Faculty of Science and Engineering
School of Earth and Planetary Sciences

Vocal Repertoire, Social Structure and Feeding Preferences of Australian and Antarctic Killer Whales (*Orcinus orca*)

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Doctor of Philosophy
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Declaration of authorship

I, **Rebecca Wellard**, declare that 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.

Animal Ethics:
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). The proposed research study received animal ethics approval from the Curtin University Animal Ethics Committee, Approval Number #AEC_2015_06. All Australian research was conducted under the Australian Government Department of Environment Research Permits 2014-0008, 2016-300 and 2017-0001. All Antarctic research was conducted under Antarctic Conservation Area Permit 2009-013, and Marine Mammal Protection Act Permits 774-1714 and 14097 issued to NOAA Fisheries, Southwest Fisheries Science Centre.

Signature:

Date: 21 December 2018

"In the end we will conserve only what we love; we will love only what we understand; and we will understand only what we are taught."

Baba Dioum

“Even if you never have the chance to see or touch the ocean, the ocean touches you with every breath you take, every drop of water you drink, every bite you consume. Everyone, everywhere is inextricably connected to and utterly dependent upon the existence of the sea.”

Sylvia A. Earle

“The earth has music for those who listen.”

Shakespeare

Dedication

This thesis is dedicated to my parents, who have stood by me and been my constant cheerleaders through every academic and personal endeavour in my life, have given me the support that I needed to build my dreams to pursue, and whose good examples have taught me to work hard for the things I aspire to achieve.

Abstract

Killer whales (*Orcinus orca*) are unrivalled oceanic apex predators found in all oceans of the world. Killer whales are the largest dolphin in the family Delphinidae, and while they are still considered to comprise a single species, different populations of killer whales can be categorised into distinct 'ecotypes', based on substantial differences in morphology, behaviour, diet, genetic structure and acoustic repertoire. Killer whales are currently listed as 'Data Deficient' by the International Union for Conservation of Nature (IUCN) and in Australian legislation. The aim of this study was to provide new information on the populations of killer whales found in Australian and Antarctic waters by investigating their call repertoire, social structure and feeding preferences.

The highly mobile nature of killer whales makes them difficult to study by traditional (i.e., visual) methods, and this is especially true for offshore Australia and Antarctica. Passive acoustic monitoring (PAM) is a technique that can surmount the challenges encountered with visual monitoring (e.g., PAM is independent of light and weather). Furthermore, PAM is an inexpensive and effective way of observing and studying vocal cetaceans. A detailed description of the vocal repertoire of a species is necessary for acoustic identification and for the optimisation of passive acoustic tools. These tools can then be used for species and population monitoring, in order to understand their behaviour and ecology, determine habitat usage and migration patterns and ultimately assess their population status.

The first objective of this study was thus to describe the call repertoire of Australian killer whales, specifically the population observed seasonally in the Bremer Sub-Basin, Western Australia. Acoustic data were collected approximately 50 km offshore in an area that is recognised as a biologically important and productive marine ecosystem, with a large number of megafaunal species encountered, including killer whales. Killer whales have been found in high numbers in this region during the months of January to April. Acoustic recordings of killer whales collected during this study included whistles, burst-pulse sounds and echolocation clicks. A total of 28 hours and 29 minutes of killer whale acoustics were recorded and analysed resulting in nine call types categorised by quantitative analysis. This study demonstrated that killer whales in the Bremer Sub-Basin exhibit a repertoire of whistles and burst-pulse sounds similar to those reported from killer whales in other regions.

Studies on the call repertoire of killer whale populations worldwide have identified a mix of unique and shared call types, whereby different killer whale groups exhibit distinct dialects. Given the paucity of information on the call repertoire of killer whales in the Southern Hemisphere in general, the second objective was to investigate the call repertoire of Antarctic killer whales, specifically Types B1, B2 and C. While three previous studies acoustically recorded Antarctic killer whales, only one was able to confirm the ecotype (in this case, Type C). For my Ph.D. study, data were collected from numerous locations across the Antarctic region: recordings of Type B1 killer whales in Rothera and Paradise Bay off the Antarctic Peninsula, recordings of Type B2 killer whales in the Gerlache Strait off the Antarctic Peninsula and recordings of Type C killer whales in McMurdo Sound, Ross Sea. The repertoire of both whistles and burst-pulse sounds was analysed for each ecotype. The call repertoire of Type C killer whales from McMurdo Sound was found to be complex, with the majority of calls containing multiple components and transitions from distinct pulses to burst-pulse sounds to whistles, along with almost half of all call categories containing biphonations. The call repertoires of Types B1 and B2 exhibited simpler structural characteristics, mostly consisting of single-component calls, with only 6.2% and 1.9% of calls containing multiple components for Types B1 and B2, respectively. The proportion of biphonic calls was also lower: 0% and 3% for Types B1 and B2, respectively. These findings agree with those of other studies demonstrating that sympatric killer whale ecotypes may exhibit different vocal repertoires.

Differences in vocal repertoire have been hypothesised to reflect distinct prey choices. A call comparison performed in this study demonstrated acoustic variation amongst Antarctic killer whale ecotypes B1, B2 and C. Type C was the most acoustically distinct of all three ecotypes. The call repertoires of Types B1 and B2 also showed some difference, although not as strong as the divergence of Type C. The large and complex vocal repertoire of Type C killer whales likely reflects the feeding ecology or the behavioural state during the recording, or possibly both. Type C killer whales prey on fish which are unlikely to hear killer whale calls. Type B1 killer whales prey on mammals, which are likely hear killer whale calls. Interestingly, Type B1 emitted predominantly singular-component and monophonic calls. With a diet containing a large proportion of fish and squid, seemingly both with poor hearing abilities at the frequency range

of killer whale vocalisations, one would expect Type B2 killer whales to have more complex calls, however this study did not support this hypothesis. The apparent simplicity of the Type B2 calls analysed in this study may not be representative of their entire repertoire but rather due to undersampling of this ecotype. Furthermore, vocal behaviour and feeding preferences are only two aspects of this species' ecology, and may be shaped by additional factors.

Sociality is another aspect of a species' ecology and might ultimately correspond to feeding preferences. The sociality of Australian killer whales had never been investigated prior to this thesis. The relative ease of access of the Bremer Sub-Basin enabled this first study of the social organisation of an offshore killer whale population in Australia. Based on boat-based surveys and photo-identification, social network techniques were applied to association analyses to examine the dynamics of the population of killer whales in the Bremer Sub-Basin. Data were collected over a period of 5 years with a total of 131 killer whales identified during 146 encounters. Association analyses revealed a well-differentiated society, with non-random associations and some individuals forming strong and persistent associations. Like other killer whale societies, killer whales in the Bremer Sub-Basin exhibited preferential patterns in which individuals associated with specific individuals throughout the entire length of the study. These non-random associations between individuals, coupled with the persistence of such associations, indicated the presence of strong, stable and long-term social bonds among killer whales in the Bremer Sub-Basin. These long-term social bonds and the social structure of this population may be influenced by non-social factors such as resource availability, prey preference and distribution, hence it is important to consider all factors when investigating sociality.

Information on the prey preferences and foraging behaviour of Australian killer whales is lacking –despite killer whales being sighted in all Australian state and territory waters. While encounters with killer whales are typically rare and unpredictable in Australian waters, the area offshore from Bremer Bay appears to support a large number of killer whales during the austral summer and autumn and provides an opportunity to study this relatively understudied population. Foraging was often observed in the Bremer Sub-Basin with observations of killer whales seemingly feeding on fish and squid. In addition, this study presented field observations of killer whales preying upon beaked whales (*Mesoplodon* spp.). Killer whales feeding on beaked whale carcasses have been previously reported, however, there has not been a documented

account of killer whales hunting and preying on beaked whales to date. Although the entire diet of this killer whale population is yet to be determined, these observations provide insight into what prey species constitute some part of their diet, and indicate the population of killer whales in the Bremer Sub-Basin are generalist feeders.

Overall, this thesis describes the vocal repertoire of killer whales found in Australian and Antarctic waters, compares vocal repertoire across sympatric ecotypes in the Antarctic region, and investigates the sociality and feeding preferences of the population of killer whales observed in the Bremer Sub-Basin. The results from this study provide a foundation for further research on Antarctic and Australian killer whales. Implications from this study warrant ongoing research effort in Australia and Antarctica to increase our knowledge on this data-deficient species. Future research should focus on comparing the killer whale vocal repertoires of all Antarctic ecotypes to allow for the development of effective passive acoustic monitoring tools. Long-term population monitoring of the killer whales in the Bremer Sub-Basin should focus on understanding their feeding ecology and investigating the social dynamics further by delineating connections between the extrinsic factors shaping sociality. Understanding the role killer whales occupy within the ecosystem is important for management and conservation.

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My PhD journey has been supported by many people and organisations who were instrumental in me completing this research. I am sincerely thankful to all who contributed.

Thank you to my PhD supervisors Christine Erbe and Rob McCauley for providing support, guidance, feedback and the freedom to develop my ideas and continue going out in the field for ‘one last trip’. I was never destined to be chained to a desk and was grateful for the time you allowed me to learn more about these animals out on the water. My continuous thirst to collect more data was never disputed by you, and I sincerely appreciate the faith you instilled in me to get things done once I returned from sea. You have both been remarkable mentors, always went above and beyond for me, and I feel honoured to have learnt from you both.

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Thank you to the great team of collaborators who assisted with the collection and collation of Antarctic data. It was such a great experience working with everyone from all over the world and building up this database- what a great opportunity to be the first to collate and analyse this precious acoustic data of Type B and C killer whales! Thank you, Ari Friedlander, Jared Towers, John Durban and Bob Pitman.

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Thank you to everyone who supported Project ORCA, without so many volunteers, supporters and collaborators helping, I would not have been able to reach funding targets, conduct my research and interact with the public. I built Project ORCA as a platform to communicate the science and to connect people worldwide with this unique population of killer whales here in Western Australia. For what is science without communication? Communication is the key to connection – and we must connect people before we can expect them to protect it. Science cannot be truly valued until it has been communicated.

Thank you to the family of CMST –past and present. Moving to Western Australia and joining this lab with such a warm welcoming put all my trepidations at ease. What an incredible lab to be welcomed into. Mal, thank you for always gearing me up for field work- your constant enthusiasm and brilliant engineering ideas have been so delightful to work alongside and allowed me to collect some unique data. To my fellow prisoners in the Dungeon and PhD students- Jamie, Claire, Capri, Rhi, Shyam, Sylvia, Angela - thank you for making this journey so much more fun and bearable, it was so nice to experience this life-changing milestone amongst such inspiring scientists. Monse and Arti, a special thanks to you both, as without our daily coffee, donuts and afternoon wines I don't think I would have survived. Thank you for being my rock during those hard and dark times in the dungeon.

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Publications and Reports

This thesis has produced the following publications and reports:

I. Wellard, R., Erbe, C., Fouda, L. & Blewitt, M. (2015) Vocalisations of killer whales (*Orcinus orca*) in the Bremer Canyon, Western Australia. PLOS ONE 10(9), e0136535.

(Chapter 2)

II. Wellard, R., Lightbody, K., Riggs, D., Fouda, L., Blewitt, M. & Erbe, C. (2016) Killer whale (*Orcinus orca*) predation on beaked whales (*Ziphiidae* spp.) in the Bremer Sub Basin, Western Australia. PLOS ONE 11(12): e0166670.

(Chapter 6)

III. Wellard, R., & Erbe, C. (2017). Killer Whales of the Bremer Sub-Basin: A photo-ID catalogue. Perth, Australia.

IV. Wellard, R., Pitman, R., Durban, J., & Erbe, C. (2020) Cold Call: The Acoustic Repertoire of Ross Sea Killer Whales (*Orcinus orca*, Type C) in McMurdo Sound, Antarctica. R. Soc. Open Sci. 7: 191228.

(Chapter 3)

Related publications and reports

I. Wellard, R., Erbe, C., Sheehan, S., Blewitt, M. (2014) Preliminary killer whale (*Orcinus orca*) acoustics in Australian waters and the acoustic ecology of the Bremer Sub-Basin. Presentation at the 51st AMSA Conference 2014, Canberra, Australia.

II. Salgado Kent C, Parnum I, Wellard R, Erbe C and Fouda L (2017) Habitat preferences and distribution of killer whales (*Orcinus orca*) in the Bremer sub-basin, Australia. Report prepared for the National Environmental Science Programme, 39 p.

III. Bouchet PJ, Meeuwig JJ, Wellard R, Erbe C, Pattiaratchi CB (2018) Bremer Canyon Emerging Priorities Project EP2: Final Report. National Environmental Science Programme (NESP) Marine Biodiversity Hub, Australia, 37 p.

IV. Bouchet PJ, Wellard R, Erbe C, Meeuwig JJ. (2018) Aerial visual survey of cetaceans and other megafauna in the Bremer Marine Park and surrounding areas. Short communication produced for the NESP Marine Biodiversity Hub and Parks Australia, 4 p.

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VI. Wellard, R., Pitman, R., Durban J. & Erbe, C. (2018) Antarctic Type C Killer Whale (*Orcinus orca*) Call Repertoire from McMurdo Sound, Ross Sea. Presentation at the 176th meeting of the Acoustical Society of America, November 2018, Victoria, Canada.

Media and Communication

The following media articles and communication tools were produced from the research completed during this PhD program:

- Project website: established in July 2015. http://www.projectorca.com.au
- Project Facebook: established in September 2015. https://www.facebook.com/orcatalkoz
- Project Instagram: established in March 2016. https://www.instagram.com/orcatalkoz
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Orca Research & Conservation Australia

PROJECT
ORCA

Statement of candidate contributions

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

These papers were primarily developed from my own ideas and approaches, with the support and guidance from my supervisors and collaborators.

Dr Christine Erbe assisted in developing code for analyses of acoustic data and provided assistance with statistical analysis of acoustic data. I built relationships amongst fellow cetacean scientists worldwide and a collaborative effort was made to collate acoustic data from the Antarctic regions, with data donated from Robert Pitman, Dr John Durban, Dr Ari Friedlaender and Jared Towers for Chapters 3 and 4. Robert Pitman provided expertise in killer whales, guidance and a review of chapters. Other contributors to fieldwork and logistics are included in the acknowledgements.

Thesis chapters were written by me, with feedback from supervisors Dr Christine Erbe, Dr Rob McCauley and collaborators.

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Christine Erbe

Dr Christine Erbe
(Primary Supervisor)

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List of Abbreviations

BSS	Beaufort Sea State
CCAMLR	Commission for the Conservation of Antarctic Marine Living Resources
CCC	Cophenetic Correlation Coefficient
DD	Data Deficient
FFT	Fast Fourier Transform
GPS	Global Positioning System
HWI	Half-weight Index
ID	Identification
IUCN	International Union for Conservation of Nature
IWC	International Whaling Commission
h	Hours
km	Kilometres
km^2	Kilometres squared
LAR	Lagged Association Rate
m	Metres
min	Minutes
MLDB	Monkey Lips/Dorsal Bursae
NFFT	Number of samples per window that is Fourier transformed
nm	Nautical Miles
Photo-ID	Photo-Identification
QAIC	Quasi Akaike Information Criterion
RSRMPA	Ross Sea Region Marine Protected Area
SD	Standard Deviation
SNR	Signal-to-Noise Ratio
WST	Australian Western Standard Time

1 Introduction

1.1 Killer Whales (*Orcinus orca*)

Killer whales (*Orcinus orca*) can be found in each of the world's oceans in a variety of marine environments, from polar regions to tropical seas. As a top predator, the role of killer whales in the ecosystem cannot be undervalued. Long-term studies of different killer whale populations have been undertaken for many decades and have proven to be valuable for ecosystem conservation and management (Baird, 2006; Bigg, 1987; Heithaus, Frid, Wirsing, & Worm, 2008; Olesiuk, Bigg, & Ellis, 1990).

Killer whales are the largest member of the family Delphinidae and one of the most readily-identifiable cetaceans with their unmistakable black-and-white colour pattern. Given their worldwide distribution, they are difficult to census. However, it is estimated that their global population is at least 50,000, with perhaps over half occurring in Antarctic waters alone (Forney & Wade, 2006; Reeves, Pitman, & Ford, 2017b). With the exception of the southern resident population off British Columbia, Canada and Washington, USA, killer whales are not listed as endangered or threatened. Their conservation status is assessed by the International Union for Conservation of Nature (IUCN), which has classified killer whales as 'Data Deficient' (DD) due to taxonomic uncertainty (Reeves et al., 2017b). This listing of DD may continue until proper taxonomic units are described and assessments can be carried out.

Unlike some other cetacean species, killer whales do not migrate to particular calving or breeding regions distant from their feeding grounds. Research for more than 40 years on killer whales in the Northeast Pacific has determined that killer whales shift their movement patterns and distributions seasonally to exploit prey aggregations (Hoelzel et al., 2007; Nichol & Shackleton, 1996), but they seldom disseminate permanently from their natal home ranges (Ford, Ellis, & Balcomb, 1994). Similar movements for foraging on seasonally changing prey distributions have been described for killer whales in Antarctic waters (Andrews, Pitman, & Ballance, 2008). Skin cell regeneration may also influence movement for killer whales in Antarctic waters, deemed as physiological maintenance migrations (Durban & Pitman, 2012).

Killer whales have evolved unique behavioural ecologies and have radiated to occupy a range of ecological niches, and as such they are recognised as top-predators capable of adapting their social and hunting behaviour to their environment (Jefferson, Stacey, & Baird, 1991). Although killer whales are considered to comprise a single species, different populations of killer whales can be categorised into distinct 'ecotypes', based on substantial differences in morphology, behaviour, diet, genetics and acoustic repertoire. Ecotypes have been defined as conspecific groups with similar ecological adaptations regardless of genealogical relationship (Cronin, 2006; Cronin & Mech, 2009). It has been suggested that speciation may result from ecotypic variation if the divergence in physiology, morphology and behaviour is sufficient to cause reproductive isolation and enable evolution by natural selection (De Bruyn, Tosh, & Terauds, 2013). This has yet to be demonstrated with killer whales.

Ten killer whale ecotypes have been described to date (Bigg, 1987; Dahlheim et al., 2008; Durban, Fearnbach, Burrows, Ylitalo, & Pitman, 2017; Foote, Newton, Piertney, Willerslev, & Gilbert, 2009; Foote et al., 2011; Ford et al., 1994; Pitman et al., 2011; Pitman & Ensor, 2003). Sympatric ecotype assemblages are documented from three different geographical regions: the eastern North Atlantic, the eastern North Pacific and Antarctica (Barrett-Lennard, Ford, & Heise, 1996; Foote et al., 2009; Ford et al., 1998; Pitman & Ensor, 2003), with some populations displaying substantial variation in diet, behaviour, morphology, size, stability and composition of social structure and mitochondrial genomics (Baird & Whitehead, 2000; Barrett-Lennard & Heise, 2006; Ford & Ellis, 2014; Ford et al., 1998), that has led some researchers to propose separate killer whale species (Morin et al., 2010).

In Antarctic waters, three morphological forms of killer whales were originally identified (Pitman & Ensor, 2003), with differences in the suggested ecological specialisations possibly being even more pronounced than those reported for the three eastern North Pacific resident, Bigg's (formerly transient) and offshore ecotypes (Bigg, 1987; Dahlheim et al., 2008; Ford et al., 1994). Currently, five distinct killer whale ecotypes have been described in Antarctic waters including Types A, B (two forms), C and sub-Antarctic Type D, each with their own physiological, morphological and social adaptations (Durban et al., 2017; Pitman et al., 2011).

Australia has seen less dedicated research on killer whales, despite sightings occurring in all state and territory waters (Chatto & Warneke, 2000; Ling, 1991; Ross, 2006). Currently no defined killer whale ecotypes have been described in Australian waters due to limited knowledge of their feeding ecology, morphology, behaviour and genetic structure. To date, there has been no reliable estimate of the population size of killer whales in Australian waters. Killer whale population trends are unknown, with much of the information on distribution and occurrence obtained from incidental sightings and from one sighting program undertaken on Macquarie Island (Morrice, 2004). Notably, historical records and anecdotal evidence suggest that killer whales are most commonly sighted in coastal waters and along the continental shelf around south-eastern Tasmania, Victoria and southern New South Wales, and also in some parts of the Australian Antarctic Territory (Bannister, Kemper, & Warneke, 1996; Chatto & Warneke, 2000; Kasamatsu & Joyce, 1995; Ling, 1991; Morrice, 2007; Morrice & Gill, 2008; Mustoe, 2008; Parker, 1978; Ross, 2006; Thiele, Chester, & Gill, 2000; Thiele & Gill, 1999; Van Waerebeek et al., 2010).

Dedicated surveys are required to quantify killer whale distribution, movements, habitat use, population size and trends off Australia. Furthermore, similar dedicated effort is also warranted in the Antarctic region, where year-round boat-based surveys are challenging due to restricting conditions such as inclement weather, limited daylight and ice coverage. The highly mobile nature of killer whales makes them difficult to study by traditional methods (such as visual, boat-based surveys) and this is especially true for the offshore waters of Australia and Antarctica. However, passive acoustic monitoring is a technique that can surmount these challenges.

Passive acoustic monitoring is an inexpensive and effective way of recording the distribution, migration, behaviour and population density of vocal species. A detailed description of the temporal and spectral acoustic characteristics is necessary for species acoustic identification and for the development of passive acoustic tools. Such tools are useful for population monitoring, in order to determine habitat usage, migration patterns, and in due course assess their population status.

1.2 Cetacean Acoustic Communication and Sound Production

Acoustic communication is widely used by cetaceans (i.e., whales, dolphins and porpoises). In an environment where light is often limiting and does not travel far under water, other sensory modalities such as vision, have limitations in effective speed and range of transmission. Sound propagates faster and farther in water than in air (Urick, 1983), so cetaceans have evolved sophisticated sound production and sensitive hearing systems. Acoustic communication in cetaceans is used in a wide range of contexts, including social interactions, group cohesion, detection of predators and prey, mother-calf contact, travelling and foraging, and the interpretation of their environment (Au, 2000b; Jones & Sayigh, 2002; Tyack & Clark, 2000). The abundance and variety of underwater sounds produced by cetaceans reflect their important role in the ecology and social lives of these marine mammals, and therefore are of great interest for our understanding of animal communication.

Unlike most mammals, odontocetes (toothed whales) do not produce sounds in the larynx but in the nasal passages above the larynx (Mackay & Liaw, 1981; Ridgway et al., 1980). Studies have theorised that mysticetes (baleen whales) use their larynx and vocal folds to produce sounds, but evidence is lacking (Reidenberg & Laitman, 2007). Research on sound production in cetaceans has extensively focused on odontocetes, with numerous studies investigating the evolution and mechanism of sound production in delphinids (Cranford, Amundin, & Norris, 1996; Cranford et al., 2011; Mackay & Liaw, 1981; Madsen, Kerr, & Payne, 2004; Madsen, Wisniewska, & Beedholm, 2010).

Research has shown that delphinids produce echolocation clicks and whistles in the nasal system by forcing air through two pairs of lips (Au & Simmons, 2007; Cranford, 2000; Cranford et al., 1996). Commonly referred to as the monkey lips/dorsal bursae (MLDB) complex, or phonic lips, they are situated about 3 cm below the blowhole (Cranford, 1992). The nasal system possesses several air sacs, which can be compressed by associated muscles. Sounds are produced when air is pressed into the nasal passage from the nasal sacs and then through the phonic lips, which are pressed together by muscles (Figure 1.1). It is thought that the sound is transmitted through specialized fatty tissue adjacent to the phonic lips. This fatty tissue, also known as posterior and anterior bursa, consists of ‘acoustic fat’. The anterior bursa is often referred to as the melon and acts as an acoustic lens by focussing the sound energy forward (Zimmer, Madsen, Teloni, Johnson, & Tyack, 2005).

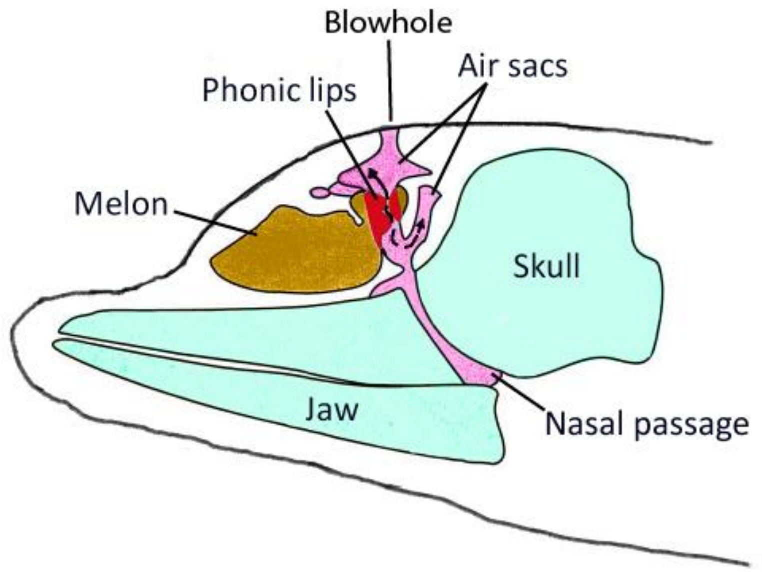

Figure 1.1 Diagram illustrating the nasal and sound production system of a dolphin. Delphinids produce sounds with their phonic lips, which are vibrated when air is pressed into the nasal passage from the nasal sacs. Sounds are transmitted via the fatty tissue (anterior and posterior bursae) into the water. Dashed lines indicate air flow. Image drawn by Rebecca Wellard, which was modified from Cranford et al. (1996), Gerhardt and Huber (2002), Ladich and Winkler (2017) and Suthers (2010).

Odontocetes produce a variety of sounds that are typically separated into three categories: echolocation clicks, whistles and burst-pulse sounds (Janik, 2009; Richardson, Green, Malme, & Thomson, 1995). Research from the Northern Hemisphere has demonstrated that killer whales, like other delphinids, predominantly produce these three commonly grouped sounds.

Echolocation clicks are short-duration (< 250 µs), broadband (10 kHz – 100 kHz) pulses of up to 224 dB re 1 µPa @ 1 m peak-to-peak source level, typically emitted in trains with a several-second duration (Au, Ford, Horne, & Allman, 2004; Barrett-Lennard et al., 1996; Evans, 1973; Ford, 1989; Gassmann, Henderson, Wiggins, Roch, & Hildebrand, 2013; Simon, Wahlberg, & Miller, 2006). Whistles and burst-pulse sounds are thought to be communicative signals most commonly used in social contexts (Ford, 1989; Thomsen, Franck, & Ford, 2002).

Whistles are frequency-modulated, tonal sounds, with or without harmonics and sidebands, and a fundamental frequency ranging from 1 to 36 kHz and source levels up to 193 dB re 1 µPa @ 1 m peak-to-peak recorded from the North Pacific killer whale populations (Filatova, Ford, et al., 2012; Ford, 1989; Riesch, Ford, & Thomsen, 2006; Simonis et al., 2012; Thomsen, Franck, & Ford, 2001). Fundamental frequencies up to 74 kHz have been recorded in Norwegian and Icelandic killer whales (Samarra et al., 2010). The fundamental frequency is the lowest frequency of an oscillating system (ANSI, 1994). Harmonics are sinusoids at frequencies that are integer multiples of the fundamental frequency (ANSI, 1994), whilst sidebands are not harmonically related to the fundamental frequency (Watkins, 1968).

Burst-pulse sounds consist of rapidly repeated pulses with inter-pulse intervals shorter than in echolocation click trains, and are considered to function as contact signals in group recognition and coordination of behaviour (Ford, 1989; Miller, Shapiro, Tyack, & Solow, 2004). In spectrograms, burst-pulse sounds typically appear as frequency-modulated sounds with numerous sidebands and harmonics, and the contours seen are related to the pulse repetition rate. The pulse repetition rate can always be read off the spectrogram as the ‘harmonic interval’ between neighbouring contours (Watkins, 1968). Frequency-modulation of the contours in burst-pulse sounds is related to changing pulse repetition rates. The main energy of killer whale burst-pulse sounds usually lies between 500 Hz and 25 kHz, lasting 0.5 – 1.5 s, with source levels of 131-176 dB re 1 µPa @ 1 m root-mean-square (Filatova, Fedutin, Nagaylik, Burdin, & Hoyt, 2009; Filatova, Fedutin, Burdin, & Hoyt, 2007; Ford, 1987, 1989, 1991; Gassmann et al., 2013; Holt, Noren, & Emmons, 2011; Miller, 2006; Richlen & Thomas, 2008; Strager, 1995). In order to differentiate between whistles and burst-pulse sounds and to describe the different components of the recorded calls, I used the default from Watkins (1968) and categorised sounds with fewer than five harmonics as a whistle, and those with more as a burst-pulse sound.

Throughout this thesis, the three types of killer whale vocalisations (i.e., echolocation clicks, whistles and burst-pulse sounds) are collectively termed as sounds, calls or vocalisations interchangeably. The chosen terminology (‘calls’, ‘sounds’ or ‘vocalisations’) does not imply a calling function or vocal chords for sound production. Killer whale calls can vary from simple structures with a single component (e.g., a whistle) to more complex structures with multiple components (e.g., a whistle-component immediately followed by a burst-pulse component without a gap in time). Some calls can comprise two simultaneous components, where two independent but simultaneous contours are present, which is usually referred to as a ‘biphonation’ (Fitch, Neubauer, & Herzel, 2002; Wilden, Herzel, Peters, & Tembrock, 1998). The term ‘two-voiced’ implies two independent sound sources within the same vocalising animal (Greenewalt, 1968; Zollinger, Riede, & Suthers, 2008). As the mechanism responsible for the occurrence of the two simultaneous, but independent, vocalisations is still not fully understood, I consistently used the term ‘biphonation’ in my thesis. While some studies found that biphonations always consisted of a low-frequency component (LFC) and an upper-frequency component (UFC) e.g., Yurk, Barrett-Lennard, Ford, and Matkin (2002), I did not find this. In fact, in the majority of biphonic calls that I analysed, both components covered the same frequency band. Sometimes, one contour started out as the lower-frequency component, but increased in frequency over time, while the initially higher-frequency component ended lower than the former component. As my data did not confirm the LFC/UFC separation, I did not use this terminology in my thesis.

1.3 Social Learning and Killer Whale Vocal Culture

Culture is the transmission of behaviours within or between generations based on social learning through either imprinting, teaching or imitation (Rendell & Whitehead, 2001; Zentall, 2006). Cultural transmission of a trait commences when a new behaviour is introduced and subsequently diffuses through all or part of the population as increasing numbers of individuals learn the behaviour from one another (Laland & Hoppitt, 2003). A prime example of social learning and animal culture is vocal behaviour. Vocal learning occurs when an animal alters its acoustic signals due to experience with other individuals and creates signals that are similar to the model that it hears (Janik & Slater, 1997, 2000). It is a social process that can lead to the transmission of an acoustic repertoire, or vocal culture, between signallers and receivers.

Vocal culture resulting from social learning has been identified in birds, bats, marine mammals and humans (Boughman, 1997; Esser & Schubert, 1998; Janik & Slater, 2003) and is expressed as a dialect, i.e., a different repertoire of song type, call type or human speech variation (Yurk, 2005). Dialects are frequent in birds (Baker & Cunningham, 1985), but are rare in mammals, with dialects only found in cetaceans (Ford, 1991; Rendell & Whitehead, 2003), bats (Boughman, 1997; Esser & Schubert, 1998) and humans (Labov, 2001).

Dialects have been described in both killer whale (Ford, 1989, 1991) and sperm whale (*Physeter macrocephalus*) populations (Rendell & Whitehead, 2003; Weilgart & Whitehead, 1997). In both species, the vocal repertoire and group specific communication is learned vertically from parent to offspring – in the case of the matrilineal societies of killer and sperm whales, from mother to offspring – but also horizontally through conspecifics or other group members (Filatova, Burdin, & Hoyt, 2010; Ford, 1991; Rendell, Mesnick, Dalebout, Burtenshaw, & Whitehead, 2012; Whitehead, 1998).

Call structure differs between allopatric, parapatric and sympatric killer whale populations. Studies of the vocal behaviour of different killer whale populations have identified a mix of unique and shared call types and documented vocal culture, whereby different killer whale groups exhibit distinct dialects (Ford, 1991; Strager, 1995; Yurk et al., 2002). These dialects are stable through time (Foote, Osborne, & Hoelzel, 2008; Ford, 1984) and are a learned behaviour (Deecke, Ford, & Spong, 2000; Filatova et al., 2015; Yurk et al., 2002). This learned behaviour is evidenced by the fact that calves inherit the repertoire of only the maternal pod, despite the fact that the mother and father usually belong to different pods, which was verified by detailed molecular–genetic studies (Barrett-Lennard, 2000).

Groups with similar repertoires have been shown more closely related than groups that share fewer calls, with some pods of related matrilines sharing many or all of the elements in their repertoire (Barrett-Lennard, 2000; Ford, 1989, 1991). Differences in calls amongst spatially separated populations of killer whales are apparent from studies worldwide (Filatova et al., 2007; Ford, 1989; Strager, 1995; Yurk et al., 2002) and have resulted in effective monitoring of these populations by the use of passive acoustic listening.

1.4 Social Structure in Killer Whales

Studies investigating the social organisation and group stability of cetaceans have been performed rigorously in several odontocete species over the last two decades. The majority of these studies have focused on bottlenose dolphins (*Tursiops* spp.) (Baker, O'Brien, McHugh, Ingram, & Berrow, 2018; Chabanne, Finn, Salgado-Kent, & Bejder, 2012; Connor, Heithaus, & Barre, 2001; Gero, Bejder, Whitehead, Mann, & Connor, 2005; Lusseau et al., 2006), pilot whales (*Globicephala* spp.) (De Stephanis et al., 2008; Mahaffy, Baird, McSweeney, Webster, & Schorr, 2015; Ottensmeyer & Whitehead, 2003), sperm whales (Gero, Engelhaupt, & Whitehead, 2008; Whitehead, 2003) and killer whales (Baird & Whitehead, 2000; Beck, Kuningas, Esteban, & Foote, 2011; Esteban et al., 2016; Ivkovich, Filatova, Burdin, Sato, & Hoyt, 2010; Parsons, Balcomb, Ford, & Durban, 2009; Reisinger, Hoelzel, & De Bruyn, 2017). Four of these species of cetacean have demonstrated stable social structures, where hierarchical group associations remain constant for generations: sperm whales, long-finned pilot whales (*G. melas*), short-finned pilot whales (*G. macrorhynchus*) and killer whales (Amos, Schlotterer, & Tautz, 1993; Baird & Whitehead, 2000; Cantor & Whitehead, 2015; De Stephanis et al., 2008; Mahaffy et al., 2015).

The social structure of killer whales has been studied extensively in the Northern Hemisphere, in particular the Northeast Pacific for more than 40 years. These long-term studies have discovered three sympatric killer whale populations, each with their own defined ecotype: resident, Bigg's and offshore. The resident killer whales exhibit a multi-level social structure with matrilineal units as the foundation and high levels of philopatry at the population and subpopulation level (Barrett-Lennard, 2000; Hoelzel, Dahlheim, & Stern, 1998). Matrilines typically consist of 2-4 maternally related generations with no permanent dispersal for identified individuals of either sex among communities or populations. Genetic studies indicate continuous gene flow among matrilines as a result of mating during temporary interactions (Pilot, Dahlheim, & Hoelzel, 2010).

Less is known about the Bigg's killer whale population, but studies have shown this population is also moulded by matrilineal units, composed of mothers and their descendants, however social groups are smaller and seem less stable, with some social dispersal of individuals observed (Baird & Whitehead, 2000; Bigg, Olesiuk, Ellis, Ford, & Balcomb, 1990; Ford & Ellis, 1999). Information on the sociality of offshore killer whales is limited, with reports describing stable mixed-sex groups within the population and sightings of large groups frequently found similar to those reported for resident killer whales (Dahlheim et al., 2008; Ford et al., 1994).

Other studies worldwide have investigated social organisation within killer whale communities and have described variation in group sizes and sociality. Studies undertaken in the North Atlantic, as well as off Gibraltar, Russia, Norway and the Marion Islands (Beck et al., 2011; Esteban et al., 2016; Ivkovich et al., 2010; Jourdain, Vongraven, Bisther, & Karoliussen, 2017; Reisinger et al., 2017) present a variety of social structures, ranging from communities similar to those of the Northeast Pacific, both fish-eating and mammal-eating, to other communities, showing diversification and being neither a match for either the 'resident' or the 'Bigg's' model.

Only one study has investigated the social structure of killer whales in the Southern Hemisphere: at Marion Island in the Southern Ocean (Reisinger et al., 2017). This study revealed long-term associations among killer whales but the social group relationships were dynamic. Reisinger et al. (2017) noted that the killer whale social structure at Marion Island was not a perfect match for either the ‘resident’ or the ‘Bigg’s’ model from the Northeast Pacific studies. Stable social units and a long period of post-reproductive senescence in killer whales are believed to be important drivers of life history evolution and may contribute to gene-culture divergence (Brent et al., 2015; Whitehead & Rendell, 2015). Understanding the social organisation of killer whale populations is an important step towards identifying factors that shape the social structure of each population.

1.5 Diet and Feeding Ecology in Killer Whales

The killer whale has an incredibly diverse diet. This cosmopolitan predator has been documented preying on species across a variety of taxa including cephalopods, fishes, sea birds, sea turtles, pinnipeds, mustelids and other cetaceans (dos Santos & Haimovici, 2001; Ford, 2009; Jefferson et al., 1991; Martinez & Klinghammer, 1970; Pitman & Dutton, 2004). Although the killer whale can be considered a generalist feeder at the species level with such a large variety of prey species, different populations of killer whales have unique feeding behaviours with foraging specialisations and distinct prey preferences.

Long-term studies in the Northeast Pacific have resulted in a great wealth of knowledge on prey preferences in both the resident and Bigg’s killer whale populations. These two sympatric killer whale ecotypes feed almost exclusively on fish and marine mammal prey, respectively (Baird & Dill, 1995; Ford & Ellis, 2006; Ford et al., 1998). In fact, the resident killer whales are so selective in their prey choice, Ford and Ellis (2006) reported the southern resident population have a strong preference for just one species of salmon: chinook salmon (*Oncorhynchus tshawytscha*). Studies in the Northern Hemisphere have demonstrated other killer whale populations also have specific prey preferences and employ unique feeding strategies. In the waters off Norway, killer whales are known to employ a cooperative hunting technique to feed on herring (*Clupea harengus*) known as carousel feeding (Similä, Holst, & Christensen, 1996). This feeding strategy involves groups of killer whales herding a school of herring to the surface and keeping them in a tightly packed ball by circling them, whilst individual killer whales will periodically slap the school with their tail allowing other killer whales in the group to feed on the debilitated herring that fall outside of the school (Nøttestad & Similä, 2001).

In the Southern Hemisphere, off Argentina, Antarctica and New Zealand, killer whale populations also exhibit prey specialisation and unique foraging strategies. One of these unique foraging strategies includes killer whales intentionally stranding themselves to catch southern elephant seals (*Mirounga leonina*) and South American sea lions (*Otaria flavescens*) on Possession Island in the Crozet Archipelago (Guinet, 1991) and the Peninsula Valdes, Argentina (Hoelzel, 1991; Lopez & Lopez, 1985). This stranding technique involves the killer whales exposing most of their body out the water on the beach whilst attempting to grab a pinniped with their teeth and then moving quickly back into deeper waters. Elasmobranchs, in particular rays, have been observed to be a selective prey choice for killer whale populations in waters off New Zealand (Visser, 1999), where benthic foraging strategies are employed using the bottom of the sea floor as a barrier to trap and kill the targeted ray.

Observations of Antarctic ecotypes show prey specialisation across all ecotypes, with the five defined ecotypes each documented to have specialised diets. Type A killer whales have been reported to prey on marine mammals, in particular Antarctic minke whales (*Balaenoptera bonaerensis*) (Pitman & Ensor, 2003). Large Type B killer whales, herein referred to as 'B1', also known as pack ice killer whales, feed mainly on ice seals, such as Weddell seals (*Leptonychotes weddellii*), crab-eater seals (*Lobodon carcinophagus*) and leopard seals (*Hydrurga leptonyx*) and are well known for employing a specialised foraging technique known as 'wave-washing' pinnipeds (Durban et al., 2017; Pitman & Durban, 2010, 2012; Pitman et al., 2011; Pitman & Ensor, 2003). This unique feeding strategy begins with a group of killer whales spy-hopping together around the edge of an ice floe, seemingly to locate the seal and assess which species of seal is present. When a seal is detected on the ice floe, the response of the killer whales depends on the species of the seal. Crab-eater and leopard seals are usually left alone due to their aggressiveness, but some attacks on these species have been recorded (Visser et al., 2008). The 'wave-washing' technique involves a group of killer whales approaching an ice floe in parallel formation while beating their flukes in a synchronised pattern to create waves. The waves then break over the small ice floe and wash the seal into the water, whilst if the ice floe is large, the killer whales will continue to create waves to break it into smaller pieces (Pitman &

Durban, 2012; Visser et al., 2008). This technique has only been seen with Type B1 killer whales off the Antarctic Peninsula and nowhere else in the world.

Small Type B killer whales, herein referred to as ‘B2’, also known as Gerlache killer whales, are often seen foraging in relatively ice-free waters where they appear to feed on fish or squid and the occasional penguin (Jefferson, Webber, & Pitman, 2015; Pitman & Ensor, 2003). Type C killer whales have been observed to eat fish, while the diet of Type D is virtually unknown, apart from the consumption of Patagonian toothfish (*Dissostichus eleginoides*) observed during longline interactions (Ainley & Ballard, 2012; Ballard & Ainley, 2005; Eisert et al., 2015; Pitman & Durban, 2010; Pitman et al., 2011; Pitman & Ensor, 2003).

This variety of specialised foraging techniques and prey preferences observed across killer whale populations, where groups have carved out specialised niches and sophisticated hunting strategies, implies that behavioural traditions are passed on by social learning (Ford et al., 1998; Saulitis, Matkin, Barrett-Lennard, Heise, & Ellis, 2000). These behavioural traditions and learned feeding strategies are part of a species’ culture, with information being passed among individuals and across generations through social learning, such as imitation (Rendell & Whitehead, 2001). These cultural feeding traditions may determine the specialised foraging techniques employed by the population and the selected prey, but other variables likely play a role in prey selection, too, such as rates of encounters with prey and its cost-effectiveness.

The passing of information between individuals and conspecifics is vital to a species’ survival and adaptability to a changing environment. With so many cultural differences being identified across killer whale populations and regions, it is important to consider the feeding ecology of each killer whale population and treat each separately when formulating protection measures. The needs of one population may be greatly different from those of another population, and this needs to be taken into account in the way we approach conservation and management of each population.

1.6 Killer Whales in Western Australia

Until recently, sightings of killer whales around Australia were incidental with no documented aggregations. On the east coast, sightings of killer whales have been collated since 1994 with the help of citizen scientists. This database produced a photo-identification catalogue of 59 killer whales (Donnelly, McInnes, Morrice, & Andrews, 2016) from numerous locations off the east coast of Australia and no reliable sighting locations described. Over recent years, Western Australia has become a reliable location to study killer whales, in particular at two aggregation sites: the Ningaloo Reef and the Bremer Sub-Basin, both comprising different killer whale populations at different times of the year.

The Ningaloo Reef is a World Heritage Site located in the north west coastal region of Australia (Department of Environment, 2010). The reef is 260 km long and is Australia's largest fringing coral reef. Although mostly famed for the high number of whale sharks feeding there during March to July, supporting a large tourism industry, the reef is also rich in other marine life, including dolphins, dugongs, elasmobranchs, humpback whales and turtles (Duffy, Layton, & Dwyer, 2018).

Western Australia is now home to the largest population of humpback whales worldwide, known as Breeding Stock D. This population has increased rapidly since the cessation of whaling in 1963. The population was estimated to have been reduced to 568 individuals by the end of 1963 (Bannister, 1964), but may have been even lower since this estimation did not account for the large-scale illegal whaling by the Soviet Union that included this population in Antarctic waters until at least 1968 (Clapham et al., 2009). The pre-exploitation population size of Western Australian humpback whales was modelled to be 21,686 by the IWC (2014). Given an annual population growth of between 10.15% (Bannister & Hedley, 2001) and 13% (Salgado Kent, Jenner, Jenner, Bouchet, & Rexstad, 2012), the population is now thought to include over 30,000 individuals (IWC, 2014; Salgado Kent et al., 2012).

With the steady increase of humpback whale numbers along the Western Australian coast, predator populations might also grow. The steady increase of sightings of killer whales recorded off the Ningaloo Reef in the austral winter coinciding with the humpback whale migration off this coast appears to support this theory. Pitman et al. (2015) proposed a local population of killer whales preying on extensively on Western Australian humpback calves prior to whaling, would have also collapsed alongside the humpback whale population collapsing in the 1960s. Hence after whaling depleted Western Australian humpback whales, killer whales that preyed on them would have either declined in numbers or were extirpated, resulting in any subsequent recovery of those killer whales trailing behind the humpback whales.

Sightings of killer whales over the last decade in the Ningaloo region have steadily increased, with killer whales observed predating upon mostly neonate humpback whales (Pitman et al., 2015). Killer whales are sighted annually off the Ningaloo region in March - August preying on abundant humpback whale calves. Although 27 individual killer whales have been documented off Ningaloo in a photo-identification study (Totterdell, 2015), the sighting rate and occurrence of killer whales are variable from year to year. This variability in sighting rate means the Ningaloo region is not as dependable as the Bremer Sub-Basin to find killer whales, and hence wasn't the main Australian site targeted in this study. This study spent 3 seasons of dedicated field effort over 3 consecutive years (2015-2018) off Ningaloo, but due to the low encounter rate of killer whales across this study period, had to omit this population of killer whales from this study.

In comparison to the Ningaloo region, the Bremer Sub-Basin has proven to be a more reliable site for killer whale sightings, with an aggregation documented annually between January and April with a sighting rate of 94% - 98% throughout this season (Wellard, Erbe, Fouda, & Blewitt, 2015; Wellard et al., 2016). The Bremer-Sub-Basin is located off the southwest continental shelf of Australia and extends over an area of 11,500 km^2 in water depths of 100 to 4500 m (Exon, Hill, Mitchell, & Post, 2005).The Bremer Sub-Basin contains numerous submarine canyons and forms part of the Albany Canyons complex (Figure 1.2). The region is recognised as a biologically important and productive marine ecosystem, with a large number of marine megafaunal species, including killer whales (Bouchet, Meeuwig, Wellard, Erbe, & Pattiaratchi, 2018; Department of Environment, 2012). Killer whale occurrence in the Bremer Sub-Basin is most likely linked to seasonal productivity and prey abundance. However, the physical and environmental features that are responsible for driving productivity, prey abundance and, ultimately, killer whale occurrence remain unknown.

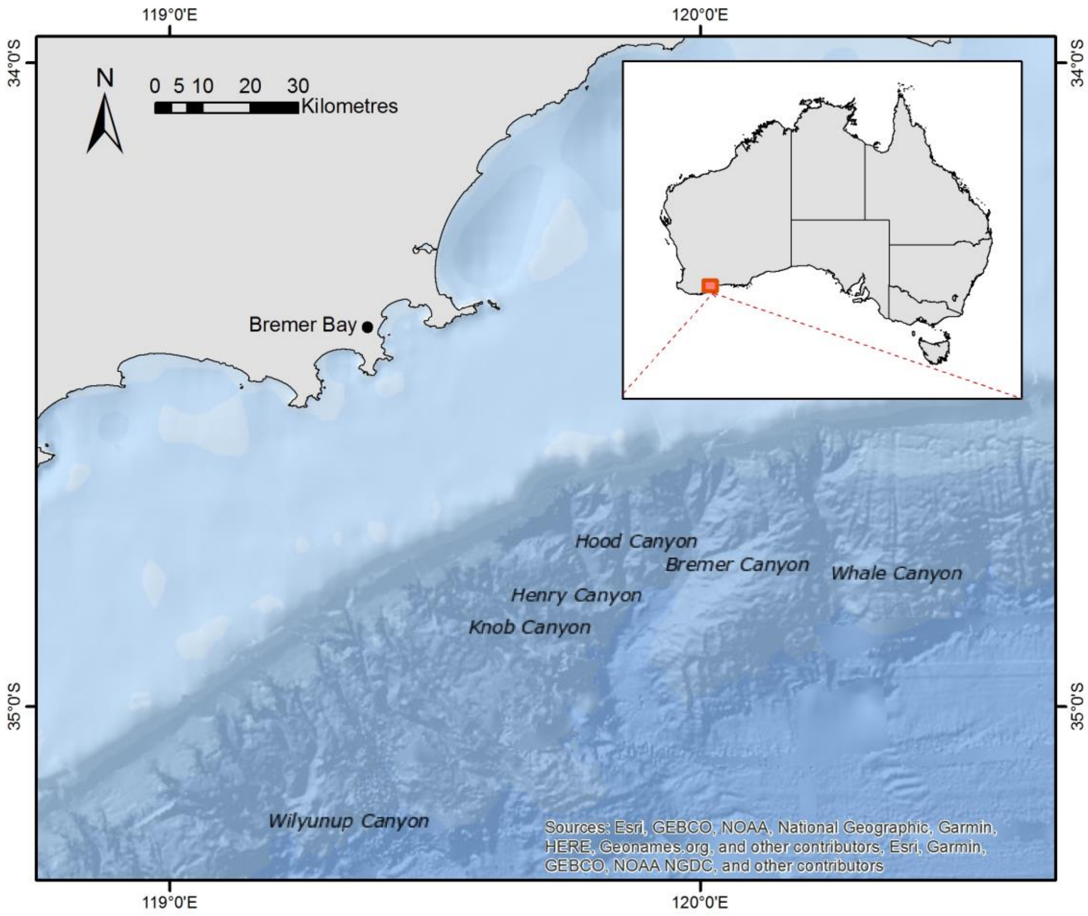

Figure 1.2 Map of the south coast of Western Australia. Survey effort during this study in the Bremer Sub-Basin was mostly focused on Knob, Henry and Hood canyon as detailed in this map. Inset map indicates the location of Bremer Bay. Map produced using ArcMap GIS software and ESRI World Ocean Base data (ArcGIS, 2012, Redlands, California, United States).

1.7 Killer Whales in Antarctica

It is estimated that over half of the worldwide population of killer whales occur in Antarctic waters alone (Forney & Wade, 2006; Jefferson et al., 2015). Despite this, little research has been undertaken, until very recently, with limited dedicated surveys addressing killer whales as the focal species. Killer whales have been observed in Antarctic waters since the early 1900s with whalers reporting frequent sightings of killer whales scavenging on baleen whale carcasses (Whitehead & Reeves, 2005). Whaling in the twentieth century targeted large baleen whales, with killer whales considered to have little commercial value. However, Soviet whalers are reported to have taken over 1,600 killer whales between 1961 and 1980, including 916 in the final season between 1979 and 1980 (Mikhalev, Ivashin, Savusin, & Zelenaya, 1981).

Since the early 1980s, research on Antarctic killer whales has increased, with various institutions and independent researchers. A combination of researchers on Soviet fleets, aboard tourist vessels and aboard Japanese research vessels on cetacean survey cruises under the auspices of the International Whaling Commission (IWC), meant more comprehensive information on the distribution and abundance of killer whales in Antarctic waters was collected. In 1981 and 1983, two groups of Soviet scientists independently described two new forms of killer whales from Antarctica. Mikhalev et al. (1981) proposed a new species: *Orcinus nanus*, based on whaling samples taken by Soviet whalers. However, other than body lengths and deeming these samples as dwarf forms, no diagnostic details were presented, and no holotype was collected. Soon after, Berzin and Vladimirov (1983) also proposed a new species: *Orcinus glacialis*, based on whaling samples taken by Soviet whalers during the 1979-1980 season. A more detailed description was provided, with the authors noting it was a dwarf form, ate mainly fish and had a thick coating of diatoms giving the skin a yellowish tinge. A holotype was taken, but later lost in a storm that flooded the museum (Pitman, Perryman, LeRoi, & Eilers, 2007). Due to the loss of holotype specimens and the lack of diagnostic details, the proposals for revised taxonomy of killer whales received no support from the scientific community (Dahlheim & Heyning, 1999).

Research over the last few decades on Antarctic killer whales has investigated feeding behaviours and prey preferences (Ballard & Ainley, 2005; Krahn, Pitman, Burrows, Herman, & Pearce, 2008; Lauriano, Vacchi, Ainley, & Ballard, 2007; Pitman, 2011; Pitman & Durban, 2010, 2012; Visser et al., 2008), photo-identification of individuals (Chambellant, Garrigue, Petier, Ridoux, & Charrassin, 2012), morphology and ecotypes (Pitman et al., 2011; Pitman & Ensor, 2003; Pitman et al., 2007), distribution and satellite telemetry studies (Andrews et al., 2008; Durban & Pitman, 2012), genetic variation (LeDuc, Robertson, & Pitman, 2008; Morin et al., 2010), and abundance trends (Pitman, Fearnbach, & Durban, 2018). Little to no research has been conducted on the social structure and vocal behaviour of Antarctic killer whales.

In Antarctic waters only three previous studies have described the vocal behaviour of killer whales (Awbrey, Thomas, Evans, & Leatherwood, 1982; Richlen & Thomas, 2008; Schall & Van Opzeeland, 2017). Of these, only one was able to confirm the ecotype of vocalising killer whales with confidence

– Type C near the Eckström Ice Shelf, eastern Weddell Sea (Schall & Van Opzeeland, 2017). This limited description of Antarctic killer whale vocal repertoires results in tools, such as passive acoustic monitoring, not being applicable to monitor this species. Such tools would be beneficial when studying a mobile species in a remote and challenging environment like Antarctica. The nature of ever-growing tourism has meant that regions previously considered inaccessible or challenging for data collection are becoming more accessible to scientists, such as Antarctic region, where tourism has increased measurably in the past few decades (Shaw, Terauds, Riddle, Possingham, & Chown, 2014; Tin, Lamers, Liggett, Maher, & Hughes, 2014). Given the high logistical cost of research in the Antarctic, tour vessels are increasingly used as cost-effective platforms. Acoustic recordings of Antarctic Types B1, B2 and C analysed in this study were collected throughout the Antarctic region (Figure 1.3) by using numerous tourism vessels as platforms of opportunity in addition to research vessels.

At a time when the climate is dramatically changing and is found to be most extreme in the polar regions, it is crucially important to understand all working mechanisms of the ecosystem, perhaps even more so for the apex predators in these environments, who have been described as a major force in the structuring of Southern Ocean food webs and play a keystone role (Ballance et al., 2006). The rapidly changing polar environment warrants continued efforts to obtain baseline data of understudied marine predators and gain a better understanding of the functional role they play within the ecosystem.

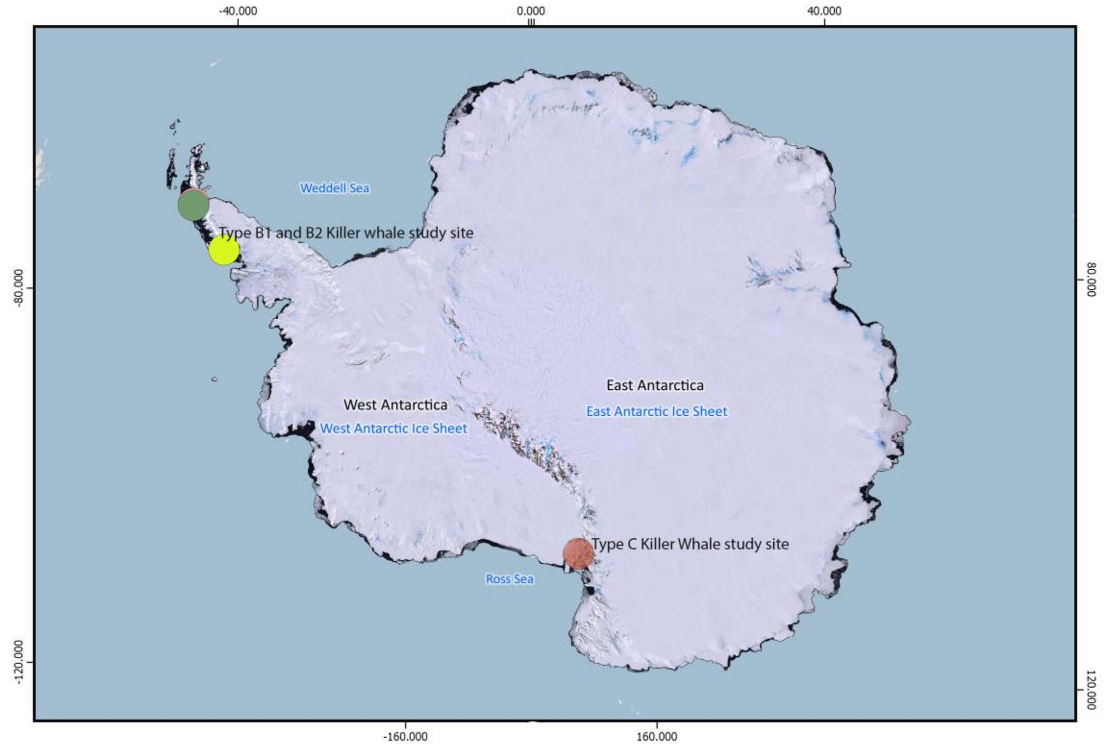

Figure 1.3 Map of Antarctica. Circular symbols indicate the location of study sites and survey effort researching Type B1, Type B2 and Type C killer whales in Antarctic waters between 2009 – 2018. Map produced using QGIS mapping software (QGIS Develpment Team, 2018, Open Source Geospatial Foundation Project, Boston, Massachusetts, United States) and Norwegian Polar Institute's Quantarctica Package (Matsuoka, Skoglund, Roth, Tronstad, & Melvær, 2018).

1.8 Objectives

This project aims to improve our understanding of killer whale populations in the Australian and Antarctic region. The specific objectives are:

1. Describe the vocal repertoire of Australian killer whales, specifically the population observed seasonally in the Bremer Sub-Basin, Western Australia and compare basic signal characteristics of the vocalisations of killer whales from the Bremer Sub-Basin

with other reported vocalisations of killer whales in the Southern Hemisphere (Chapter 2).

2. Describe and categorise the vocal repertoire of Type C killer whales recorded in McMurdo Sound, Ross Sea and compare call types with other killer whale call types described in acoustic studies on killer whale repertoire in the Southern Ocean (Chapter 3).
3. Describe the vocal repertoire of Type B1 and Type B2 killer whales found around the Antarctic Peninsula and investigate acoustic divergence amongst sympatric ecotypes of killer whales in the Antarctic region (Chapter 4).
4. Investigate the social structure of the population of killer whales in the Bremer Sub-Basin, Western Australia and determine association patterns and temporal stability of associations (Chapter 5).
5. Investigate feeding ecology of killer whales in the Bremer Sub-Basin, Western Australia (Chapter 6).

1.9 Significance of Research

This PhD thesis provides a quantitative assessment of the acoustic features of killer whale vocalisations in Australian and Antarctic waters and presents an acoustic comparison between sympatric ecotypes in Antarctic waters. It further examines the social structure and feeding ecology of killer whales in the Bremer Sub-Basin, the first study of its kind in Australian waters.

As an apex predator, killer whales play an important role in the ecosystem and can be considered an indicator species due to the position they hold at the top of the trophic food chain (Sergio, Newton, & Marchesi, 2005; Sergio, Newton, Marchesi, & Pedrini, 2006). Indicator species can be used to monitor environmental changes, signal a change in the biological condition of the ecosystem, provide warning signals for impending ecological shifts and be used as a proxy to diagnose the health of an ecosystem (McDonough, David Jaffe, Watzin, & McGinley, 2009; Siddig, Ellison, Ochs, Villar-Leeman, & Lau, 2016). Killer whales currently face many threats being at the top of food chain, including contaminants, such as high concentrations of PCBs and other organic pollutants (Desforges et al., 2018; Hickie, Ross, Macdonald, & Ford, 2007; Jepson et al., 2016; Ross, Ellis, Ikonomou, Barrett-Lennard, &

Addison, 2000), reduced prey availability and prey vulnerability (Ford, Ellis, Olesiuk, & Balcomb, 2010) and climate change (Lusseau et al., 2004; Simmonds & Isaac, 2007). Populations of killer whales can be small in size, show little to no dispersal, and may be highly specialized in their prey preferences, and therefore vulnerable to disturbance, prey reductions and habitat deterioration. Killer whales are currently listed as 'Data Deficient' on the IUCN list (Reeves, Pitman, & Ford, 2017a), and also listed as 'Data Deficient' in Australian legislation (Department Of Environment, 2014; Woinarski, Burbidge, & Harrison, 2014). Obtaining a detailed description of the acoustic characteristics, social structure and feeding ecology of killer whales will help us understand this species and provide baseline information needed for effective management of killer whales within Australian and Antarctic waters. Understanding more about this apex predator, and how it plays a role within the marine ecosystem, is critical for the conservation of this species and for the environment in which it resides. This study makes a substantial, original and significant contribution to the knowledge and understanding of killer whales found in Australia and Antarctica. Results from this study will deliver key scientific data and provide valuable information to scientists, policy makers and conservation management.

1.10 Layout of Thesis

This thesis contains five data chapters, each addressing one of the objectives detailed above. As the data chapters are in the format of scientific papers, each comes complete with its own Abstract, Introduction, Methods, Results and Discussion. Every effort has been made to provide a comprehensive yet non-repetitive literature review and methodology; however, it is inevitable that some overlap occurs given the preparation of chapters as ‘papers’. The content of the data chapters is detailed below:

Chapter 2: Vocalisations of killer whales (*Orcinus orca*) in the Bremer Sub-Basin, Western Australia.

This chapter has been published in the peer-reviewed journal PLOS One as:

> Wellard, R., Erbe, C., Fouda, L., & Blewitt, M. (2015). Vocalisations of Killer Whales (*Orcinus orca*) in the Bremer Canyon, Western Australia. *PLOS ONE, 10*(9), e0136535.

Chapter 3: The Call Repertoire of Antarctic Type C killer whales (*Orcinus orca*) in the Ross Sea Marine Protected Area.

This chapter has been published in the peer-reviewed journal Royal Society Open Science as:

> Wellard, R., Pitman, R., Durban, J., & Erbe, C. (2020) Cold Call: The Acoustic Repertoire of Ross Sea Killer Whales (Orcinus orca, Type C) in McMurdo Sound, Antarctica. R. Soc. Open Sci. 7: 191228.

Chapter 4: The Call Repertoire of Type B Killer Whales (*Orcinus orca*) off the Antarctica Peninsula and a Comparison between Antarctic Ecotypes.

Chapter 5: The Social Structure and Population Dynamics of Killer Whales (*Orcinus orca*) in the Bremer Sub-Basin, Western Australia.

Chapter 6: Killer whale (*Orcinus orca*) predation on beaked whales (*Mesoplodon* spp.) in the Bremer Sub-Basin, Western Australia.

This chapter has been published in the peer-reviewed journal PLOS One as:

> Wellard, R., Lightbody, K., Fouda, L., Blewitt, M., Riggs, D., & Erbe, C. (2016). Killer Whale (*Orcinus orca*) Predation on Beaked Whales (*Mesoplodon* spp.) in the Bremer Sub-Basin, Western Australia. *PLOS ONE, 11*(12), e0166670.

The thesis concludes with a general discussion intended to reflect on the significant findings from the project and identifies limitations and future research directions.

2 Vocalisations of Killer Whales (*Orcinus orca*) in the Bremer Sub-Basin, Western Australia

Abstract

A detailed description of the acoustic characteristics is necessary for species acoustic identification and for the development of passive acoustic tools , in order to determine habitat usage, migration patterns, behaviour and acoustic ecology. To date, there has been no dedicated study in Australian waters on the acoustic behaviour of killer whales (*Orcinus orca*). This study presents the first analysis of recordings collected off the Western Australian coast. Underwater sounds produced by Australian killer whales were recorded during February and March 2014 and 2015 in the Bremer Sub-Basin in Western Australia. Vocalisations recorded included echolocation clicks, whistles and burst-pulse sounds. A total of 28 hours and 29 minutes of killer whale acoustics were recorded and analysed, with 2376 killer whale whistles and burst-pulse sounds detected. Recordings of poor quality or signal-to-noise ratio were excluded from analysis, resulting in 142 whistles and burst-pulse vocalisations suitable for analysis and categorisation. These were grouped based on their spectrographic features into nine call types. The frequency of the fundamental contours of all call types ranged from 600 Hz to 29 kHz. Calls ranged from 0.05 to 11.3 seconds in duration. Echolocation clicks were also recorded, but not studied further. Surface behaviours noted during acoustic recordings were categorised as either travelling or social behaviour. This study provides the first quantitative assessment and report on the acoustic features of killer whales vocalisations in Australian waters and presents an opportunity to further investigate this little-known population.

2.1 Introduction

The killer whale (*Orcinus orca)* is found in all oceans of the world (Ford, 2002). Currently considered one species, different populations of killer whales can be categorised into distinct ‘ecotypes’, based on substantial differences in morphology, behaviour, diet and acoustic repertoire. Sympatric ecotype assemblages are currently documented from three different geographical regions: the eastern North Atlantic, the eastern North Pacific and Antarctica (Barrett-Lennard et al., 1996; Foote et al., 2009; Ford et al., 1998; Pitman & Ensor, 2003).

Three different morphological forms (morphotypes) of killer whales were originally identified in Antarctic waters, with differences in the ecological specialisations possibly being more pronounced than those reported for the Northeast Pacific ecotypes (Pitman & Ensor, 2003). Research to date describes five distinct killer whale morphotypes in Antarctic waters- Types A, B (two forms), C and sub-Antarctic Type D- each with their own physiological, morphological and social adaptations (Pitman et al., 2011).

In Australia, killer whales have been sighted in all state and territory waters (Chatto & Warneke, 2000; Ling, 1991; Ross, 2006). Nonetheless, no defined killer whale ecotypes have been described due to limited understanding of their distribution, movements, habitat use and population status. To date, there has been no reliable estimate of the population size of killer whales in Australian waters, and population trends are unknown, with much of the information on distribution and occurrence obtained from incidental sightings, and from one sighting program undertaken on Macquarie Island (Morrice, 2004). Notably, they are more commonly sighted in coastal waters, along the continental shelf around south-eastern Tasmania, Victoria and southern New South Wales, around sub-Antarctic Macquarie Island, as well as in some parts of the Australian Antarctic Territory (Bannister et al., 1996; Chatto & Warneke, 2000; Kasamatsu & Joyce, 1995; Ling, 1991; Morrice, 2007; Morrice & Gill, 2008; Mustoe, 2008; Parker, 1978; Ross, 2006; Thiele et al., 2000; Thiele & Gill, 1999; Van Waerebeek et al., 2010). Limited knowledge of the spatial and temporal extent of killer whale movements throughout the Australian region means that dedicated surveys of killer whales are required to quantify distribution, movements, habitat use, population size and trends.

Acoustic communication is widely used by cetaceans in a range of contexts, including social interactions, group cohesion, mating, mother-calf contact, travelling and foraging (Tyack & Clark, 2000). In addition, odontocetes use echolocation during navigation and hunting (Au, 2000a). Research from the Northern Hemisphere has demonstrated that killer whales, like other delphinids, produce three commonly grouped sounds: echolocation clicks, whistles and burst-pulse sounds.

Echolocation clicks are short-duration (< 250 µs), broadband (10 kHz – 100 kHz) pulses of up to 224 dB re 1 µPa @ 1 m peak-to-peak source level, typically emitted in trains with a several-second duration (Au et al., 2004; Barrett-Lennard et al., 1996; Evans, 1973; Ford, 1989; Gassmann et al., 2013; Simon et al., 2006). Whistles and burst-pulse sounds are thought to be communicative signals most commonly used in social contexts (Ford, 1989; Thomsen et al., 2002). Whistles are frequency-modulated, tonal sounds, with or without harmonics, and a fundamental frequency ranging from 1 to 36 kHz and source levels up to 193 dB re 1 µPa @ 1 m peak-to-peak reported from North Pacific killer whale populations (Filatova, Ford, et al., 2012; Ford, 1989; Riesch et al., 2006; Simonis et al., 2012; Thomsen et al., 2001), and fundamental frequencies up to 74 kHz recorded in Norwegian and Icelandic killer whales (Samarra et al., 2010). Burst-pulse sounds consist of rapidly repeated pulses with inter-pulse intervals shorter than in echolocation click trains, and are thought to function as contact signals in group recognition and coordination of behaviour (Ford, 1989; Miller et al., 2004). In spectrograms, burst-pulse sounds typically appear as frequency-modulated sounds with numerous sidebands and overtones. The energy of burst-pulse sounds usually lies between 500 Hz and 25 kHz, lasting 0.5 – 1.5 s, with source levels of 131-176 dB re 1 µPa @ 1 m root-mean-square (Filatova et al., 2009; Filatova et al., 2007; Ford, 1987, 1989, 1991; Gassmann et al., 2013; Holt et al., 2011; Miller, 2006; Richlen & Thomas, 2008; Strager, 1995).

Call structure varies amongst allopatric, parapatric and sympatric killer whale populations. Differences in calls amongst spatially separated populations of killer whales are apparent from studies across the world, e.g. the North Pacific (Deecke et al., 2000; Filatova et al., 2007; Ford, 1989; Yurk et al., 2002), Norway (Strager, 1995), and Antarctica (Richlen & Thomas, 2008). There has also been evidence of dialect variation amongst social groups within a population. The resident populations off British Columbia, Canada and Washington, USA consist of four acoustic clans, each clan containing group-specific repertoires reflecting the maternal genetic relationship of the groups (Ford, 1991). Pods within a clan share call types, but exhibit pod-specific variation, i.e. dialects, of shared call types. Such group-specific dialects have also been documented in killer whale populations in Norway and Iceland (Moore, Francine, Bowles, & Ford, 1988; Strager, 1995).

Passive acoustic monitoring can be an inexpensive and effective way of documenting cetacean distribution, migration, behaviour and population density (Erbe, 2013). However, no information has been published on the sounds produced by killer whales from the Australian region. A detailed description of the acoustic characteristics is necessary for species acoustic identification, as well as establishing a basis for comparison of the acoustics of other killer whale populations and uncovering potentially distinctive repertoires in the Australian population. Identifying call repertoires can also aid in identifying potential sympatric ecotypes in Australia.

2.1.1 Objectives

This objectives of this study were to: (1) record vocalisations of killer whales observed seasonally in the Bremer Sub-Basin, Western Australia, (2) describe the vocal repertoire, (3) conduct a quantitative analysis on acoustic features of vocalisations and group them accordingly, and (4) compare basic signal structure characteristics of the vocalisations of killer whales from the Bremer Sub-Basin with other reported vocalisations from killer whales in the Southern Hemisphere.

2.2 Methods

2.2.1 Study Area

The Bremer Sub-Basin is located off the southwest continental shelf of Australia and extends over an area of 11,500 km^2 in water depths of 100 to 4500 m (Exon et al., 2005). The Sub-Basin contains numerous submarine canyons and forms part of the complex Albany Canyons group. The Bremer Sub-Basin region is recognised as a biologically important and productive marine ecosystem, with a large number of marine megafauna observed utilising this area, including a large number of toothed cetaceans such as killer whales (Bouchet et al., 2018; Department of Environment, 2012). Killer whales may occupy this region at any time of the year but have been found to be in a large number during the months of January through to April (Wellard et al., 2015; Wellard et al., 2016).

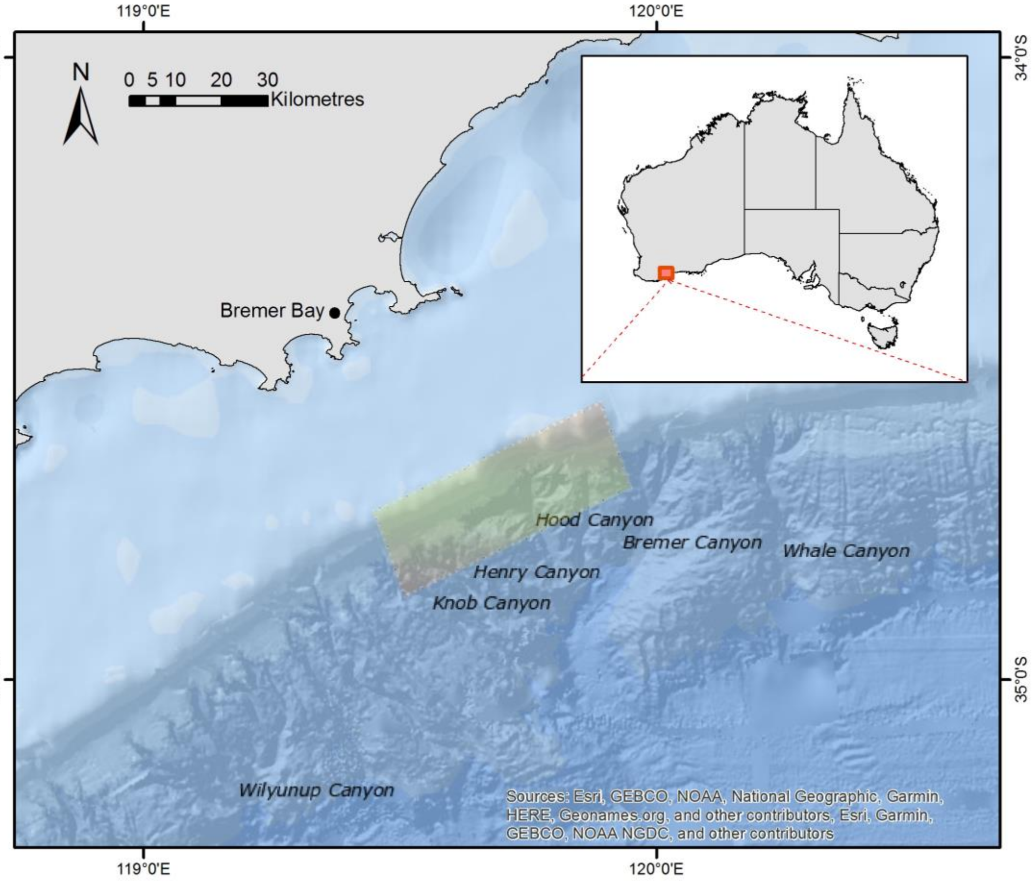

Figure 2.1 Map of the south coast of Western Australia. Highlighted region indicates the area of survey effort undertaken in the Bremer Sub-Basin in 2014 and 2015. Inset map shows the location of Bremer Bay. Map produced using ArcMap GIS software and ESRI World Ocean Base data (ArcGIS, 2012, Redlands, California, United States).

2.2.2 Data Collection

Non-systematic surveys were conducted in the Bremer Sub-Basin between February and March 2014 and again in February and March 2015 (study area within 20 nautical mile radius of centre point: 34°44.30'S and 119°35.55'E, Figure 2.1). Data was collected from a research vessel and a commercial ecotourism vessel, during daylight hours and in variable weather conditions. A total of 34 field trips were conducted with more than 278 h spent at sea, resulting in 85 encounters with killer whales.

Upon an encounter with a group of killer whales, information on group composition, number of animals and behavioural state was recorded. Behaviour was assigned to one of four categories, which were adapted from previous killer whale studies (Baird & Dill, 1995; Barrett-Lennard et al., 1996; Ford, 1989; Weiß, Symonds, Spong, & Ladich, 2007; Williams, Lusseau, & Hammond, 2006): (1) travelling, (2) feeding, (3) milling/resting and (4) socialising (Table 2.1). Photo-identification was collected for each group encountered following established methodologies for killer whale photo-identification studies (Bigg, 1982, 1987).

Table 2.1 Definition of killer whale behavioural states modified from Ford (1989) and Baird and Dill (1995).

Behavioural State	Definition
Travelling (T)	Killer whales moving steadily in a constant direction, respirations usually synchronous, swimming with short relatively constant dive intervals. Group spacing varies.
Feeding (F)	Killer whales seen with direct evidence of feeding, i.e. prey seen in mouths or in the water. Other indications of feeding and foraging include changes in direction, high-speed swimming with direction, and erratic swimming and diving. Large numbers of birds may also be observed either diving or with food in their mouths.
Milling (M)/ Resting (R)	Killer whales engaged in slow movements or 'logging' at the surface. There is little surface-active behaviour (e.g. breaching or tail-slapping) observed during this behavioural state. Both milling and resting are included in this category.
Socialising (S)	Killer whales engaged in a variety of interactive behavioural events, including body contact, sexual interactions, chasing, breaching or hitting the water surface with body parts.

Acoustic recordings were obtained using two devices. The majority of recordings were made using an HTI-96-MIN hydrophone (High Tech Inc., Long Beach, MS, USA) with built-in pre-amplifier (flat frequency response of 2 Hz to 30 kHz; sensitivity -164.1 dB re 1 V/µPa), fitted to a Sound Devices 722 digital recorder (Sound Devices Corp., Reedsburg, WI, USA) sampling at 96 kHz, 24-bit. Recordings commenced once the vessel was manoeuvred into a close proximity of no less than 100 m to the focal group, the engine was switched off and the hydrophone was deployed over the side of the vessel, suspended from a buoy by a bungee including a damper, and lowered down to a depth of 5 m using a small 100g weight strapped to the cable. In addition, a SoundTrap (Ocean Instruments, Auckland, New Zealand) —a self-contained underwater sound recorder—was attached to a tow-line and deployed during an encounter when the vessel was travelling less than 5 knots. The SoundTrap sampled at 192 kHz, 16-bit.

2.2.3 **Data Analysis**

Acoustic recordings were downloaded onto a computer and inspected visually and aurally using acoustic software Raven Pro 1.5 (Cornell Lab of Ornithology, 2014, Ithaca, New York, USA). Calls with a good signal-to-noise ratio (SNR) were selected and analysed using custom software written in MATLAB (The MathWorks Inc., 2014b, Natick, Massachusetts, United States). A 1024-point Hamming window was used to compute spectrograms, with 50% overlap. Given the recordings had been sampled at 96 kHz, the frequency resolution of the spectrograms was about 90 Hz. Only recordings made during confirmed visual sighting of killer whales were included in analysis. Data was excluded when another identified or unidentified odontocete species was observed within sight of the focal group of killer whales.

All sounds were classified as whistles, burst-pulse sounds or echolocation clicks. No quantitative analysis was performed on clicks, as these are not expected to be population-specific or characteristic, but instead this study focussed on whistles and burst-pulse sounds. Whistles were defined as continuous, frequency-modulated, tonal sounds consisting of the fundamental frequency, and in some cases with harmonics at frequencies that were integer multiples of the fundamental. Burst-pulse sounds consisted of rapidly repeated broadband pulses and appeared in spectrograms as constant-wave or frequency-modulated contours with many sidebands and harmonics.

For each whistle, the following parameters of its fundamental were measured: minimum frequency (Min f), maximum frequency (Max f), frequency range (Delta f, i.e. Max f – Min f), start frequency (Start f), end frequency (End f), duration, number of extrema, number of inflection points, and frequency modulation rate (FM rate). Harmonics were also documented. Extrema are local maxima and local minima in fundamental frequency, i.e. stationary points, where the first derivative (the slope) is 0 and changes sign (from positive to negative in the case of a local maximum and from negative to positive in the case of a local minimum). At inflection points, the fundamental contour changes curvature, and the first derivate has a local extremum. FM rate was computed as the ratio of the number of inflection points and the duration (Figure 2.2).

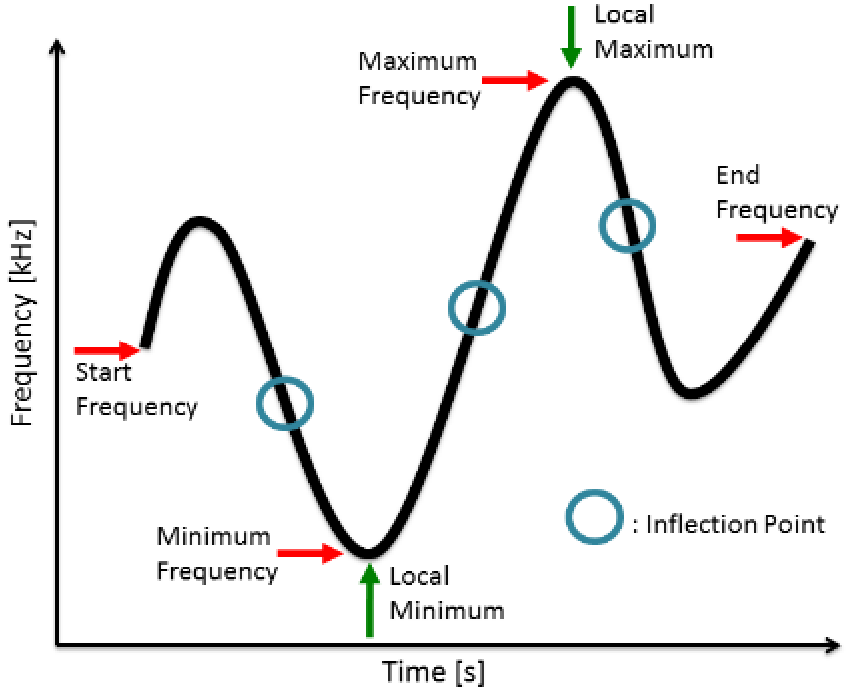

Figure 2.2 Diagram of a hypothetical whistle contour showing parameters that are measured for sound analysis of killer whale vocalisations.

In the case of burst-pulse sounds, the Min f and the Max f of the lowest contour were measured, Start f, End f, Delta f, duration, number of extrema, number of inflection points, FM rate, and the sideband spacing of the burst-pulse sound.

2.2.4 Statistical Analysis

The measured parameters of the call characteristics were used to create a feature vector for each call. K-means clustering (MacQueen, 1967), a simplification of Gaussian mixture modelling, was applied to group the calls into categories by minimising the Euclidian distance between all feature vectors and the cluster centroids. This analysis was performed in MATLAB (The MathWorks Inc., 2014b, Natick, Massachusetts, United States), using the k-means algorithm of the MATLAB statistics toolbox.

2.3 Results

Acoustics recordings were collected during 85 encounters with killer whales in the Bremer Sub-Basin with group sizes ranging from 2 to 30 individuals, including adults, sub-adults and calves. A total of 28 h and 29 min of underwater recordings was examined with 2376 killer whale vocalisations detected. Vocalisations with poor SNR were excluded from analysis, resulting in 142 vocalisations suitable for analysis and categorisation, with all groupings presented in this chapter.

Animals sighted during recordings displayed phenotypic characteristics consistent with ecotype Type A as described by Pitman and Ensor (2003) (Figure 2.3 and Figure 2.4). Although it must be noted, categorising these animals into such ‘ecotypes’ should be with caution, since Type A is described for animals specifically sighted in the Antarctic region.

All behaviours documented during acoustic recordings were categorised as either travelling or socialising. No acoustic recordings were made whilst observing feeding or milling/resting behaviour.

Figure 2.3 Photograph of the right flank of a killer whale (*Orcinus orca*) sighted in the Bremer Sub-Basin off Western Australia sighted during acoustic recordings showing phenotypic characteristics consistent with Type A killer whales.

Figure 2.4 Photograph of the right flank of a killer whale (*Orcinus orca*) sighted in the Bremer Sub-Basin off Western Australia sighted during acoustic recordings showing phenotypic characteristics consistent with Type A killer whales.

Whistles were categorised into 4 groups as a result of the k-means cluster analysis: BSB01, BSB02, BSB03 and BSB04 (BSB = Bremer Sub-Basin). Table 2.2 summarises the measurements of whistles for each group and displays these measured parameters: Min f: minimum frequency of the fundamental; Max f: maximum frequency of the fundamental; Start f: frequency at which the fundamental commenced; End f: frequency at which the fundamental finished; Delta f = Max f – Min f; Duration (s); Number of extrema; Number of inflection points; and FM rate = Number of inflections points / duration.

Table 2.2 Summary of parameters measured for categorised whistles produced by killer whales recorded in Bremer Sub-Basin. Results from the k-means analysis categorised whistles into 4 groups: BSB01, BSB02, BSB03 and BSB04. Number of whistles per group: n. For each group, the range over all the whistles belonging to that group is given.

GROUP	n	Min f [kHz]	Max f [kHz]	Start f [kHz]	End f [kHz]	Delta f [kHz]	Duration [s]	Number of Extrema	Number of Inflection Points	FM Rate [1/s]
BSB01	18	2.2 - 11.8	3.9 - 14.6	2.2 - 12.8	2.9 - 14.5	1.1 - 6.2	0.2 - 3.7	9 - 21	8 - 20	3.4 - 50.2
BSB02	35	1.0 - 5.4	1.8 - 8.4	1.1 - 6.3	1.0 - 8.4	0.4 - 4.4	0.1 - 1.5	0 - 9	0 - 8	0 - 38
BSB03	5	6.8 - 8.2	10.0 -11.5	7.6 - 8.4	7.5 - 9.7	3.2 - 3.8	3.9 - 11.3	15 - 72	14 - 71	3.3 - 6.3
BSB04	61	3.9 - 15.0	9.1 - 29.3	3.9 - 27	5.7 - 29.1	0.3 - 20.3	0.05 - 1.4	0 - 7	0 - 6	0 - 14.3

Burst-pulse sounds were categorised into three categories (BSB05, BSB06 and BSB07) and the remaining calls were categorised into two categories (BSB08 and BSB09) following the k-means cluster analysis. Table 2.3 summarises the measurements of burst-pulse sounds and remaining groups and displays these measured parameters: Min f: minimum frequency of the lowest contour; Max f: maximum frequency of the lowest contour; Start f: frequency of where the lowest contour commenced; End f: frequency of where the lowest contour finished; Delta f = Max f – Min f; Duration (s); Number of extrema; Number of inflection points; FM rate = Number of inflections points / duration and Sideband spacing.

Table 2.3 Summary of measurements for categorised burst-pulse sounds and remaining call groups produced by killer whales recorded in Bremer Sub-Basin. Results from the k-means analysis categorised burst-pulse sounds into 3 groups: BSB05, BSB06 and BSB07. The remaining calls were categorised into 2 groups: BSB08 and BSB09. Number of calls per group: n. For each group, the range over all the calls belonging to that group is given.

GROUP	n	Min f [kHz]	Max f [kHz]	Start f [kHz]	End f [kHz]	Delta f [kHz]	Duration [s]	Number of Extrema	Number of Inflection Points	FM Rate [1/s]	Sideband Spacing [kHz]
BSB05	5	0.6 - 1.2	1.1 - 5.6	0.6 - 1.5	0.7 - 3.4	0.3 - 4.5	0.5 - 1.2	0 - 5	0 - 4	0 - 6.5	0.3 - 0.7
BSB06	6	4.6 - 8.1	5.2 – 10.7	4.8 - 10.1	4.6 - 8.3	0.6 - 2.8	0.2 - 0.6	4 - 8	5 - 7	9.3-28.2	0.2 - 0.8
BSB07	4	2.7 - 4.7	4.1 - 6.3	3.6 - 6.3	2.9 - 6.3	1.4 - 1.6	0.1 - 0.3	1 - 6	0 - 5	0 - 18.1	0.4 - 0.7
BSB08*	2	3.6 - 4.2	5.1 - 5.2	5.4 - 8.7	3.9 - 8.0	1 - 1.6	0.1 - 0.5	1	0	0	0.8 - 0.9
BSB09**	6	0.9 - 4.1	1.5 - 5.5	1.1 - 4.4	1.2 - 5.5	0.5 - 3.4	0.1 - 1.2	1 - 10	0 - 9	0 - 13.9	0.4 - 0.9

* Whistles with pulsed middle section. Min f, Max f, Delta f were measured off the whistle fundamental. Duration, and numbers of extrema and inflection points are for the entire call. Sideband spacing was measured off the pulsed middle section.

**Burst-pulse => whistle transitions and whistle=>burst-pulse transitions. Min f, Max f, Delta f were measured off the whistle fundamental. Duration, and numbers of extrema and inflection points are for the entire call. Sideband spacing was measured off the pulsed section.

2.3.1 Call Categorisation

Whistles

Group BSB01

Of all the whistles categorised, 15.13% were BSB01 (n=18). These whistles exhibited contours with many local extrema and inflection points, had a high FM rate, and a long duration (Figure 2.5). Note the similarity of the overall upsweeping whistles in Figure 2.5b, 2.5c and Figure 2.5d. These whistles are 1.1-1.2 s in duration, and have a fundamental contour starting at about 5 kHz and ending at about 8 kHz. The differences are that Figure 2.5b shows sidebands at the beginning, Figure 2.5c lacks harmonics, and Figure 2.5d shows two similar whistles recorded almost simultaneously but with different FM rates.

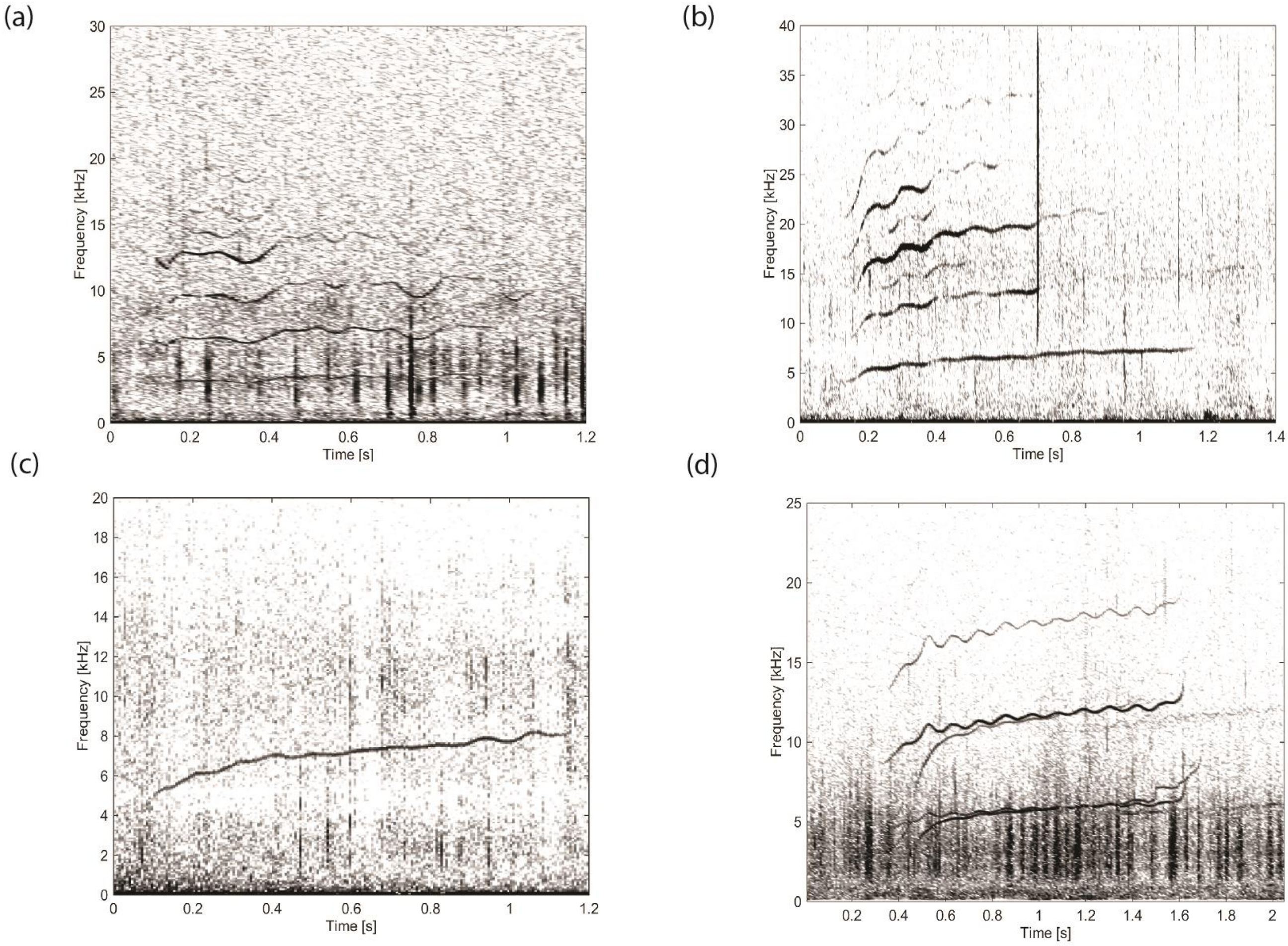

Figure 2.5 Whistles categorised into Group BSB01: (a) BSB01 whistle with high frequency modulation (fs = 96 kHz, NFFT = 512, 50% overlap); (b) BSB01 whistle with high frequency modulation and harmonic overtones. There is another faint call in the background visible at 14 kHz and 0.3 s (fs = 96 kHz, NFFT = 512, 50% overlap); (c) BSB01 whistle with long duration (fs = 96 kHz, NFFT = 512, 50% overlap); (d) BSB01 whistle with high frequency modulation and harmonic overtones. There is another call visible here which was recorded almost simultaneously as this whistle (fs = 96 kHz, NFFT = 1600, 50% overlap).

Group BSB02

Of all the whistles categorised, 29.41% were BSB02 (n=35). These whistles had the lowest frequencies and a low frequency range (Delta f). They were of short duration and had a low number of extrema and inflection points. Most whistles, except three, had harmonics at frequencies that were integer-multiples of the fundamental frequency (Figure 2.6).

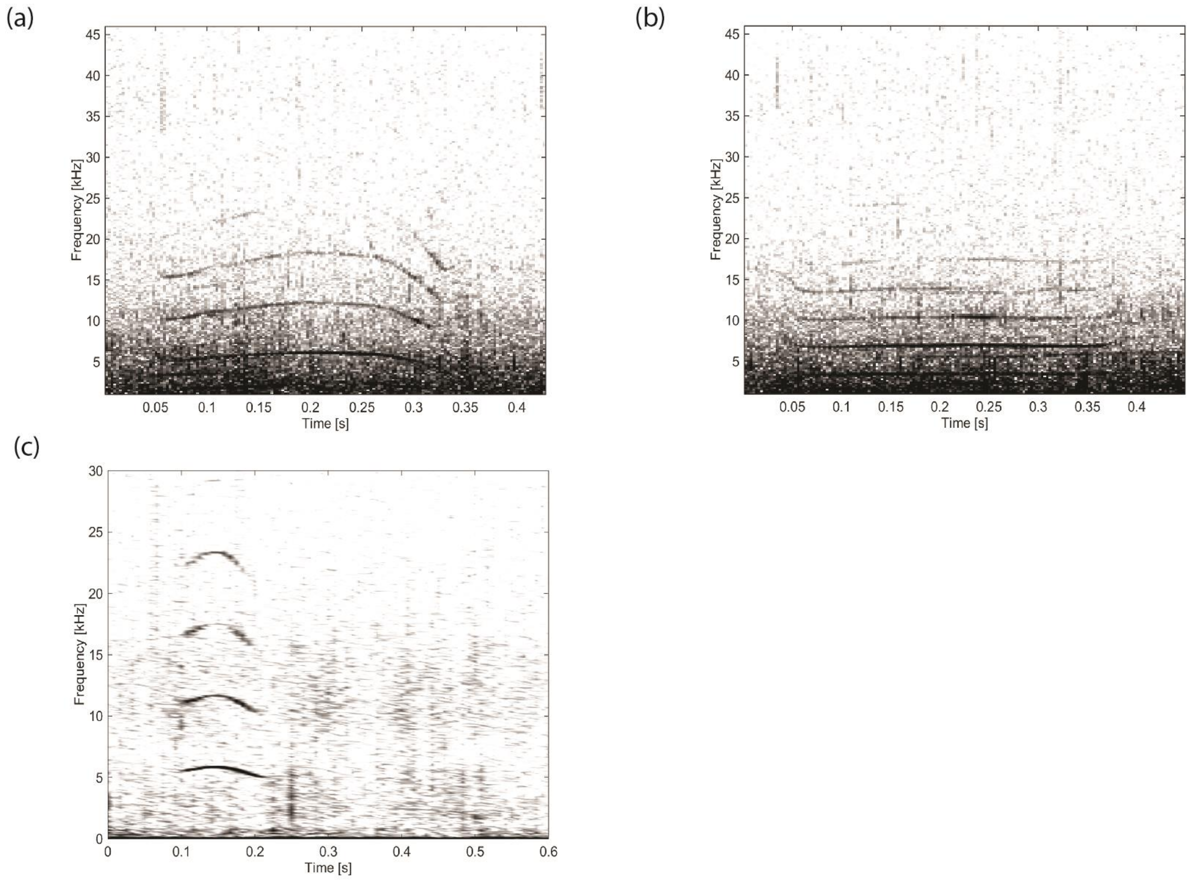

Figure 2.6 Whistles categorised into Group BSB02: (a) BSB02 whistle with a short duration and convex shape. Harmonic overtones are present (fs = 96 kHz, NFFT = 512, 50% overlap); (b) BSB02 whistle of low frequency and a constant-wave shape. This whistle also has harmonic overtones (fs = 96 kHz, NFFT = 512, 50% overlap); (c) BSB02 whistle of short duration and with low number of extrema and inflection points (fs = 96 kHz, NFFT = 512, 50% overlap).

Group BSB03

Of all the whistles categorised, 4.2% were BSB03 (n=5). These whistles had the longest duration (11.3 s) and by far the highest number of extrema and inflection points (Figure 2.7). None of these whistles had harmonics.

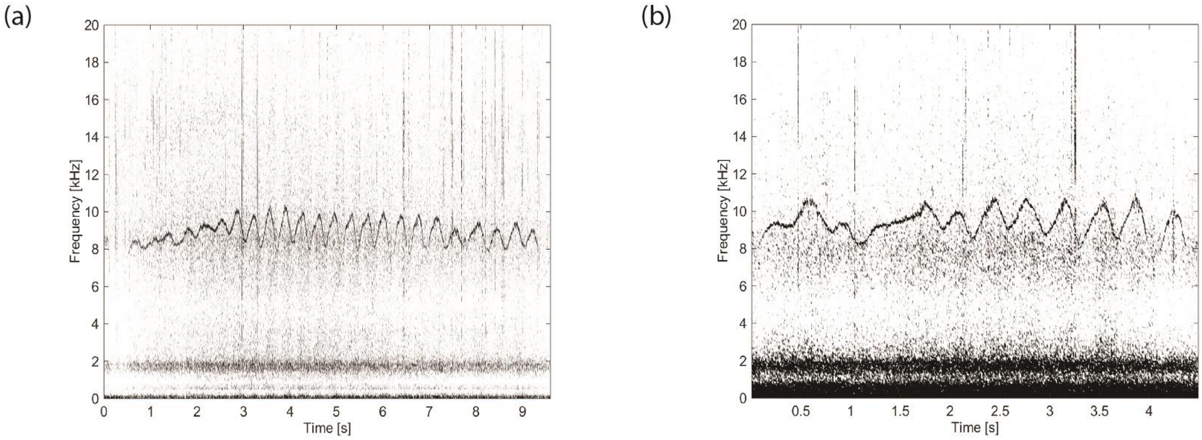

Figure 2.7 Whistles categorised into Group BSB03: (a) BSB03 whistle with a long duration and a high number of extrema and inflection points (fs = 192 kHz, NFFT = 3200, 50% overlap); (b) BSB03 whistle with a long duration and a high number of extrema and inflection points (fs = 192 kHz, NFFT = 3200, 50% overlap).

Group BSB04

Majority of whistles (51.26%, n=61) were categorised in group BSB04. These whistles were of high frequency and short duration with “simple” frequency-modulation and contours including upsweeps, downsweeps, concave and convex shapes (Figure 2.8).

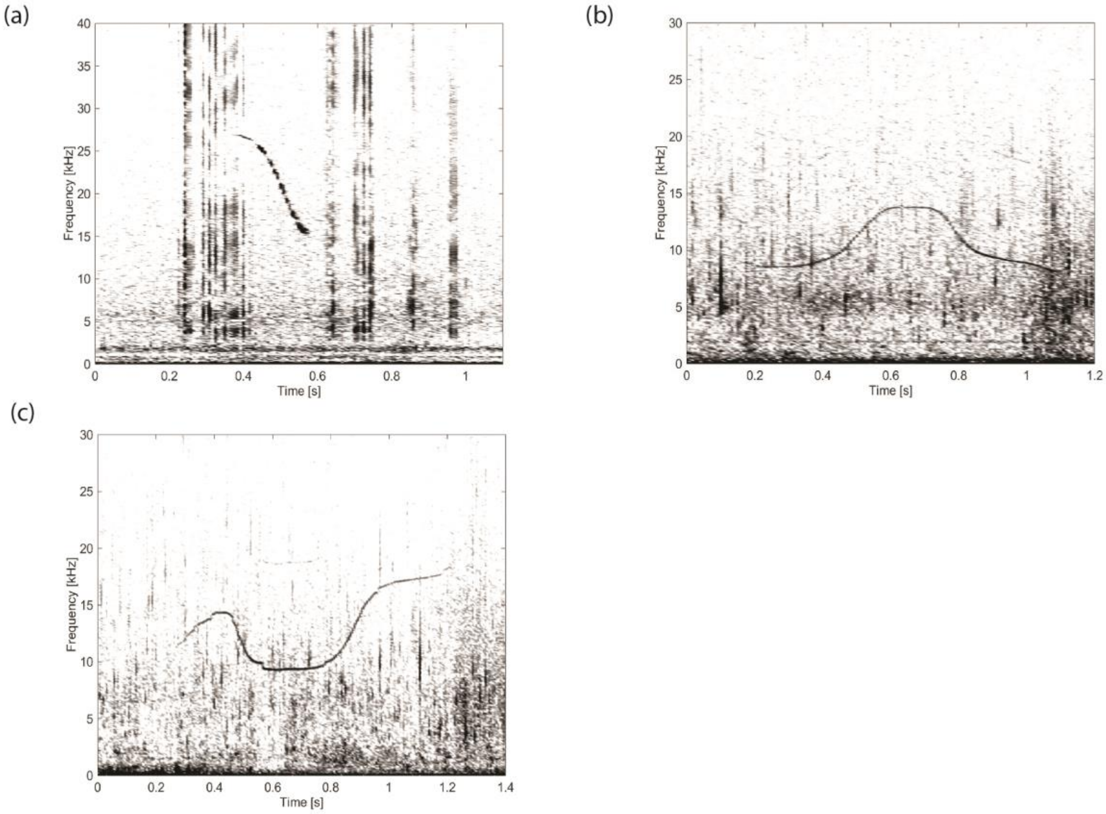

Figure 2.8 Whistles categorised into Group BSB04: (a) BSB04 whistle of short duration and high frequency, ranging up to 27 kHz (fs = 192 kHz, NFFT = 3200, 50% overlap); (b) BSB04 whistle showing "simple" frequency modulation (fs = 96 kHz, NFFT = 1600, 50% overlap); (c) BSB04 whistle showing "simple" frequency modulation and high frequency, ranging up to 19 kHz (fs = 96 kHz, NFFT = 1600, 50% overlap).

Burst-pulse Sounds

Group BSB05

Of all the burst-pulse sounds categorised, 33.33% were BSB05 (n=5). This group of burst-pulse sounds had sidebands extending to the lowest frequencies, the lowest FM rates and the longest durations (Figure 2.9).

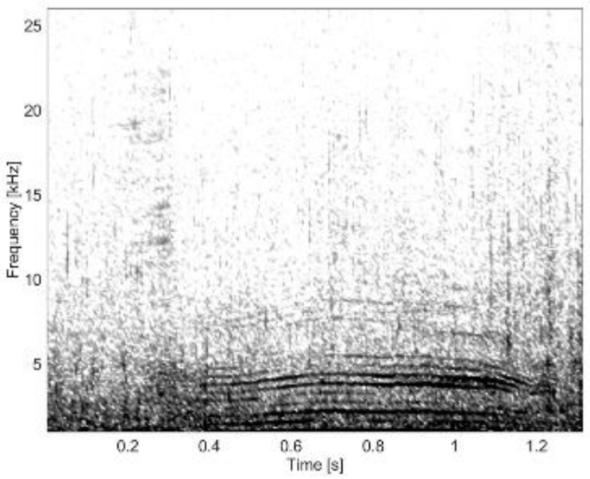

Figure 2.9 Burst-pulse sound from Group BSB05 showing little frequency modulation (fs = 96 kHz, NFFT = 1024, 50% overlap).

Group BSB06

Of all the burst-pulse sounds categorised, 40% were BSB06 (n=6). These burst-pulse sounds had the highest frequencies, the highest number of extrema and inflection points, and the highest FM rates (Figure 2.10).

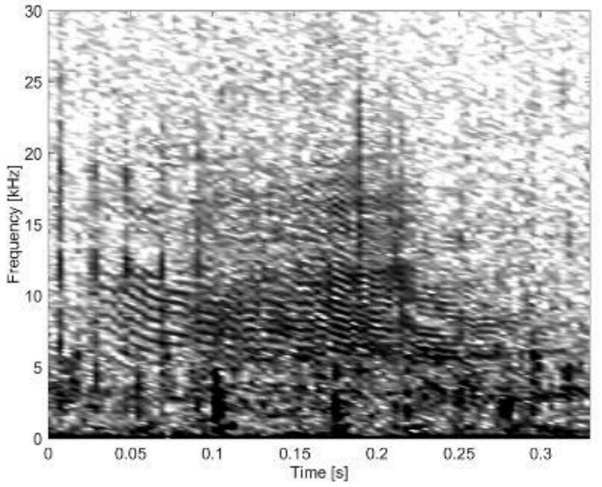

Figure 2.10 Burst-pulse sound from Group BSB06 of high frequency, and with a high FM rate and many inflection points (fs = 96 kHz, NFFT = 700, 50% overlap).

Group BSB07

Of all the burst-pulse sounds categorised, 26.67% were BSB07 (n=4). These burst-pulse sounds were intermediate in frequency and the shortest in duration (Figure 2.11).

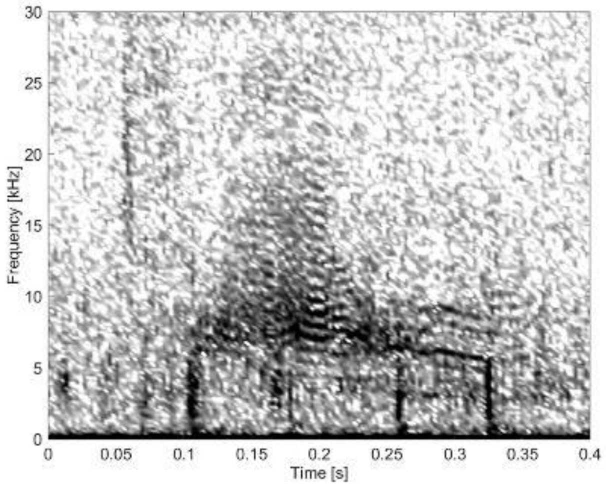

Figure 2.11 Burst-pulse sound from Group BSB07 of short duration (fs = 96 kHz, NFFT = 512, 50% overlap).

Group BSB08

Group BSB08 were whistles that were pulsed in the middle, hence exhibiting many sidebands only in the centre of the call, and harmonics at the beginning and end of the call. This call type was recorded twice, once in a convex shape (Figure 2.12) and once in a concave shape.

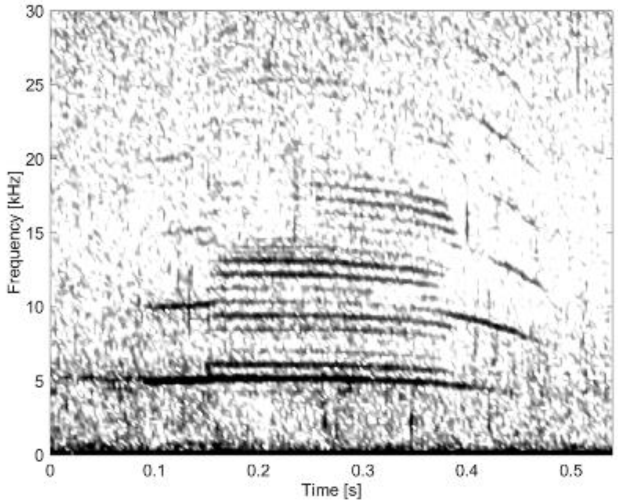

Figure 2.12 Call type BSB08- a whistle that is pulsed in the middle- with non-harmonic sidebands only in the centre of the call (fs = 96 kHz, NFFT = 512, 50% overlap).

Group BSB09

Group BSB09 was recorded six times and consisted of both burst-pulse to whistle transitions and whistle to burst-pulse transitions. Calls had a duration of 0.1 to 1.2 s, with half of the call being of burst-pulse nature and the other half a whistle (Figure 2.13).

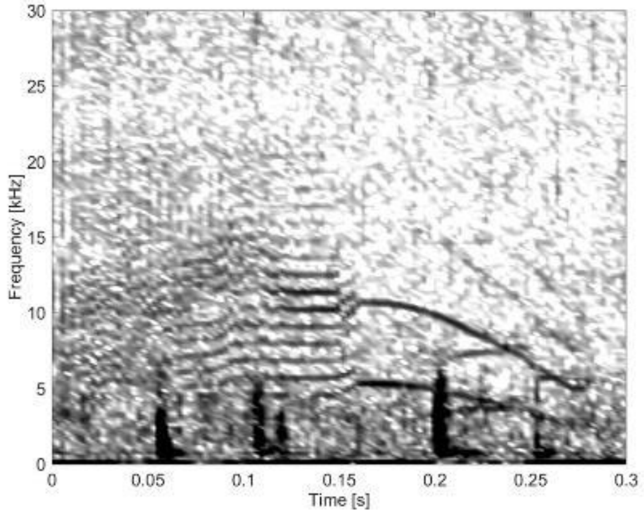

Figure 2.13 Call type BSB09, a transition burst-pulse sound with many sidebands changing into a frequency-modulated downsweep whistle with harmonics (fs = 96 kHz, NFFT = 512, 50% overlap).

Clicks

Echolocation clicks were grouped collectively (Figure 2.14, Figure 2.15 and Figure 2.16). Some clicks were recorded as slow trains with inter-click intervals of 0.1 s and sped-up ending in a buzz sound (Figure 2.14). The peak energy for clicks was between 12 and 24 kHz. Spectra and waveforms compare to those recorded from North Pacific killer whales (Au et al., 2004). Figure 2.15 shows a few clicks from a buzz sequence. The inter-click interval is 2.5 ms. Reflections are seen 0.5 ms after each click. Figure 2.15 is a zoomed-in version of Figure 2.16, showing the Gabor waveform of an outgoing click likely recorded on-axis, i.e. the animal was echolocating in the direction of the hydrophone.

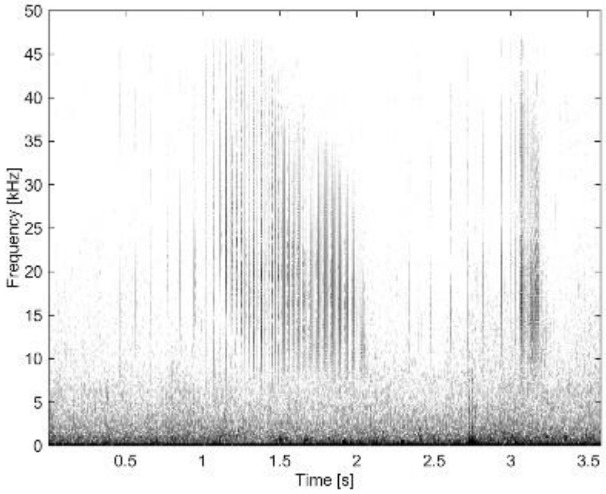

Figure 2.14 Two click trains with peak energy between 12 and 24 kHz (fs = 96 kHz, NFFT = 1600, 50% overlap).

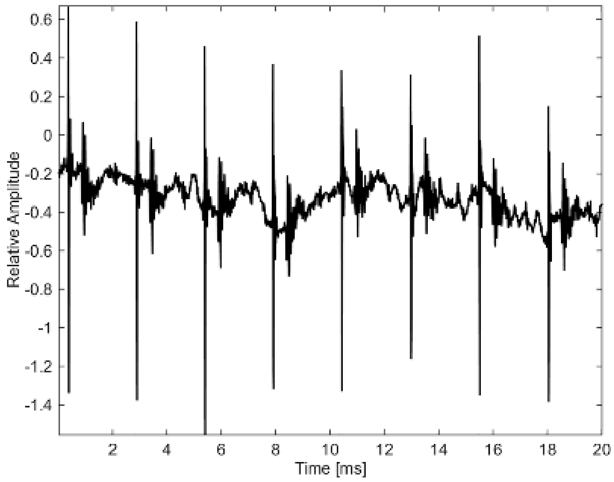

Figure 2.15 Buzz with inter-click interval of 2 ms and reflections seen 0.4 ms after the clicks (fs = 96 kHz).

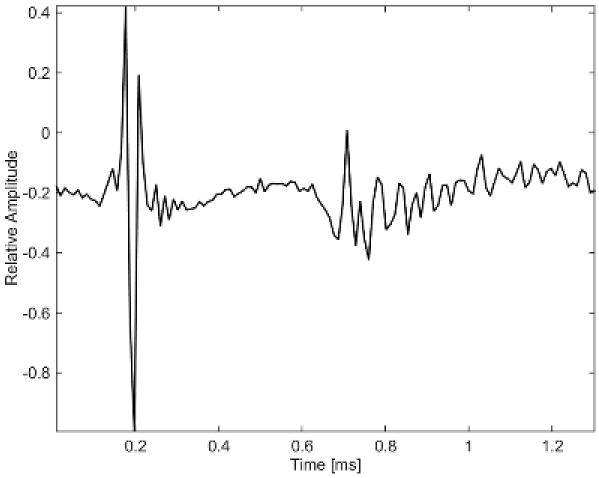

Figure 2.16 Single click of <200 µs duration in the shape of a negative Gabor function, with the reflection arriving 0.4 ms later (fs = 96 kHz).

2.4 Discussion

The Australian killer whale vocalisations analysed in this study produce a repertoire of echolocation clicks, whistles and burst-pulse sounds similar to those reported from killer whales in other regions. While echolocation clicks are not expected to vary between populations, and have not been used in the literature to distinguish between populations, the whistles and burst-pulse sounds characterised here provide a basis for initial comparison to other populations worldwide.

In this study, nine call types were categorised and compared to the only other killer whale calls reported from the Southern Hemisphere. Two whistles categorised in BSB01 were strikingly similar to call type AM4 recorded in Antarctica (Richlen & Thomas, 2008). Both vocalisations are overall upsweeping whistles of 1-1.2 s in length, fundamentals of 4 – 7 kHz plus harmonics, and with many inflection points. Some of the vocalisations in our group BSB02 were very similar to call type AM2 (Richlen & Thomas, 2008), with whistles of 0.2-0.4 s duration, fundamentals of 4-7 kHz plus harmonics, with hardly any frequency-modulation. Call type Group BSB09 which consisted of whistle and burst-pulse transitioning calls, was similar to call type AM5 (Richlen & Thomas, 2008), a buzz sequence which graded into a down-sweeping frequency-modulated signal rich in harmonics. None of the other four call types documented from Antarctic killer whales by Richlen and Thomas (2008) were recorded in this study.

Interestingly, whistle maximum frequency appears to vary substantially across killer whale populations, in contrast to what is reported for other delphinids (Ding, Würsig, & Evans, 1995). Whistle fundamental frequencies have been reported up to 36 kHz in the North Pacific region (Filatova, Ford, et al., 2012; Riesch et al., 2006; Simonis et al., 2012) and up to 74 kHz in Norwegian and Icelandic killer whales (Samarra et al., 2010). This research shows that Australian killer whales exhibit whistle frequencies well within the documented range across other regions, with whistle fundamental frequencies ranging up to 29 kHz.

While 34% of the recorded calls had no inflection points, the FM rate was 5.9/s (median 2.9/s). Some of the calls had a high FM rate (peak 50/s). High FM rates were also noted for Antarctic killer whales with a mean of 7.5/s, median 8.4/s, computed as the ratio of mean number of inflections and mean duration for all call types listed by Richlen and Thomas (2008). Resident killer whales off Vancouver Island, British Columbia, have been reported to show high FM rates of up to 20/s (Ford, 1989), often sped-up variants of slower calls. These ‘excitement’ calls were recorded during episodes of physical interactions between animals both at the surface and underwater as observed by Ford (1989).

Calls categorised in BSB09 were both burst-pulse to whistle transitions and vice versa. These calls typically consisted of two parts, either beginning with the whistle or the burst-pulse component, and then transitioning to the other component. Many of the Pacific Northwest resident killer whale calls consist of several parts with different frequency content and modulation (Ford, 1991).

Previous studies of the vocal behaviour of different killer whale populations have revealed quantitative and qualitative differences related to dietary specialisation. In the Northeast Pacific, mammal-hunting killer whales have been shown to produce echolocation clicks, pulsed calls and whistles at significantly lower rates compared to sympatric fish eaters (Barrett-Lennard et al., 1996; Deecke, Ford, & Slater, 2005). Whereas many fish species have poor hearing sensitivity at the frequencies of killer whale vocalisations, marine mammals can detect killer whale vocalisations at significant distances, and this eavesdropping from their potential prey makes vocal behaviour costly for mammal hunting killer whales (Barrett-Lennard et al., 1996; Deecke et al., 2005; Deecke, Slater, & Ford, 2002). Therefore, since acoustic behaviour can be a tool for indicating foraging specialists, the analysis of Australian killer whale sounds may be able to determine acoustic differences and geographic variations associated with different foraging strategies, and potential undescribed different ecotypes in this region.

Obtaining a detailed description of the acoustic characteristics of killer whales in Australia is necessary for species acoustic identification and is important when visual surveys are limited or lacking, and thus allowing the use of passive acoustic monitoring as a tool for monitoring the population. Passive acoustic monitoring is potentially a powerful, non-lethal, non-invasive and cost-effective method for assessing killer whale abundance and trends, defining habitat use and population monitoring. This would further enhance the limited knowledge and provide an understanding of both spatial and temporal distribution of killer whales in Australian waters.

2.4.1 Conclusion

This study has identified some basic signal structure characteristics found in the Australian killer whale population and provides the foundation to continue further analysis and comparison. In addition to comparing Australian killer whale sounds to other populations worldwide, further investigation and comparison of killer whale populations found within Australian waters could greatly benefit the limited knowledge of this species in this region, with the ability to uncover potential distinctive acoustic repertoires and possible sympatric ecotypes in Australia.

3 The Call Repertoire of Type C Killer Whales (*Orcinus orca*) in the Ross Sea Marine Protected Area

Abstract

Killer whales (*Orcinus orca*) are top marine predators found in all oceans of the world. In Antarctic waters, five ecotypes have been described, each displaying distinct morphological and genetic features, with variability in described foraging behaviours, habitat and diet preferences. Among these, Type C killer whales are the smallest form of killer whale known. They are found off eastern Antarctica, in particular the Ross Sea region, the world's largest marine protected area, where they inhabit mainly inshore waters along the fast ice edge and far into the fast ice leads where they hunt for fish. Acoustic recordings of Type C killer whales were collected between December 2012 and January 2013 in McMurdo Sound, Ross Sea. A total of 3 hours and 33 minutes of killer whale acoustics were recorded and quantitatively analysed resulting in 6386 killer whale vocalisations detected and rated for quality. Spectrograms were examined for characteristic patterns and a call type catalogue was produced, with the call classification yielding a total of 29 categories, including 4 subtypes. Acoustic parameters of each call type for both whistles and burst-pulse sounds were measured. Analysis of calls revealed that Type C killer whales produce many biphonations and complex calls with multiple frequency-modulated and pulsed components. The limited accessibility of Antarctic regions year-round makes passive acoustic monitoring (PAM) a very effective tool to obtain information on ecotype-specific distribution and seasonal occurrence.

3.1 Introduction

The Ross Sea Region Marine Protected Area (RSRMPA) is 1.55 million km^2 in size and the largest high-seas protected area in the world. The first of its kind in international waters, it was established in 2016 by the Commission for the Conservation of Antarctic Marine Living Resources (CCAMLR) following scientific advice (CCAMLR, 2016). The RSRMPA was designed to conserve natural ecological structure, dynamics and function throughout the Ross Sea region, at all levels of biological organisation, by protecting habitats that are important to native mammals, birds, fishes and invertebrates (CCAMLR, 2017). The Ross Sea is an ecologically important area, providing habitat to a unique range of species assemblages (Ballard, Jongsomjit, Veloz, & Ainley, 2012) with a high number of upper-trophic-level predators including large fishes, birds, pinnipeds and cetaceans (Ainley, Ballard, & Weller, 2010). The area is not only an important marine ecosystem but is also currently listed as the least directly anthropogenically affected marine area on Earth (Halpern et al., 2008). This is in part due to its remoteness, which also makes the region difficult to access for ecosystem monitoring.

The creation of such a region means that fundamental baseline data are needed to facilitate proper management of resources, monitor ecosystem health and maintain ecological integrity of the system, the major goal of designating the Ross Sea as an MPA. The utility of upper-trophic-level species, or ‘top predators’, as ecosystem indicators and their effectiveness in assisting management has been discussed and studied intensively (Boyd & Murray, 2001; Camphuysen, 2006; Caro & O'Doherty, 1999; Sergio et al., 2008; Steneck & Sala, 2005). These top-level predators can serve as indicators of change within the broader ecosystem. Understanding the movements, relative abundance, distribution and habitat use of top predators, such as the killer whale (*Orcinus orca*), can help to assess the RSRMPA and assist the development of policies and management decisions.

Killer whales are one of the most cosmopolitan top predators. The killer whale’s global distribution and recognition of its ecological importance as a top predator is reflected by several long-term studies (Bigg et al., 1990; Ford et al., 1994; Matkin, Ellis, Olesiuk, & Saulitis, 1999). Although killer whales are still considered to comprise a single species, studies have established that some populations demonstrate distinct morphological and genetic differences, as well as different behaviours, social structures, diet preferences and acoustic repertoires (Baird, 2000; Durban et al., 2017; Foote et al., 2009; Ford et al., 1998; LeDuc et al., 2008; Morin et al., 2010; Pitman & Ensor, 2003).

In Antarctic waters, five killer whale ecotypes have been described, including Type A, Type B (two forms: large ‘B1’ and small ‘B2’), Type C and sub-Antarctic Type D, with each ecotype displaying morphological differences and distinct habitat preferences, prey specialisation and foraging behaviours (Durban et al., 2017; Pitman et al., 2011; Pitman & Ensor, 2003) (see Figure 3.1).

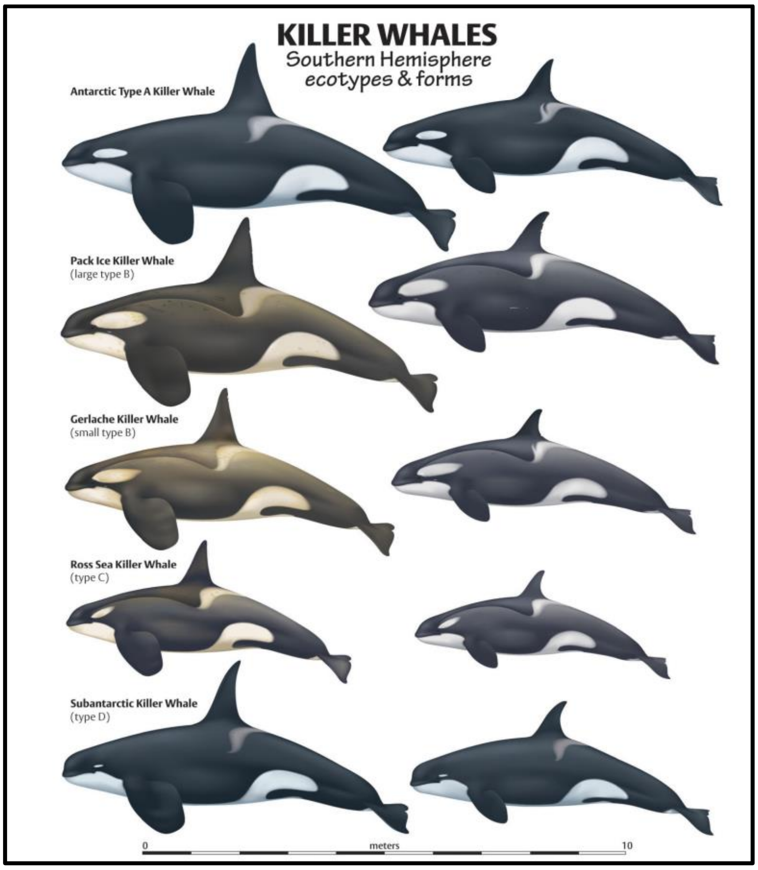

Figure 3.1 The five described killer whale ecotypes of the Southern Hemisphere. Artwork by Uko Gorter. Image source: Riesch, Barrett-Lennard, Ellis, Ford, and Deecke (2012).

Type A is circumpolar in Antarctic waters and is usually found in ice-free areas, where it preys mainly on Antarctic minke whales (*Balaenoptera bonaerensis*; Pitman & Ensor, 2003) . Type A has a medium-sized eyepatch oriented parallel to the body axis, no dorsal cape, and has been recorded to migrate to lower latitudes (Jefferson et al., 2015).

Type B killer whales also have a circumpolar distribution but are found in more inshore pack-ice areas. Large Type B, also known as B1, killer whales exhibit a very large eyepatch oriented parallel to the body axis and a darker gray dorsal cape. They appear to spend most of the year in Antarctic waters. Large Type B feed mainly on ice seals, such as Weddell seals (*Leptonychotes weddellii*), crab-eater seals (*Lobodon carcinophagus*) and leopard seals (*Hydrurga leptonyx*). Small type B, also known as B2, are found in the Gerlache Strait region and are known feed on fish or squid and, occasionally, penguin (Pitman & Ensor, 2003). Small Type B killer whales are about 1 m shorter than large Type B and are found in the western Antarctic Peninsula and western Weddell Sea (Jefferson et al., 2015; Pitman & Ensor, 2003).

Type C killer whales are currently known mainly from eastern Antarctica, where they inhabit the inshore waters along the fast ice edge. They also occur deep in the leads where they hunt for fish, such as Antarctic toothfish (*Dissostichus mawsoni*) and smaller fish species documented by stable isotope analysis (Ainley, Ballard, & Olmastroni, 2009; Krahn et al., 2008) and field observations (Lauriano et al., 2007; Pitman, 2014; Pitman et al., 2018). Type C are the smallest killer whale form known worldwide, with the largest Type C measuring 6.1 m (Pitman et al., 2007), and are easily identifiable by the presence of a dorsal cape and the narrow, slanted eyepatch that is oriented at about a 45° angle to the long axis of the body (Jefferson et al., 2015; Pitman & Ensor, 2003). It is likely that Type C are the same as those described by Berzin and Vladimirov (1983) from eastern Antarctica – *O. glacialis*- but current evidence is inconclusive. Studies have shown that Type C have movement patterns consistent with fish-eating residents from the eastern North Pacific, with a more localised distribution and more predictable occurrence (Andrews et al., 2008).

Type D killer whales have a circum-global range in subantarctic waters and can be easily identified by their extremely small eyepatch that lies parallel to the body axis. Little is known about Type D diet, but this ecotype has been recorded interacting with toothfish longlines, suggesting that its diet probably includes fish (Jefferson et al., 2015; Pitman et al., 2011).

Given only relatively recent recognition of Antarctic killer whale ecotypes, little is known about their distribution, movement patterns and social structures throughout the Southern Ocean. Despite these limitations, our target ecotype for this study – Type C – has been commonly reported in McMurdo Sound for more than a century and sightings are more consistent than for other ecotypes due to its location and accessibility (Ainley et al., 2017; Ballard & Ainley, 2005; Eisert et al., 2015; Jehl, Evans, Awbrey, & Drieschmann, 1980; Pitman & Ensor, 2003; Pitman et al., 2018; Wilson, 1907). Since the early 1970s, killer whales have been recorded annually in McMurdo Sound shortly after the icebreaking has begun. They are found to take advantage of foraging habitat made available when an icebreaker opens up the channel for supply ships to gain access to McMurdo Station, resulting in opportunities for data collection at close range (Pitman & Ensor, 2003). Studies indicate that there may be a seasonally resident population of

Type C killer whales in McMurdo Sound, with tag data and a photo-identification revealing localised distribution and a more predictable occurrence (Andrews et al., 2008; Pitman et al., 2018).

The highly mobile nature of killer whales makes them difficult to study by traditional methods, but passive acoustic monitoring is a technique that can overcome this. Using autonomous recording systems in remote and isolated regions, such as the Ross Sea, allows year-round data collection independent of inclement weather, limited daylight and ice coverage. Quantitatively describing the acoustic repertoire of a species and potentially identifying sympatric ecotypes is important for establishing effective passive acoustic monitoring programmes and essential when using autonomous systems. Describing a species' or ecotype's repertoire and understand their vocal behaviour requires concurrent visual sightings with acoustic recordings, with sufficient visual sightings to identify not only species, but ecotype as well.

Studies of the vocal behaviour of different killer whale populations have identified a mix of unique and shared call types and documented vocal culture whereby different killer whale groups exhibit distinct dialects (Deecke, Barrett-Lennard, Spong, & Ford, 2010; Ford, 1991; Strager, 1995; Yurk et al., 2002). These dialects are stable through time (Foote et al., 2008; Ford, 1984) and are a learned behaviour (Deecke et al., 2000; Filatova et al., 2015; Yurk et al., 2002). Groups with similar repertoires have been shown to be more closely related than groups that share fewer calls, with some pods of related matrilines sharing many or all of the elements in their repertoire (Barrett-Lennard, 2000; Ford, 1989, 1991). Differences in call types amongst spatially separated populations of killer whales are apparent from studies worldwide (Deecke et al., 2000; Filatova et al., 2007; Ford, 1989; Strager, 1995; Yurk et al., 2002) and have resulted in effective monitoring of these populations through the use of passive acoustic listening stations (Yurk, Filatova, Matkin, Barrett-Lennard, & Brittain, 2010).

Like other delphinids, killer whales have an acoustic repertoire that consists of three types of vocalisations: echolocation clicks, whistles and burst-pulse sounds. Echolocation clicks are broadband pulses (10 kHz to 100 kHz) with a short duration, typically emitted in trains lasting several seconds; they are used for navigating and foraging (Au et al., 2004; Barrett-Lennard et al., 1996; Evans, 1973). Whistles are tonal signals with the fundamental frequency ranging from 1 kHz to 36 kHz in the case of the North Pacific killer whale populations (Filatova, Ford, et al., 2012; Ford, 1989; Riesch et al., 2006; Simonis et al., 2012; Thomsen et al., 2001), and with fundamental frequencies up to 74 kHz in eastern North Atlantic killer whale populations (Samarra et al., 2010). Burst-pulse sounds are broadband sounds that consist of rapidly repeated pulses which, along with whistles, have been used reliably to categorise calls specific to killer whale populations (Deecke et al., 2005; Ford, 1987; Strager, 1995). Both whistles and burst-pulse sounds are believed to be communicative signals used in social contexts, functioning as contact signals in group recognition and in coordination of behaviour (Ford, 1989; Miller et al., 2004; Thomsen et al., 2002).

Despite the reliability of sightings of Type C killer whales in McMurdo Sound, few acoustic studies have been conducted on the call repertoire of this ecotype. In McMurdo Sound, both Type B and Type C have been sighted using the ice channel, hence why confirming ecotype is pertinent for concurrent acoustic recordings. There have been four previous studies describing killer whale vocal behaviour in the Southern Ocean (Awbrey et al., 1982; Richlen & Thomas, 2008; Schall & Van Opzeeland, 2017; Wellard et al., 2015). Three of these focused on calls recorded in Antarctic waters, with only one report having concurrent photographs confirming ecotype Type C with certainty (Schall & Van Opzeeland, 2017).

Preliminary reports briefly described the underwater sounds of killer whales in the Ross Sea (Awbrey et al., 1982; Thomas, Leatherwood, Evans, Jehl Jr, & Awbrey, 1981), but no concurrent imagery could confirm the ecotype. Richlen and Thomas (2008) analysed recordings made in 1979 along a lead in the fast-ice in McMurdo Sound from a group of seven to nine killer whales. Seven discrete call types were identified, with Richlen and Thomas (2008) reporting the acoustic repertoire similar to sounds described from fish-eating killer whale populations in other oceans, and suggesting a pod-specific repertoire due to the consistent repetition of call types. Concurrent photographs were taken during this encounter, which showed only the body and dorsal cape of the animals, with no other diagnostic features evident in the photographs making confirmation of ecotype impossible.

Schall and Van Opzeeland (2017) analysed opportunistic acoustic data collected concurrently with visual confirmation of Type C killer whales near the Eckström Ice Shelf in the eastern Weddell Sea. However, this study had limitations such as a 15 kHz bandwidth, which meant that the classification analyses in this study were restricted and the whole spectrum of a call may not be captured if it was above 15 kHz. Another limitation was the low encounter rate; only four killer whales were sighted during the acoustic recording. This low encounter rate of individuals may bias the described call repertoire. When describing the repertoire of a species or ecotype, the study would ideally maximise data representation and avoid oversampling specific groups or individuals. Acoustic data would ideally be collected from different groups and individuals, displaying a multitude of varying behaviours, to capture the potentially broad acoustic repertoire of the subject.

This study conducted in McMurdo Sound, Ross Sea, Antarctica, is the first to extensively describe the call repertoire of confirmed Type C killer whales. A detailed description of acoustic characteristics provides an initial step towards comparing and distinguishing Type C call repertoire with those of other killer whale populations in the Southern Hemisphere and is essential for PAM to be effective in this newly assigned MPA.

3.1.1 Objectives

The objectives of this study were to: (1) record vocalisations of Type C killer whales, along with concurrent photographs, in McMurdo Sound, Antarctica, (2) describe the vocal repertoire, (3) categorise call types accordingly and create a call catalogue, (4) conduct an interobserver reliability test to confirm the initial classification of call categories, (5) measure parameters of whistles and burst-pulse sounds, and (6) compare call types in this study with other killer call types described in acoustic studies on killer whale repertoire in the Southern Ocean.

3.2 Methods

3.2.1 Study Area and Data Collection

Acoustic data were collected near the fast ice edge in McMurdo Sound, Ross Sea, Antarctica, between December 2012 and January 2013 (Figure 3.2). Most of the data collection consisted of a primary scouting flight by a helicopter from McMurdo Station. Upon detecting killer whales, the helicopter landed on the fast ice approximately 200 m from the ice edge. Killer whales usually travelled along the fast ice edge but were sometimes found along leads in the fast ice or at isolated breathing holes, 0.5 km or more from the fast ice edge. The hydrophone was hand-deployed into the water at the ice edge in the immediate vicinity of killer whales (i.e., at < 100 m range). Acoustic recordings were obtained with a custom-made hydrophone (flat frequency response of 20 Hz to 20 kHz) and M-Audio Microtrack 24-96 recording unit. Sound was sampled at 96 kHz or 44.1 kHz (sampling frequency, fs), providing a minimum bandwidth of 48 kHz and 22.05 kHz, respectively.

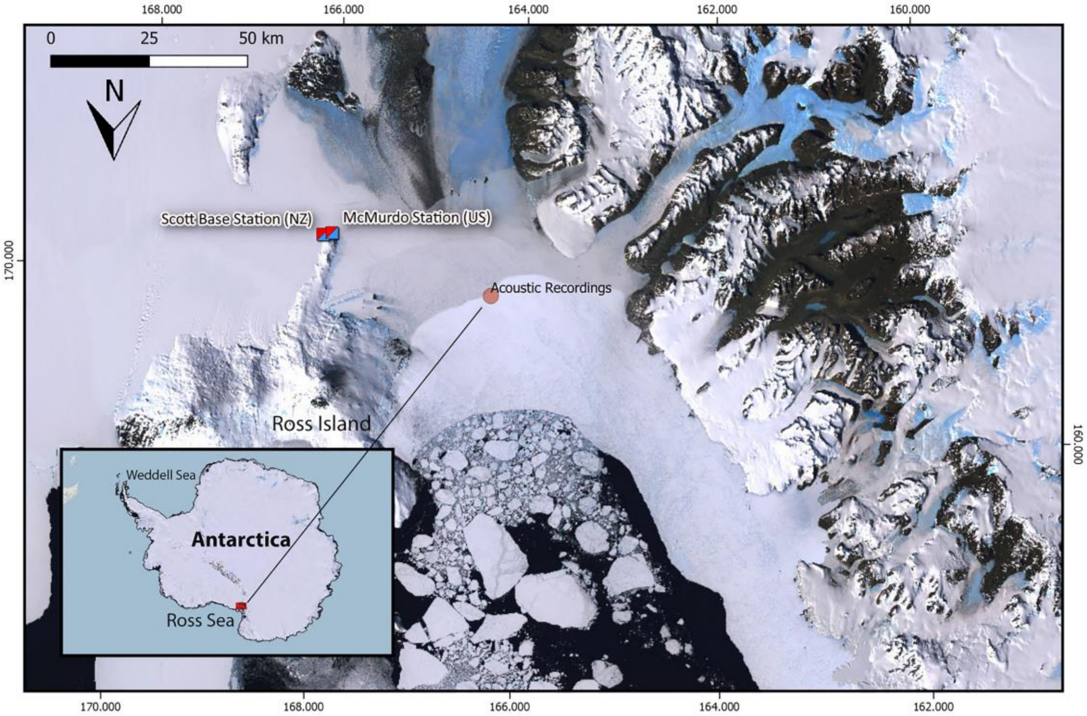

Figure 3.2 Map of Antarctica showing the location of study area and marked point where acoustic recordings were taken in McMurdo Sound between December 2012 and January 2013. Map produced using QGIS mapping software (QGIS Develpment Team, 2018, Open Source Geospatial Foundation Project, Boston, Massachusetts, United States) with Quantarctica package (Matsuoka et al., 2018). Satellite imagery provided by Norwegian Polar Institute based on Landsat satellite images from previous years does not reflect sea ice coverage during the 2012/2013 season.

During the recording, killer whale ecotype, group composition, number of animals, and behaviour was noted. Individual whales were photographed as part of a photo-identification study (Pitman et al., 2018). Behaviour was assigned to one of four behavioural states, which were adapted from previous killer whale studies (Baird & Dill, 1995; Barrett-Lennard et al., 1996; Ford, 1989; Weiß et al., 2007; Williams et al., 2006): (1) travelling, (2) foraging, (3) milling/resting and (4) socialising (Table 3.1).

Table 3.1 Definition of killer whale behavioural states modified from Ford (1989) and Baird and Dill (1995).

Behavioural State	Definition
Travelling (T)	Killer whales moving steadily in a constant direction, respirations usually synchronous, swimming with short relatively constant dive intervals. Group spacing varies.
Foraging (F)	Killer whales seen with direct evidence of feeding, i.e. prey seen in mouths or in the water. Other indications of feeding and foraging include changes in direction, high-speed swimming with direction, and erratic swimming and diving. Large numbers of birds may also be observed either diving or with food in their mouths.
Milling (M)/ Resting (R)	Killer whales engaged in slow movements or 'logging' at the surface. There is little surface-active behaviour (e.g. breaching or tail-slapping) observed during this behavioural state. Both milling and resting are included in this category.
Socialising (S)	Killer whales engaged in a variety of interactive behavioural events, including body contact, sexual interactions, chasing, breaching or hitting the water surface with body parts.

3.2.2 Acoustic Analysis

Acoustic recordings were inspected both visually and aurally using the acoustic software Raven Pro 1.5 (Cornell Lab of Ornithology, 2014, Ithaca, New York, USA). Spectrograms were computed at consistent frequency resolution. A 1024-point Fast Fourier Transform (FFT) was used for the recordings sampled at 96 kHz, and a 512-point FFT was used for the recordings sampled at 44.1 kHz, resulting in a frequency resolution of about 90 Hz in both cases. All Fourier transforms were computed with 90% overlap of successive Hann windows. Only recordings made during a confirmed encounter with ecotype Type C were included in the analysis. Calls were visually rated based on their signal-to-noise ratio (SNR): Grade 1 ('Poor') if the signal was faint, but still visible; Grade 2 ('Average') if the signal was distinct and clear; and Grade 3 ('Good') if the signal was strong and prominent. Only Grade 2 and 3 calls were selected for analysis.

3.2.3 Call Type Categorisation

Calls rated 2 and 3 were sorted into preliminary call types to produce a call catalogue. These call categories were principally based on features that are discernible in spectrograms and demonstrate the unique aural characteristics of a call, such as the number of successive components (single or multi-component call), duration of the call, presence of simultaneous components (biphonic call) and the overall shape of the call's contour. This methodology was based on previous studies using aural and spectrographic comparison for categorising killer whale calls (Ford, 1984; Ford & Fisher, 1982; Yurk et al., 2002). If call types contained less than two examples, the call type was discarded. Original call categorisation was conducted by two experienced bioacousticians and was subsequently confirmed by a test for interobserver reliability.

Several call types were found to have subtypes (i.e., variations of the primary call type). The primary call type was the call type most frequently recorded and variants were subtypes. Subtypes were assigned if there were (1) consistent differences in the frequency contour of an element or the addition/deletion of one component following Strager (1995) and Yurk et al. (2002), and (2) at least two occurrences of the subtype were found. Calls were classified as biphonic if they had two simultaneous but independently modulated frequency components, otherwise they were classified as monophonic (Filatova et al., 2009; Wilden et al., 1998).

3.2.4 Interobserver Reliability Test

To confirm the initial classification of call categories, a subset of 50 calls were randomly chosen and given to independent observers for classification (Janik, 1999; Kriesell, Elwen, Nastasi, & Gridley, 2014; Rehn, Teichert, & Thomsen, 2007; Riesch & Deecke, 2011; Riesch et al., 2006). Spectrograms were printed on individual sheets and shown in random order. Four observers with little or no acoustic analysis experience were asked to group the calls independently into an unspecified number of categories based on (1) call duration, (2) number of components, and (3) similar contour modulations. A Kappa statistic was then used to test for interobserver reliability (Siegel & Castellan, 1988).

3.2.5 Call Measurements

Each call that was included in the analysis had up to 20 parameters measured in Raven Pro 1.5 to quantify its spectro-temporal structure (Table 3.2). Some of the parameters are more useful for quantifying broadband calls like burst-pulse sounds (e.g., entropy measures and quartile frequencies), while others are more useful for whistles (e.g., start, end, minimum and maximum frequencies of the contour). For each call type category, a minimum of 20% of Grade 2 and Grade 3 calls were measured, and in the case of call types with 10 or less, all calls were measured.

Table 3.2 List of parameters measured to quantify the spectro-temporal structure of call types recorded from Type C killer whales in McMurdo Sound, Antarctica. (V): measured visually from spectrograms in Raven; (R): computed by Raven.

Parameter	Abbreviation	Description
Duration (R)	Dur	Time duration [s] of the entire call
Duration 90% (R)	Dur90%	Useful for burst-pulse sounds and whistles, the time [s] during which the cumulative energy of the call rises from 5% to 95%
Minimum Frequency (V)	Fmin	Lowest frequency [Hz] of the call in the case of burst-pulse sounds and lowest frequency of the fundamental contour in the case of whistles
Maximum Frequency (V)	Fmax	Highest frequency [Hz] of the call in the case of burst-pulse sounds and highest frequency of the fundamental contour in the case of whistles
Start Frequency (V)	Fstart	Useful for whistles, the frequency [Hz] at the start of the fundamental contour
End Frequency (V)	Fend	Useful for whistles, the frequency [Hz] at the end of the fundamental contour
Delta Frequency (R)	Fdelta	Range of frequencies spanned by the burst-pulse sound or the fundamental whistle contour (Fdelta = Fmax - Fmin)
Bandwidth 90% (R)	BW90%	Useful for burst-pulse sounds, the bandwidth [Hz] containing 90% of the call energy (i.e., difference between the frequencies at the 5th and 95th energy percentiles)
Peak Frequency (R)	Fpeak	Useful for burst-pulse sounds, the frequency [Hz] at which the call spectrum has its maximum energy
Centre Frequency (R)	Fcentre	Useful for burst-pulse sounds, the frequency [Hz] that divides the call spectrum into two frequency bands of equal energy
1st Quartile Frequency (R)	Q1F	Useful for burst-pulse sounds, the frequency [Hz] that divides the call spectrum into two frequency bands containing 25% and 75% of the energy in the call
3rd Quartile Frequency (R)	Q3F	Useful for burst-pulse sounds, the frequency [Hz] that divides the call spectrum into two frequency bands containing 75% and 25% of the energy in the call
Minimum Entropy (R)	MinEnt	Useful for burst-pulse sounds, the minimum entropy over all time bins in the call spectrogram [bits]
Maximum Entropy (R)	MaxEnt	Useful for burst-pulse sounds, the maximum entropy over all time bins in the call spectrogram [bits]
Average Entropy (R)	AvgEnt	Useful for burst-pulse sounds, the average entropy over all time bins in the call spectrogram [bits]
Number of Extrema (V)	Ext	Extrema are local maxima and minima in the whistle contour, i.e., where the first derivative of the whistle contour with respect to time is zero

Parameter	Abbreviation	Description
Inflection points (V)	Infl	At inflection points, the curvature of the whistle contour changes from clockwise to counter-clockwise or vice versa. The second derivative of the whistle contour with respect to time is zero.
FM rate (V)	FM	The ratio of the number of inflection points and duration [1/s]
Number of Steps (V)	Steps	A discontinuity in the whistle contour, where the contour makes a jump in frequency without any gap in time
Harmonics (V)	Harm	The presence of harmonics in whistles was noted as a binary response (y/n)

The parameters in Table 3.2 were measured separately for all components of a call. Calls consisted of one or more components, with many calls consisting of both whistle and burst-pulse components. Some calls also had simultaneous biphonic components. For whistles, measurements were taken from the fundamental contour; however, it was often easier to measure features from higher harmonics where the noise floor was less. Features such as duration, extrema, inflections, FM rate, and steps are the same in harmonics and fundamental. Frequency measurements such as start, end, minimum, and maximum frequency are scaled down when measurements were made on the higher bands ; i.e., a factor n+1 higher for the n^{th} harmonic. For example, if measurements were done off the first harmonic, then the measurements were divided by 2 in order to correspond to the fundamental.

Most recordings were too noisy (ice noise, overlapping sounds from other killer whales, and recording artefacts) to investigate the sound pressure waveform and thus distinguish between pure tones (whistles) and burst-pulse sounds at high pulse-repetition rates. In spectrographic analysis, burst-pulse sounds appear as frequency contours with sidebands. All of the contours seen may occur at harmonic intervals, being integer multiples of a fundamental, making it impossible to tell whether the underlying call is a whistle with harmonics or a series of rapid pulses. In spectrographic analysis, changes in the pulse-repetition rate of burst-pulse sounds appear as frequency-modulation of contours. In order to describe the different components of the recorded calls, we used the default from Watkins (1968) calling sounds with fewer than five harmonics a whistle, and those with more contours a burst-pulse sound. We also note that the majority of calls recorded transitioned gradually from burst-pulses to whistles and vice versa by increasing the pulse-repetition rate and decreasing the inter-pulse interval until continuous tones were formed, and vice versa. This category of transition calls follows Murray, Mercado, and Roitblat (1998) and their definition of characterizing graded vocalisations and the continuum from whistle to pulses.

3.3 **Results**

Acoustic recordings were collected during nine separate encounters with Type C killer whales that were confirmed to ecotype by diagnostic features (Figure 3.3), with group sizes ranging from 8 to 125 individuals, including adults, sub-adults and calves. A total of 353 killer whales were estimated in these encounters, although some of these individuals were likely re-sights while submerged individuals may have been missed during counting. Behaviour documented during acoustic recordings included all four behaviour states, with predominant behaviours of socialising, foraging and travelling observed. For most sightings, the killer whales were either travelling along the fast ice edge or foraging under the ice; i.e., they disappeared under the ice edge and often resurfaced in the same area several minutes later. Often, younger animals stayed at the surface near the ice edge while the adults foraged, so group behaviour often included simultaneous foraging and socialising. Type C killer whales tend to aggregate in large groups, and therefore it was difficult to discern stable constituent sub-groups and likely matrilines.

Figure 3.3 Photograph of a Type C killer whale encountered during acoustic recordings on 04 January 2013. The photograph shows the narrow, slanted eyepatch that is oriented at a 45° angle to the long axis of the body and the presence of a dorsal cape. Image by R.L. Pitman.

A total of 3 h and 33 min of killer whale recordings were analysed resulting in 6386 killer whale vocalisations detected and subsequently rated. After removing Grade 1 calls, 1252 vocalisations were sorted into 35 call categories with 6 subtypes. Following the review of these categories, classes with fewer than two examples of each type were eliminated. The final classification of calls yielded a total of 29 categories, including 4 subtypes. Summary statistics for the acoustic parameters for each call type are listed in Appendix 2 and a spectrogram of each call type with all parameters measured is given in the call catalogue (Appendix 3).

3.3.1 Interobserver Reliability Test

The visual inspection conducted by four inexperienced judges showed that observers agreed on the classification of the killer whale calls and the majority of calls were placed into the same categories by each observer, with a moderate level of agreement in classification of calls across the 29 categories (Fleiss-Kappa statistic, $K = 0.515, z = 41.8, p < 0.0001$). These results show that clearly defined call types exist in the repertoire of Type C killer whales and support the authors' visual categorisation of the calls in this study.

3.3.2 Call Categorisation

The most common call types were McM3, McM2, McM1, McM10, McM15, McM7 and McM5 (n=130, 10.4%; n=111, 8.9%; n=101, 8.1%; n=95, 7.6%; n=89, 7.1%; n=88, 7.0%; n=84, 6.7%; respectively), while the other 22 call types comprised the remaining vocalisations analysed (n=554, 44.2%).

Four call categories were deemed subtypes of other call types. The majority of call categories (McM1a, McM5a, McM10a, and McM15a) were designated subtypes on the basis that there was an addition or deletion of one or more components from the primary call type, whilst the remaining category (McM3a) had a variation in the frequency contour of one component (Figure 3.4).

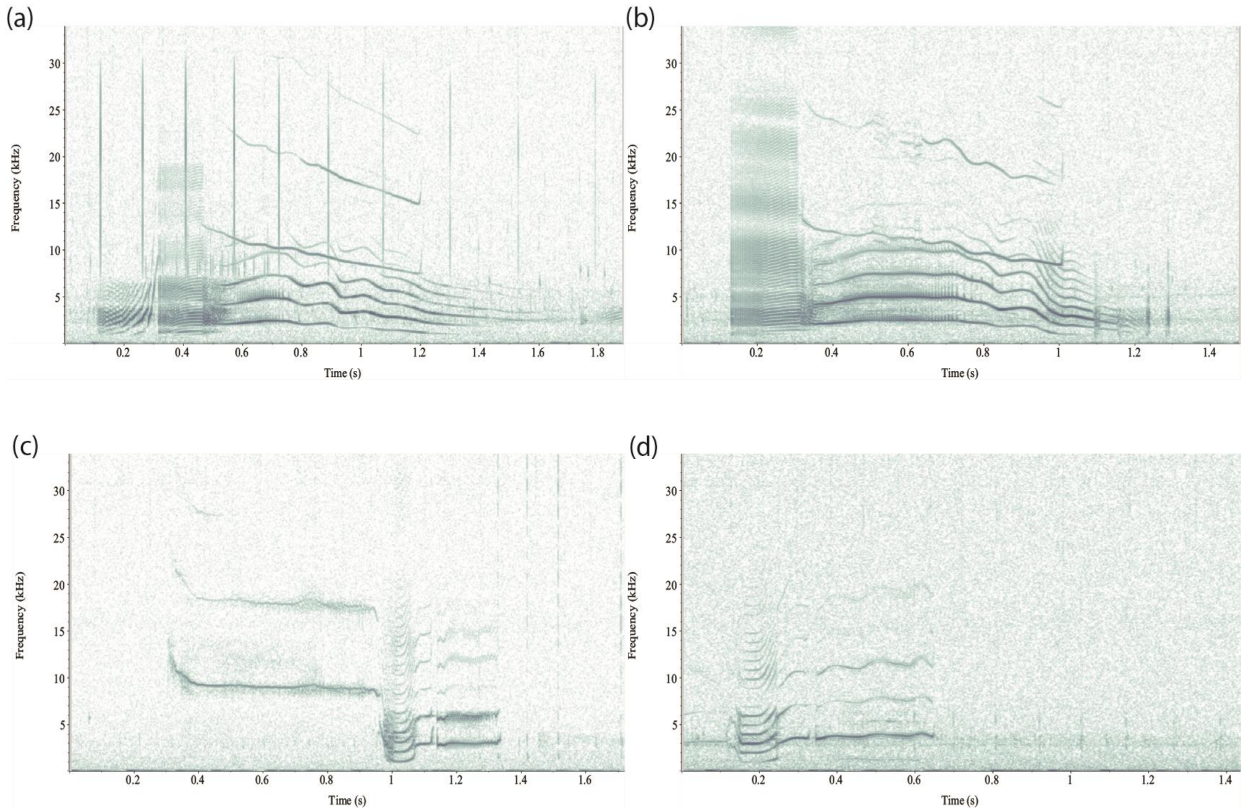

Figure 3.4. Spectrograms of call categories and the subtypes of these call categories: (a) call type McM1, a multi-component call with a biphonation; (b) subtype McM1a, a variant of call type McM1 where the first component of the original call is missing; (c) call type McM15, a multi-component call; (d) subtype McM15a; a variant of call type McM15 where the first component of the original call is missing (fs = 96 kHz, NFFT = 1024, 90% overlap, Hann window).

The number of multi-component calls was significantly higher (n=888, 71%) than the number of single- component calls (n=364, 29%), and 21 out of the 29 call categories consisted of multi-component calls, representative of the complexity of these signals (Figure 3.5).

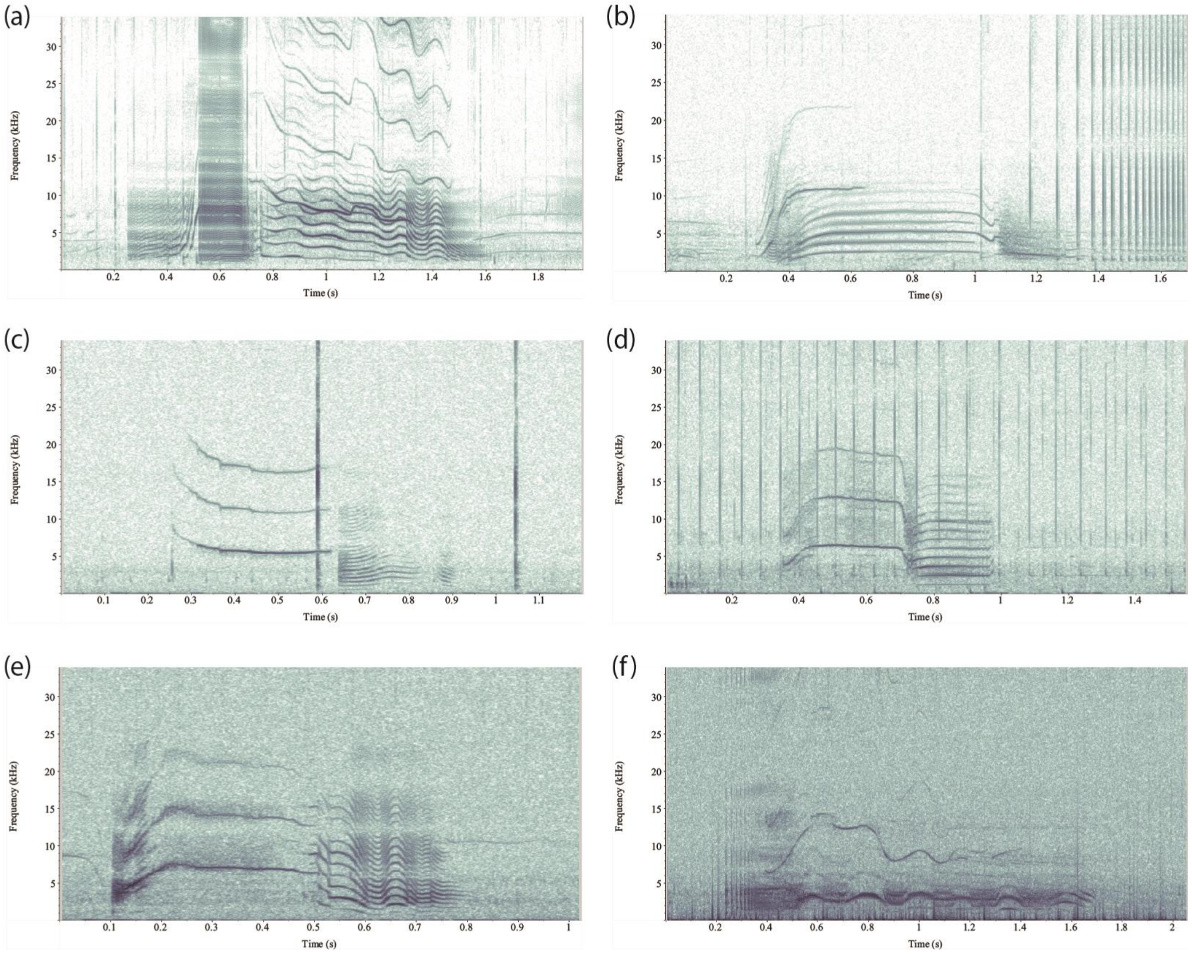

Figure 3.5: Spectrograms of multi-component calls recorded from Type C killer whales in McMurdo Sound: (a) call type McM1, a multi-component call with a biphonation; (b) call type McM3, a 2-component biphonic call; (c) call type McM5, a multi-component call; (d) call type McM9, a multi-component call; (e) call typeMcM10, a multi-component call; and (f) call type McM18, a multi-component call (fs = 96 kHz, NFFT = 1024, 90% overlap, Hann window).

Of the 29 call types, 45% were biphonic call categories (n=13) and 55% were monophonic call categories (n=16). In total, 532 biphonic calls were measured and analysed. All biphonic calls had two or more components (Figure 3.6).

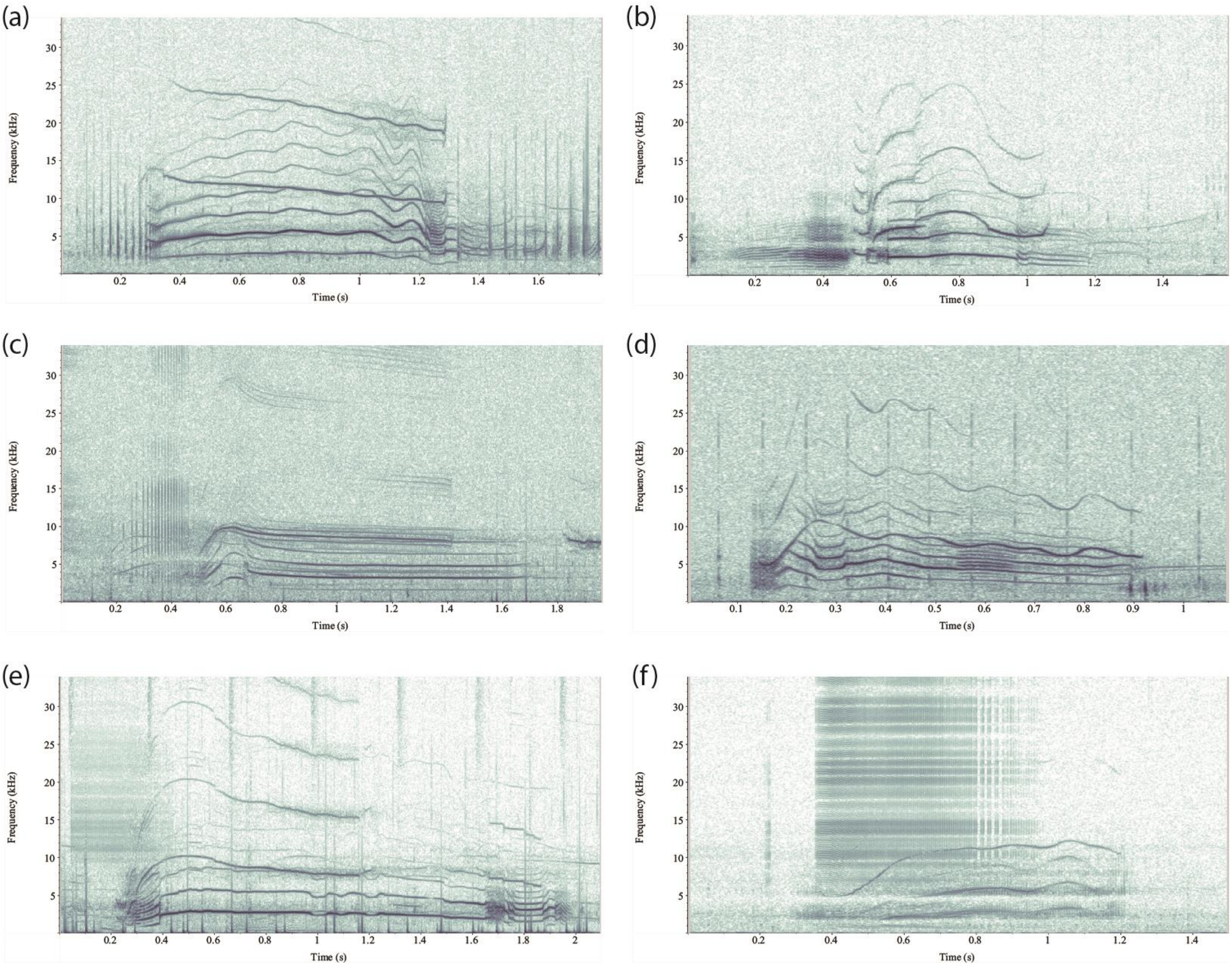

Figure 3.6: Spectrograms of biphonic calls recorded from Type C killer whales in McMurdo Sound: (a) call type McM2, a multi-component biphonic call, with distinct harmonics in the biphonation (b) call type McM3a, a multi-component biphonic call, this call is a variant of call type McM3 where the first pulse starts well before the biphonic whistle commences; (c) call type McM4, a multi-component biphonic call, with harmonics and weak sidebands in the biphonation; (d) call type McM8, a biphonic call, with distinct harmonics in the biphonation; (e) call type McM23, a multi-component biphonic call, with the biphonation evident at the start of the call at a low start frequency; and (f) call type McM24, a multi-component biphonic call (fs = 96 kHz, NFFT = 1024, 90% overlap, Hann window).

3.3.3 Call Comparison with Killer Whale Call Repertoires described in the Southern Ocean

All call types in this study were compared with other call types described in acoustic studies on killer whales in the Southern Ocean. Of the 29 call categories described here for McMurdo

Sound, seven call types were distinctly similar to calls previously documented. Call type McM1a, a multicomponent and biphonic call starting with a series of pulses and followed by a burst-pulse sound with a biphonic whistle, has the same components and biphonation as call "AM1" in Richlen and Thomas (2008) and call "1" in Schall and Van Opzeeland (2017) (see Figure 3.7a). Both singular and multi-component call types McM4, McM5, McM5a and McM14 were similar in structure to call types B_7, A_2, A_{18} and F_1, respectively, described by Billon (1984) (see Figure 3.7b, 3.7c, 3.7d and 3.7g). Call type McM7, a whistle with high frequency-modulation, is noticeably similar to call "BC01" in Wellard et al. (2015) and call "AM4" in Richlen and Thomas (2008) (see Figure 3.7e). Call type McM8, a two-component biphonic call with a burst-pulse sound and highly frequency-modulated biphonic whistle, is strikingly similar to call "AM7" described by Richlen and Thomas (2008) (see Figure 3.7f).

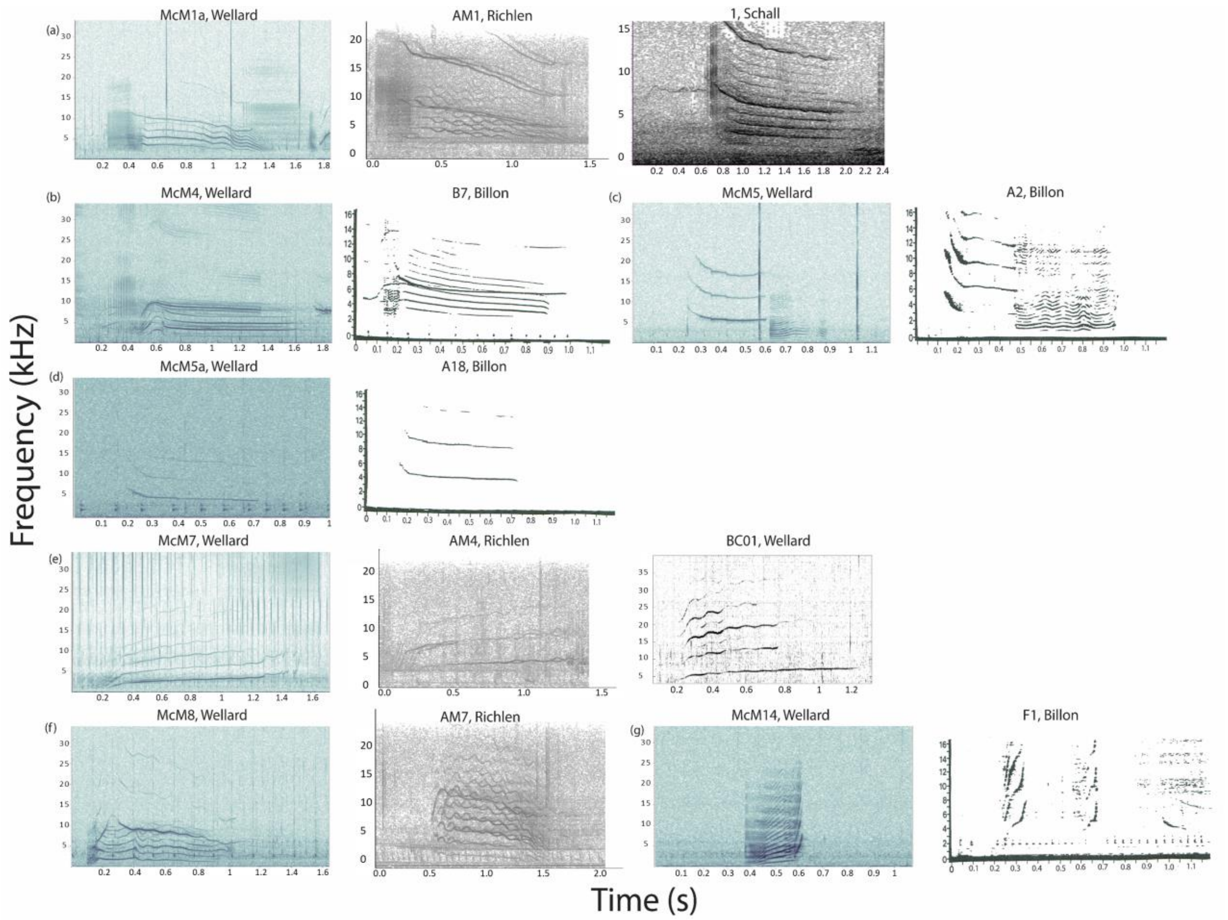

Figure 3.7 Spectrograms of call types recorded from Type C killer whales in McMurdo Sound *(left panels fs = 96 kHz, NFFT = 1024, 90% overlap, Hann window)* compared to similar call types recorded from killer whales in the Southern Hemisphere: (a) call type McM1a compared with (from left) call type AM1 (Richlen & Thomas, 2008) and call type 1 (Schall & Van

Opzeeland, 2017); (b) call type McM4 compared with call type B_7 (Billon, 1984); (c) Call type McM5 compared with call type A_2 (Billon, 1984); (d) call type McM5a compared with call type A_{18} (Billon, 1984); (e) call type McM7 compared with (from left) call type AM4 (Richlen & Thomas, 2008) and call type BC01 (Wellard et al., 2015); (f) call type McM08 compared with call type AM7 (Richlen & Thomas, 2008); and (g) call type McM14 compared with call type F_1 (Billon, 1984).

3.4 Discussion

This study is the first comprehensive description of the call repertoire of Type C killer whales, with a unique data set combing acoustic recordings with visual observations to confirm ecotype and many encounters and individuals sampled. Previous studies on purported Type C killer whale vocalisations have been limited in their visual confirmation of ecotype (Richlen & Thomas, 2008), in the scope of their acoustic analysis (Awbrey et al., 1982; Jehl et al., 1980; Thomas et al., 1981), and in the number of groups and individuals recorded (Schall & Van Opzeeland, 2017). This study with its larger sample size of groups and individuals and concurrent visual and acoustic observations delivers baseline data for identifying this ecotype using PAM systems and provides a foundation for future comparisons of acoustic repertoire between sympatric Antarctic killer whale ecotypes.

3.4.1 Categorising Calls and Vocal Repertoire

The analysis of these recordings of Type C killer whales demonstrate a repertoire of whistles, burst-pulse sounds, and echolocation clicks as described in other killer whale acoustic studies elsewhere. A total of 29 call types were described in the call catalogue, inclusive of four call types being variants of the primary call type. This large number of call types is comparable to the repertoire of Type C killer whales near the Eckström Ice Shelf, eastern Antarctica, reported by Schall and Van Opzeeland (2017), which comprised 26 call types from one encounter. The Type C repertoire of 29 call types is large in comparison to the seven call types of killer whales in one Ross Sea encounter in 1979 (Richlen & Thomas, 2008). It is also larger than repertoires described for Northern Hemisphere killer whale ecotypes which range from 4 to 17 call types (Deecke et al., 2005; Deecke, Nykänen, Foote, & Janik, 2011; Filatova et al., 2007; Foote et al., 2008; Ford, 1987; Strager, 1995). However, separating into call types is subjective.

A large vocal repertoire may reflect the feeding ecology of this ecotype or the behavioural state during the recording, or both factors. Previous research has shown that there is a clear distinction between call repertoires of mammal-eating and fish-eating killer whales, with the former producing fewer complex calls, exhibiting long periods of silence and most vocal activity occurring only after marine-mammal kills and during social interactions (Deecke et al., 2005; Morton, 1990; Saulitis, Matkin, & Fay, 2005). Fish-eating killer whales are known to produce sounds prolifically in all behavioural contexts (Barrett-Lennard et al., 1996; Filatova, Guzeev, Fedutin, Burdin, & Hoyt, 2013; Ford, 1989; Holt, Noren, & Emmons, 2013), possibly because their prey has poor hearing abilities at the frequencies of killer whale calls. By contrast, mammal-eating killer whales prey upon whales, dolphins and pinnipeds, with sensitive underwater hearing abilities within the frequency range of killer whale vocal communication, demonstrating that prey likely shape the vocal behaviour of the predator (Deecke et al., 2005). Type C killer whales are known to feed primarily on fish, and, similar to the fish-eating killer whales in the Northeast Pacific (Ford, 1987), their call repertoire displays a large number of call types, high calling rate and distinct acoustic variability in call types. Behavioural context may also influence call rate and call type variability within killer whale repertoire. Previous studies have reported an increase in the production of call types and call rate during observed social and foraging behaviour and a lower call rate during travelling (Ford, 1989; Rehn et al., 2007; Simon, McGregor, & Ugarte, 2007). The most common killer whale behaviours observed in this study were foraging under the ice and socialising at the surface. Hence behaviours observed in these encounters could account for an increase in call rate and call variation. Both factors of feeding ecology and behavioural context need to be considered when examining call repertoire and using PAM technologies for detection.

3.4.2 Complexity of Calls

The majority of call types described in this study are multi-component (71%), with many calls containing transitions from distinct pulses to burst-pulse sounds to whistles. This is analogous to call types described by Richlen and Thomas (2008) and Schall and Van Opzeeland (2017), with many call types containing multiple components and transitions across components. Most interestingly, nearly half of the call types described here start with a series of broadband pulses, which is similar to the one-third of call types observed by Richlen and Thomas (2008) and the two-thirds of call types described by Schall and Van Opzeeland (2017). Such an acoustic feature should be considered when describing and identifying killer whale ecotypes in Antarctic waters, as this may serve as an acoustic marker for ecotype-identification when using remote listening stations.

A large percentage (43%) of call categories in this study contained biphonations. Biphonation appears as two independent but simultaneous contours in a call spectrogram (Fitch et al., 2002; Wilden et al., 1998) and has been described across a variety of mammal taxa including primates (Brown, Alipour, Berry, & Montequin, 2003; Fischer, Hammerschmidt, Cheney, & Seyfarth, 2001), canids (Riede et al., 2000; Volodin & Volodina, 2002; Wilden et al., 1998), and cetaceans (Tyson, Nowacek, & Miller, 2007). While the function of biphonation in calls is not understood, its occurrence in the vocalisations of different species implies a potentially important communicative role. Biphonic calls have been observed in the repertoire of fish-eating killer whales in both the Northwest Pacific (Filatova et al., 2009) and Northeast Pacific (Foote et al., 2008), with these calls more common when animals occurred in mixed groupings consisting of members of different pods. This suggests that group composition influences the usage of such calls and that biphonic calls are possibly employed as markers of pod and matriline affiliation. This study demonstrated that encounters with larger group sizes had a higher rate of biphonic calls. Given the physical habitat at McMurdo Sound, characterised by a limited number of breathing holes, numerous family groups may be present within close vicinity, although information on the social structure of Type C killer whales is limited and it is unknown whether this ecotype is organised in stable groups similar to the matrilineal groups of Northern Hemisphere fish-eating killer whale. It should be noted that almost half of the encounters during these recordings had up to 50 individuals present with one encounter having up to an estimated 125 individuals. These large group sizes suggest that numerous family groups were present during recordings, which may explain a higher rate of biphonic calls used to locate group members.

The frequent use of biphonic calls could also be related to the shifting and changing habitat in McMurdo Sound. For killer whales, it was suggested that differences in the directionality of the components in biphonic calls can provide information on the orientation of a caller relative to the listener (Miller, 2002). In McMurdo Sound, 4-5 m wide ice leads can rapidly close with changing wind and weather conditions, closing killer whale habitat for miles, and breathing holes, if they exist, can be kilometres apart. It is possible that animals use this directionality feature of biphonic calls to identify the signaller's orientation and communicate amongst individuals the shifting location of the ice edge and breathing holes.

3.4.3 Qualitative vs. Quantitative

Due to the complexity of calls having multiple, successive and simultaneous components, simple quantitative techniques to group calls based on a set of frequency measurements (Wellard et al., 2015) were inapplicable and therefore calls were categorised on the basis of aural qualities and spectrographic characteristics. Currently there is no single method for objectively defining killer whale call types, nor is there a singular method for validating call-type categories. The majority of studies on killer whale repertoire have categorised call types on the aural qualities and structural characteristics examined in spectrograms by human observers (Ford, 1991; Saulitis et al., 2005; Yurk et al., 2002), with these perceptual methods of classification being validated by studies and proving to be reliable (Deecke, Ford, & Spong, 1999; Yurk et al., 2002). Criteria were used whilst classifying calls in this study and to reduce subjectivity a second independent observer was included in the initial categorisation. Additional observers undertook a test for interobserver reliability and agreed with the initial classification (Fleiss-Kappa statistic, $K = 0.515$, $z = 41.8$, $p < 0.0001$). This categorisation of Type C killer whale calls based on visual inspection of the spectrogram and characteristics of the call is a common technique that has been used in numerous other delphinid studies (Caldwell, Caldwell, & Tyack, 1990; Ford, 1989, 1991; Ford & Fisher, 1983; Hoelzel & Osborne, 1986; Janik, 1999). Nonetheless, this method has limitations and is inherently subjective, with reduced reproducibility and criteria for categorisation not clearly being defined. Previous studies have applied quantitative techniques to validate these perceptual classification methods (Brown & Miller, 2007; Deecke et al., 1999; Filatova et al., 2007; Wellard et al., 2015), hence multiple features of each component in each call were measured in this study (Table 3.2), to allow for quantitative techniques to be undertaken in future studies on other Antarctic killer whale ecotypes.

3.4.4 Comparison with Killer Whale Call Repertoires described elsewhere in the Southern Ocean

A comparison of repertoires showed that seven call types from this study had similar aural and structural characteristic call types described by other studies on Southern Hemisphere killer whales. Similar calls have been noted in the call repertoire recorded off the Eckström Shelf (Schall & Van Opzeeland, 2017), off the south coast of Western Australia (Wellard et al., 2015) and in McMurdo Sound (Billon, 1984; Richlen & Thomas, 2008). Of these 7 call types, only one from Wellard et al. (2015) and one from Schall and Van Opzeeland (2017) matched, which could be due to chance or similarity of the species' repertoire, rather than ecotype. However, 33% of all call types described by Richlen and Thomas (2008) matched with this study's catalogue. Antarctic killer whale ecotypes had not been described when Richlen and Thomas (2008) collected their recordings, and the few photographs taken at the time do not show diagnostic features. Our findings support the hypothesis that Richlen and Thomas (2008) recorded Type C killer whales in 1979. The limited similarity of calls between confirmed ecotype Type C recordings by Schall and Van Opzeeland (2017) off the Ekström Shelf may be due to limited sampling of individuals and behaviours, or may reflect geographical variation in vocal repertoire, as the Eckström Shelf is located on the opposite side of Antarctica from McMurdo Sound. The vocal repertoire of killer whales is thought to be a learned behaviour, rather than genetically controlled (Deecke et al., 2000; Foote et al., 2006; Ford, 1991), which can lead to the formation of dialects in sympatric populations and geographical variation in distant populations. Based on these findings, we hypothesise that Type C killer whales in McMurdo Sound, Ross Sea, may have a distinct dialect. Further comparative acoustic research is needed to test the hypothesis.

3.4.5 Implications for Passive Acoustic Monitoring and Conservation

This study catalogued 29 complex and recognisable call types of Type C killer whales and while the catalogue may not be complete, the number of call types and variations, along with the high encounter rate, suggests that a moderate proportion of the repertoire may have been captured. Based on this catalogue, and a future comparison of sympatric killer whale ecotypes, passive acoustic monitoring can be implemented in the Ross Sea region to provide information such as geographic range, seasonal occurrence and density of this ecotype.

During this study, other top marine predators were recorded, including leopard seals and sperm whales (*Physeter macrocephalus*), which are other candidate species for passive acoustic monitoring. To manage the RSRMPA and conserve the species that inhabit this region, we need to understand their seasonal distribution. Although passive acoustic technologies have primarily been used with cetaceans, the potential now exists for monitoring other marine animals such as pinnipeds and fishes. In order to do this, we need to gather information on sound production by individuals, groups, populations and species.

The remoteness of the Ross Sea makes access for ecosystem monitoring difficult. Autonomous acoustic recorders are an economical long-term tool for monitoring habitat usage by vocalising marine species in particular in restricted locations and during prohibitive weather when vessels cannot go to sea – a problem during the Antarctic winter season. But passive acoustic monitoring is not without its limitations. One major limitation is that animals must be vocalising to be detected. Hence, understanding not only their call repertoire, but the calling behaviour, call rates and behavioural context is important.

Future research should investigate the call repertoire of other Antarctic killer whale ecotypes and examine acoustic divergence between ecotypes. Characterising ecotype-specific call repertoires is crucial when using PAM in these remote areas and attempting to identify sympatric ecotypes in the same region. Identifying ecotype-specific dialects in the Antarctic region, in combination with genetic data, may also help us determine matrilines and gain a better understanding of cultural evolution and phylogenetic relationships.

3.4.6 **Conclusion**

Our results suggest an identifiable dialect displayed by Type C killer whales. Future research comparing sympatric Antarctic ecotypes and their vocal repertoires will ultimately allow us to passively monitor their movements, distribution and relative abundance. This is an important step towards understanding more about this species in this region and the ecological impact of the most diverse killer whale community known.

4 The Call Repertoire of Type B Killer Whales (*Orcinus orca*) off the Antarctic Peninsula and a Comparison Between Antarctic Ecotypes

Abstract

There are currently 10 ecotypes of killer whales (*Orcinus orca*) described world-wide, with five of these noted in the Antarctic region. These ecotypes exhibit differences in morphology, foraging behaviours, habitat and diet preferences, and genetic structure. Two forms of Type B ecotype killer whales are found around the Antarctic Peninsula and can be readily distinguished from other ecotypes by their dark dorsal cape, lighter lateral fields, and noticeably large postocular eyepatch. Acoustic recordings of Type B killer whales were opportunistically collected between 2009 and 2018 off the Antarctic Peninsula. A total of 3 hours and 53 minutes of killer whale recordings were analysed resulting in 2469 vocalisations detected and subsequently rated. Acoustic parameters of each call type for both whistles and burst-pulse sounds were measured and calls were categorised by a k-means cluster analysis, producing a catalogue of 20 call types. Analysis of calls revealed that Type B killer whales produced mostly single component calls, with some multi-component and biphonic calls observed. The repertoires of Antarctic killer whale ecotypes Type B1, B2 and C were compared revealing acoustic divergence between all ecotypes. This study provides new information on the call repertoire of Type B killer whales, reports on acoustic differences between Antarctic ecotypes, and examines the use of call repertoire as a reliable diagnostic tool for identifying sympatric ecotypes in Antarctic waters.

4.1 Introduction

Killer whales (*Orcinus orca*) currently comprise a single, rather variable species, however studies over the last 30 years have discovered the existence of pronounced morphological and behavioural variation among populations which has led to the designation of different “types” or “ecotypes” (De Bruyn et al., 2013). At present 10 ecotypes of killer whales are described worldwide: three in the North Pacific, five in the Antarctic region, and two in the North Atlantic (Durban et al., 2017; Foote et al., 2009; Ford et al., 1998; Pitman et al., 2011; Pitman & Ensor, 2003; Saulitis et al., 2000), with some populations displaying substantial variation in diet, behaviour, morphology and genetic structure that has led some researchers to propose calling them separate species (Morin et al., 2010). Furthermore, ecotypes show differences in movement patterns and pigmentation, as well as in the size, stability and composition of social groups (Baird & Whitehead, 2000; Barrett-Lennard & Heise, 2006; Ford & Ellis, 2014; Ford et al., 1998).

Currently five killer whale ecotypes have been described in Antarctic waters, including Type A, Type B (two forms: large ‘B1’ and small ‘B2’), Type C and sub-Antarctic Type D (Durban et al., 2017; Pitman et al., 2011; Pitman & Ensor, 2003). Each Antarctic ecotype displays distinct morphological differences, allowing easy identification at sea. Along with morphological differences, each ecotype also demonstrates distinct habitat preferences, prey specialisation and foraging behaviours.

The two forms of Type B killer whales are the most common ecotype found around the Antarctic Peninsula and can be readily distinguished from the other types by their dark dorsal cape and lighter lateral fields, and a noticeably large postocular eyepatch (Pitman & Ensor, 2003). Large Type B, herein referred to as ‘B1’, are also known as ‘pack ice killer whales’, as they mainly foraging among loose pack ice, prey upon seals and are well known for their ‘wave-washing’ technique (Pitman & Durban, 2012). Type B1 killer whales can grow to lengths of at least 9 m, have a dark gray dorsal cape and a very large eyepatch oriented parallel to the body axis. This ecotype feeds mainly on seals, predominantly Weddell seals (*Leptonychotes weddellii*), but has been observed preying upon a minke whale (*Balaenoptera bonaerensis*), and is most often found around dense pack ice (Pitman & Durban, 2012). Small Type B, herein referred to as ‘B2’, are also known as ‘Gerlache killer whales’, and are on average about 1 m shorter than large Type Bs and are found in the western Weddell Sea and around the Antarctic Peninsula. Type B2 killer whales also have a large eyepatch oriented parallel to the body axis and a dark gray dorsal cape. This ecotype is a deep diver and is regularly seen foraging in relatively ice-free waters where it seemingly feeds on squid or fish, and the occasional penguin (Jefferson et al., 2015; Pitman & Ensor, 2003). Both Type B killer whales have been reported to undertake rapid, roundtrip migrations to the tropics in an apparent periodic maintenance migration to allow skin regeneration (Durban & Pitman, 2012), but otherwise it is thought Type B killer whales spend their remaining time in Antarctic waters.

Vocal behaviour is a key feature of cetacean social behaviour and acoustic research has been used to distinguish between Northern Hemisphere killer whale ecotypes. The best-studied populations of killer whales are in the Northeast Pacific. In the Northeast Pacific, three distinct sympatrically occurring ecotypes have been described: resident, transient or Bigg's, and offshore, each differing in social structure, morphology, genetic structure and behaviour. Residents feed on fish and typically travel in large stable social units of closely related individuals (Ford & Ellis, 2006). Bigg's killer whales predominantly hunt marine mammals and travel in smaller, more fluid social groups (Baird & Dill, 1996). Offshore killer whales are usually occur in large groups with an unknown social structure and their diet is less understood, but likely comprises of mainly bony and cartilaginous fishes (Dahlheim et al., 2008; Ford et al., 2011). Each ecotype displays specific patterns of movement, behaviour and social adaptations that are connected to dietary specialisations. Resident, Bigg's and offshore ecotypes are also differentiated acoustically, with acoustic behaviour varying considerably between ecotypes. Rather than being genetically transmitted, the vocal repertoire of killer whales is thought to be learned (Deecke et al., 2000; Foote et al., 2006), which can lead to the formation of dialects between social groups in some populations. Dialects have been found both within and between populations (Ford, 1991), and where calls are shared within pods they are deemed to belong to the same acoustic clan. Call types shared within a clan typically show matriline-specific variation in call structure (Deecke et al., 2010; Miller & Bain, 2000).

Comparisons of vocal behaviour between these ecotypes occurring in the North Pacific have shown numerous differences. Resident killer whales are highly vocal and use stable acoustic repertoires of discrete pulsed calls that define family groups (Ford, 1989, 1991; Ford & Fisher, 1983), transients produce echolocation clicks and pulsed calls less frequently than residents (Barrett-Lennard et al., 1996; Deecke et al., 2005; Ford, 1984), and the call rate varies between these two ecotypes (Morton, 1990). These differences are largely attributed to the prey targeted by each ecotype. The preferred prey of the resident killer whales are salmonids, that have poor hearing abilities at the frequencies of killer whale communication (Hawkins & Johnstone, 1978) suggesting limited costs for residents from eavesdropping prey. In comparison, marine mammals have excellent underwater hearing (Au, 2000b) and can detect the communicative calls of killer whales from distances of several kilometres (Deecke et al., 2002; Miller, 2000). These differences between ecotypes are a clear demonstration of prey shaping the vocal behaviour of their predators, with potential prey able to detect predator vocalisations and responding with anti-predator behaviour.

Killer whales emit three types of vocalisations: echolocation clicks, whistles and burst-pulse sounds. Echolocation clicks are broadband pulses (10 kHz to 100 kHz) with a short duration, typically emitted in trains lasting several seconds; they are used for navigating and foraging (Au et al., 2004; Barrett-Lennard et al., 1996; Evans, 1973). Whistles are tonal signals with the fundamental frequency ranging from 1 kHz to 36 kHz for North Pacific killer whale populations (Filatova, Ford, et al., 2012; Ford, 1989; Riesch et al., 2006; Simonis et al., 2012; Thomsen et al., 2001), and with fundamental frequencies up to 74 kHz in eastern North Atlantic killer whale populations (Samarra et al., 2010). Burst-pulse sounds are broadband and consist of rapidly repeated pulses which, along with whistles, have population-specific variation (Deecke et al., 2005; Ford, 1987; Strager, 1995). Both whistles and burst-pulse sounds are believed to be communicative signals used in social contexts, functioning as contact signals in group recognition and in coordination of behaviour (Ford, 1989; Miller et al., 2004; Thomsen et al., 2002).

The recent description of the Antarctic killer whale ecotypes means that little is known about their distribution, movement patterns, social structures, and vocal behaviour. To date, there have been no dedicated acoustic studies on killer whales around the Antarctic Peninsula, and no description of Type B killer whale call repertoire. Four previous studies have described the vocal behaviour of killer whales in the Southern Ocean (Awbrey et al., 1982; Richlen & Thomas, 2008; Schall & Van Opzeeland, 2017; Wellard et al., 2015). Of these, three focused on calls recorded in Antarctic waters, with only one account able to confirm the ecotype of vocalising killer whales with confidence – Type C near the Eckström Ice Shelf, eastern Weddell Sea coast (Schall & Van Opzeeland, 2017).

Acoustic monitoring using stationary hydrophones and autonomous recorders can provide a practical alternative where boat-based surveys are difficult in remote areas year-round, such as the Antarctic Peninsula. For passive acoustic monitoring (PAM) to be effective, we must know the vocal repertoire of the target population to accurately identify its presence. This important baseline information is reliably obtained from concurrent visual observations and acoustic recordings of the population, which can be difficult with highly mobile marine animals, such as killer whales. Additionally, multi-sensor acoustic tags have been a rich source of information on sound production, diving physiology, foraging behaviour, social behaviour, and effects of noise within marine mammal populations (Baird, Hanson, & Dill, 2005; Baird, Webster, Schorr, McSweeney, & Barlow, 2008; Curé et al., 2013; Friedlaender et al., 2014; Goldbogen et al., 2015; Jensen, Perez, Johnson, Soto, & Madsen, 2011; Johnson, de Soto, & Madsen, 2009; Johnson, Tyack, Nowacek, & Shorter, 2000; Madsen et al., 2006; Miller, Shapiro, & Deecke, 2010). With multi-sensor acoustic tags, acoustic analysis may reveal behavioural components of acoustic production and social interactions that have not been possible to study with acoustic data from deployment of hydrophones alone.

This study presents the first recordings of Type B1 and B2 killer whales around the Antarctic Peninsula and investigates the use of PAM to study these animals. The acoustic divergence amongst Type B and Type C killer whales was examined and using call repertoire as a diagnostic tool for identifying sympatric ecotypes in Antarctic waters is explored.

4.1.1 Objectives

This objectives of this study were to: (1) record vocalisations of Type B killer whales, along with concurrent photographs, in Antarctic waters, (2) describe the vocal repertoire of both Type B1 and Type B2 killer whales, (3) conduct a quantitative analysis on acoustic features of vocalisations and group them accordingly to create a call catalogue, (4) measure parameters of whistles and burst-pulse sounds, and (5) examine acoustic divergence in Antarctic killer whale ecotypes by comparing Type B1 and B2 killer whale call types with Type C killer whale call types.

4.2 Methods

4.2.1 Study Area and Data Collection

Acoustic recordings were collected in several locations off the Antarctic Peninsula between 2009 and 2018 (Figure 4.1, Table 4.1). Recordings were made with different equipment and at a sampling frequencies of 44.1 kHz or higher, permitting evaluation of call features up to 22.05 kHz. Figure 4.1 shows the geographical locations of recordings used for this study.

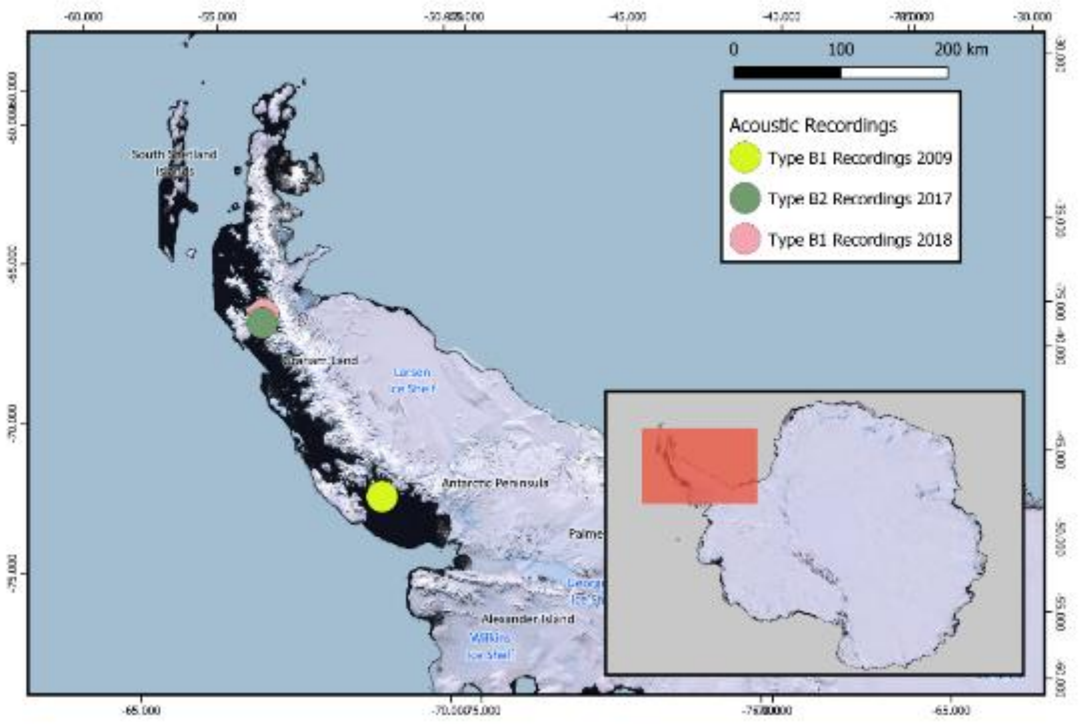

Figure 4.1 Map of the Antarctic Peninsula showing the locations of the acoustic recordings of Type B1 and B2 killer whales. Each set of recordings are displayed as circular symbols for each survey conducted between 2009 and 2018. Map produced using QGIS and the Norwegian Polar Institute's Quantarctica Package (Matsuoka et al., 2018).

Table 4.1 Sighting details and acoustic recordings collected throughout the Antarctic Peninsula between 2009 and 2018 of Ecotype B1 and B2 killer whales.

Date	Location	Recording Equipment	Sampling rate	Ecotype	Number of animals	Behaviour	Total hour/minutes of acoustic recordings
17/01/2009	Rothera, Antarctic Peninsula	M-Audio Microtrack 24-96 recording unit with a custom-made hydrophone	44.1 kHz, 24 bit	Ecotype B1	10	Feeding (F)	1:46:41

Date	Location	Recording Equipment	Sampling rate	Ecotype	Number of animals	Behaviour	Total hour/minutes of acoustic recordings
24/11/2017	Gerlache Strait, Antarctic Peninsula	Aquarian H2a-XLR hydrophone on recording unit iRig	48 kHz, 24 bit.	Ecotype B2	20	Socialising (S), Foraging (F), Milling (M)	00:36:23
03/03/2018	Paradise Bay, Antarctic Peninsula	HTI-96 hydrophone embedded in a multi-sensor digital tag	48 kHz, 16 bit	Ecotype B1	8	Travelling (T)	1:29:49
TOTAL					**38**		**3:52:53**

During every acoustic recording concurrent visual observations were also noted, including information on killer whale ecotype, group composition, number of animals, and behavioural state. Behaviour was assigned to one of four behavioural states, which were adapted from previous killer whale studies (Baird & Dill, 1995; Barrett-Lennard et al., 1996; Ford, 1989; Weiß et al., 2007; Williams et al., 2006): (1) travelling, (2) foraging, (3) milling/resting and (4) socialising (Table 4.2).

Table 4.2 Definition of killer whale behavioural states modified from Ford (1989) and Baird and Dill (1995).

Behavioural State	Definition
Travelling (T)	Killer whales moving steadily in a constant direction, respirations usually synchronous, swimming with short relatively constant dive intervals. Group spacing varies.
Foraging (F)	Killer whales seen with direct evidence of feeding, i.e. prey seen in mouths or in the water. Other indications of feeding and foraging include changes in direction, high-speed swimming with direction, and erratic swimming and diving. Large numbers of birds may also be observed either diving or with food in their mouths.

Behavioural State	Definition
Milling (M)/ Resting (R)	Killer whales engaged in slow movements or ‘logging’ at the surface. There is little surface-active behaviour (e.g. breaching or tail-slapping) observed during this behavioural state. Both milling and resting are included in this category.
Socialising (S)	Killer whales engaged in a variety of interactive behavioural events, including body contact, sexual interactions, chasing, breaching or hitting the water surface with body parts.

4.2.2 Data Analysis

Acoustic recordings were inspected both visually and aurally using acoustic software Raven Pro 1.5 (Cornell Lab of Ornithology, 2014, Ithaca, New York, USA). Spectrograms were computed at consistent frequency resolution. A 512-point FFT was used for the recordings sampled at 48 kHz and 44.1 kHz, resulting in a frequency resolution of 94 and 86 Hz respectively. All Fourier transforms were computed with 90% overlap of successive Hann windows. Only recordings made during a confirmed sighting of ecotype B1 or B2 were included in the analysis. Calls were visually rated based on their signal-to-noise ratio (SNR): Grade 1 (‘Poor’) if the signal was faint, but visible on the spectrogram; Grade 2 (‘Average’) if the signal was distinct and clear; and Grade 3 (‘Good’) if the signal was prominent and strong. Only Grade 2 and 3 calls were selected for analysis.

4.2.3 Call Measurements

All sounds were classified into whistles, burst-pulse sounds and echolocation clicks. No quantitative analysis was performed on the echolocation clicks, as these are not expected to be population-specific or characteristic, but analysis focused on whistles and burst-pulse sounds. For every call of Grade 2 and Grade 3 quality, up to 20 parameters were measured to quantify its spectro-temporal structure (Table 4.3). Some of the parameters are more useful for quantifying broadband calls like burst-pulse sounds (e.g., entropy measures and quartile frequencies), while others are more useful for whistles (e.g., start, end, minimum and maximum frequencies of the contour).

Table 4.3. List of parameters measured to quantify the spectro-temporal structure of call types recorded from Type B killer whales off the Antarctic Peninsula. (V): measured visually from spectrograms in Raven; (R): computed by Raven.

Parameter	Abbreviation	Description
Duration (R)	Dur	Time duration [s] of the entire call
Duration 90% (R)	Dur90%	Useful for burst-pulse sounds and whistles, the time [s] during which the cumulative energy of the call rises from 5% to 95%
Minimum Frequency (V)	Fmin	Lowest frequency [Hz] of the call in the case of burst-pulse sounds and lowest frequency of the fundamental contour in the case of whistles
Maximum Frequency (V)	Fmax	Highest frequency [Hz] of the call in the case of burst-pulse sounds and highest frequency of the fundamental contour in the case of whistles
Start Frequency (V)	Fstart	Useful for whistles, the frequency [Hz] at the start of the fundamental contour
End Frequency (V)	Fend	Useful for whistles, the frequency [Hz] at the end of the fundamental contour
Delta Frequency (R)	Fdelta	Range of frequencies spanned by the burst-pulse sound or the fundamental whistle contour (Fdelta = Fmax - Fmin)
Bandwidth 90% (R)	BW90%	Useful for burst-pulse sounds, the bandwidth [Hz] containing 90% of the call energy (i.e., difference between the frequencies at the 5th and 95th energy percentiles)
Peak Frequency (R)	Fpeak	Useful for burst-pulse sounds, the frequency [Hz] at which the call spectrum has its maximum energy
Centre Frequency (R)	Fcentre	Useful for burst-pulse sounds, the frequency [Hz] that divides the call spectrum into two frequency bands of equal energy
1st Quartile Frequency (R)	Q1F	Useful for burst-pulse sounds, the frequency [Hz] that divides the call spectrum into two frequency bands containing 25% and 75% of the energy in the call
3rd Quartile Frequency (R)	Q3F	Useful for burst-pulse sounds, the frequency [Hz] that divides the call spectrum into two frequency bands containing 75% and 25% of the energy in the call
Minimum Entropy (R)	MinEnt	Useful for burst-pulse sounds, the minimum entropy over all time bins in the call spectrogram [bits]
Maximum Entropy (R)	MaxEnt	Useful for burst-pulse sounds, the maximum entropy over all time bins in the call spectrogram [bits]
Average Entropy (R)	AvgEnt	Useful for burst-pulse sounds, the average entropy over all time bins in the call spectrogram [bits]

Parameter	Abbreviation	Description
Number of Extrema (V)	Ext	Extrema are local maxima and minima in the whistle contour, i.e., where the first derivative of the whistle contour with respect to time is zero
Inflection points (V)	Infl	At inflection points, the curvature of the whistle contour changes from clockwise to counter-clockwise or vice versa. The second derivative of the whistle contour with respect to time is zero.
FM rate (V)	FM	The ratio of the number of inflection points and duration [1/s]
Number of Steps (V)	Steps	A discontinuity in the whistle contour, where the contour makes a jump in frequency without any gap in time
Harmonics (V)	Harm	The presence of harmonics in whistles was noted as a binary response (y/n)

The parameters in Table 4.3 were measured separately for all components of a call. Calls consisted of one or more components, with some calls consisting of both whistle and burst-pulse components. Some calls also had simultaneous biphonic components. For whistles, measurements were taken off the fundamental contour; however, there were some cases where the lowest band was not of sufficient quality to be measured, so measurements were made on the higher bands and then scaled down. Frequency measurements such as start, end, minimum, and maximum frequency are a factor n+1 higher for the n^{th} harmonic and were therefore scaled down. For example, if measurements were done off the first harmonic, then the measurements were divided by 2 in order to correspond to the fundamental. Features such as duration, extrema, inflections, FM rate, and steps are the same in harmonics and fundamental.

4.2.4 K-means Clustering for Types B1 and B2 Killer Whale Vocalisations

The parameters described in Table 4.3 made up a feature vector for each call. K-means clustering (MacQueen, 1967),a simplification of Gaussian mixture modelling, was applied to group the calls into categories by minimising the Euclidian distance between all feature vectors and the cluster centroids. This analysis was performed in MATLAB (The MathWorks Inc., 2014b, Natick, Massachusetts, United States), using the k-means algorithm of the MATLAB statistics toolbox, separately for both ecotypes and two types of vocalisations analysed. Calls grouped into call types from the k-means cluster analysis were used to produce a call catalogue for Type B1 and B2 killer whales.

4.2.5 **Call Comparison between Antarctic Ecotypes**

An initial comparison of variables for each type of vocalisation (whistles and burst-pulse sounds) was plotted for all Antarctic ecotypes Type B1, B2 and C. In this study, recordings of Type C killer whales from McMurdo Sound, Antarctica were used for this comparison (see Chapter 3, for details). In total, 11 variables were plotted for the comparison of whistles across ecotypes: Fmin, Fmax, Fstart, Fend, Fdelta, Dur, Ext, Infl, FM, Steps and number of multi-components. A total of 10 variables were plotted for the comparison of burst-pulse sounds across ecotypes: Dur90%, Q1F, Q3F, BW90%, Fcentre, Fpeak, MinEnt, MaxEnt, AvgEnt, and number of multi-components. The logarithm of the duration measurements was taken to transform Duration into a Gaussian distribution for input into the k-means model.

4.2.6 **Multivariate Analysis of Variance (MANOVA)**

A MANOVA was undertaken to compare vocalisations between Antarctic ecotypes Type B1, B2 and C. This analysis was performed separately for whistles and burst-pulse sounds. Measurements of the following features were used for analysis of whistles: Fmin, Fmax, Fstart, Fend, Fdelta, Dur, Ext, Infl, FM, Steps and number of components. Measurements of the following features were used for analysis of burst-pulse sounds: Dur90%, Q1F, Q3F, BW90%, Fcentre, Fpeak, MinEnt, MaxEnt, AvgEnt, and number of components. The logarithm of the duration measurements was taken to transform Duration into a Gaussian distribution for input.

The MATLAB function manova1.m (MATLAB and Statistics Toolbox Release, 2014b, Natick, Massachusetts, United States) was used for this MANOVA to derive canonical variables that are linear combinations of the measurement vectors relating to the 11 features of whistles and 10 features of burst-pulse sounds that create maximum separation between the two groups.

4.2.7 **Analysis of Variance (ANOVA)**

An ANOVA for between-subject effects was then performed on whites and burst-pulse sounds. The MATLAB function anova.m (MATLAB and Statistics Toolbox Release, 2014b, Natick, Massachusetts, United States) was used to assess variability within and between the three ecotypes using a repeated measures model.

4.3 Results

Hydrophone recordings of Type B1 killer whales were made on 17 January 2009 when a group of 10 killer whales was encountered in Rothera off the Antarctic Peninsula (Figure 4.1). Animals were feeding and socialising during and after preying on an Antarctic minke whale. Ecotype B1 was confirmed from diagnostic features including the presence of a dorsal cape, large eyepatch oriented parallel to the body axis and large in body size (Figure 4.2). Recordings were made with a custom-made hydrophone and M-Audio Microtrack 24-96 recording unit at a sampling frequency of 44.1 kHz, 24 bit.

Figure 4.2 Photograph of Type B1 killer whales observed during acoustic recordings on 17 January 2009 whilst on survey. Ecotype B1 can be identified the presence of a dorsal cape and large eyepatch oriented parallel to the body axis. Photograph by R.L. Pitman.

Hydrophone recordings of Type B2 killer whales were collected on 24 November 2017 when a group of approximately 20 killer whales was encountered in Gerlache Strait (Figure 4.1). Behavioural states during included socialising, foraging and milling. A few individuals of this group were observed chasing a gentoo penguin (*Pygoscelis papua*), although once this penguin was caught, they did not feed on it but instead peeled the skin off the head and neck (Figure 4.3). Animals then continued to socialise and mill. Recordings were made with an Aquarian H2a-XLR hydrophone on recording unit iRig at a sampling frequency of 48 kHz, 24 bit.

Figure 4.3 Photograph of a Type B2 killer whale observed during acoustic recordings on 24 November 2017 in the Gerlache Strait, Antarctic Peninsula, seen here with a gentoo penguin in the mouth. Ecotype B2 identifiable by diagnostic features such as the presence of a dorsal cape and large eyepatch oriented parallel to the body axis. Photograph by R.L. Pitman.

Opportunistic tagging occurred off the Antarctic Peninsula in March 2018 when a group of approximately 8 Type B1 killer whales were encountered in Paradise Bay (Figure 4.1). Behavioural state noted during this encounter was travelling. Ecotype B1 confirmed by identifiable diagnostic features such as the presence of a dorsal cape and large eyepatch oriented parallel to the body axis (see Figure 4.4). The whales were approached in a rigid-hulled inflatable boat and tagged using a 6 m carbon-fibre pole. A Customized Animal Tracking Solutions (CATS; Queensland, Australia; Oberstdorf, Germany) tag was fixed to the dorsal surface of an individual female killer whale with suction cups (see Figure 4.5). Acoustic recordings from this encounter were extracted from data obtained with the digital acoustic recording tag. Recordings were made with a HTI-96 hydrophone embedded in the digital tag and sampling at a frequency of 48 kHz, 16 bit.

Figure 4.4 Photograph of a Type B1 killer whale tagged with CATS suction-cup tag in Paradise Bay, Antarctic Peninsula on 3 March 2018. Ecotype B1 identifiable by diagnostic features such as the presence of a dorsal cape and large eyepatch oriented parallel to the body axis. Photograph by Ari Friedlaender.

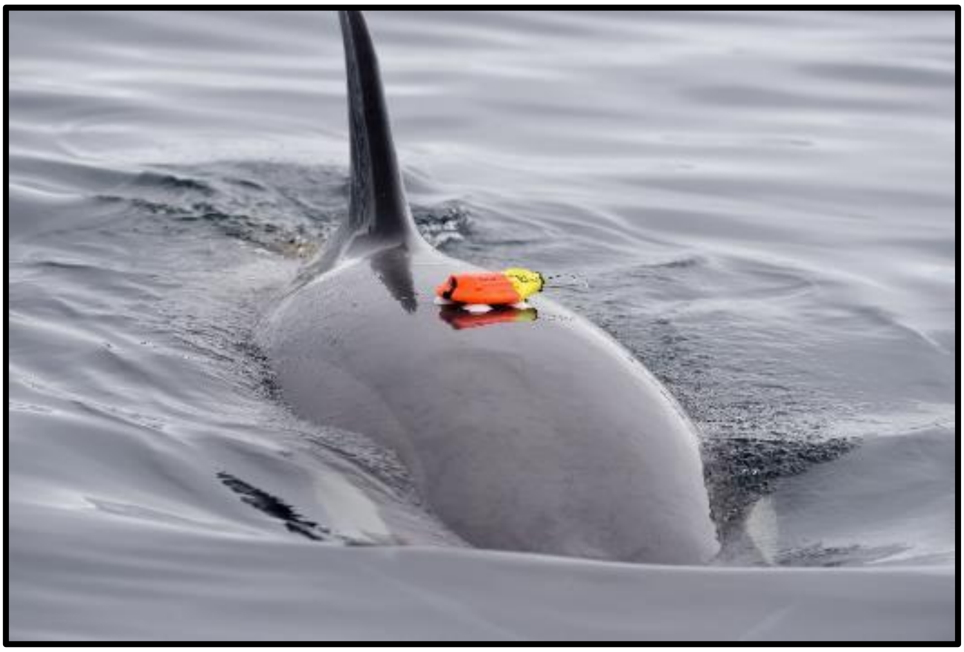

Figure 4.5 Photograph showing a close-up of CATS suction-cup tag deployed on Type B1 female killer whale in Paradise Bay, Antarctic Peninsula on 3 March 2018. Photograph by Ari Friedlaender.

A total of 3 h and 53 min of killer whale recordings were analysed resulting in the detection of 2469 killer whale vocalisations which were subsequently rated. After removing Grade 1 calls, 1986 vocalisations were suitable for analysis and categorisation. A total of 1694 and 292 vocalisations from Type B1 and Type B2 killer whales were analysed, respectively. Of the Type B1 killer whale vocalisations, 62.69% were whistles (n=1062), 32% were burst-pulse sounds (n=542) and 5.31% were multi-component vocalisations (n=90). From the Type B2 killer whale vocalisations, 73.63% were whistles (n=215), 21.23% were burst-pulse sounds (n=62) and 5.14% were multi-component vocalisations (n=15). Summary statistics for the acoustic parameters for each vocalisation type are listed in Table 4.4.

Table 4.4 Descriptive statistics of whistles and burst-pulse sounds recorded from Type B1 and Type B2 killer whales off the Antarctic Peninsula. Measurements of the fundamental frequency for whistles and measurements of the entire call for burst-pulse sounds are presented here. Sample sizes for each ecotype are included in the brackets. For each parameter, values given are the range and the mean ± standard deviation.

		Type B1 (*n* = 1062)			Type B2 (*n* = 215)		
		Minimum	Maximum	Mean ± Standard Deviation	Minimum	Maximum	Mean ± Standard Deviation
WHISTLES	**Minimum Frequency (Hz)**	51	20526	6065 ± 3791	97	16806	5266 ± 2533
	Maximum Frequency (Hz)	428	22050	8774 ± 4311	519	21077	8036 ± 3309
	Start Frequency (Hz)	186	21467	6753 ± 4176	242	19332	6637 ± 3081
	End Frequency (Hz)	155	21921	7808 ± 4572	208	21077	6563 ± 3081
	Bandwidth 90% (Hz)	151	8204	1874 ± 1347	199	6938	1883 ± 1078
	Delta Frequency (Hz)	250	18215	2708 ± 1882	369	18278	2769 ± 1947
	Duration (s)	0.02	2	0.3 ± 0.3	0.05	6	0.5 ± 0.5
	Number of extrema	0	23	1.5 ± 2.1	0	39	2.2 ± 4.4
	FM rate (1/s)	0	67	8.8 ± 10.3	0	34	7.3 ± 8.5

		Type B1 (*n* = 542)			Type B2 (*n* = 62)		
		Minimum	Maximum	Mean ± Standard Deviation	Minimum	Maximum	Mean ± Standard Deviation
BURST-PULSE SOUNDS	**1st Quartile Frequency (Hz)**	94	13664	2410 ± 1293	82	5438	1798 ± 1143
	3rd Quartile Frequency (Hz)	94	20180	4279 ± 1942	258	14719	2996 ± 168
	Bandwidth 90% (Hz)	47	20953	4916 ± 2130	258	14344	3086 ± 2138
	Centre Frequency (Hz)	94	17273	3213 ± 1523	152	8625	2334 ± 1384
	Peak Frequency (Hz)	94	20602	3106 ± 1808	70	5813	2126 ± 1296
	Average Entropy (bits)	1	9	5.2 ± 1	3	7	5.1 ± 0.8
	Minimum Entropy (bits)	0.2	8	3.8 ± 1.3	2	7	3.8 ± 1.1
	Maximum Entropy (bits)	2	10	6.6 ± 0.9	4	8	6.1 ± 0.9
	Duration (s)	0.04	3	0.7 ± 0.4	0.1	1.2	0.5 ± 0.3

4.3.1 **K-means Cluster Analysis**

Calls analysed for Type B1 killer whales were grouped into 12 categories: 5 whistle classes, 4 burst-pulse classes and 3 multi-component classes. Calls analysed for Type B2 killer whales were grouped into 8 categories: 3 whistle classes, 3 burst-pulse classes and 2 multi-component classes. Figure 4.6, Figure 4.7and Figure 4.8 illustrate spectrographic examples of call types of Type B1 killer whales. Figure 4.9, Figure 4.10 and Figure 4.11 illustrate spectrographic examples of call types of Type B2 killer whales. A full description and further images of calls are presented in the Type B Call Catalogue (Appendix 4).

ECOTYPE B1

Calls analysed for Type B1 killer whales were grouped separately for whistles and burst-pulse sounds, with whistles grouped into five categories and burst-pulse sounds grouped into four categories. There were also three categories of calls that contained multi-components. Figure 4.6, Figure 4.7 and Figure 4.8 illustrate spectrographic examples of whistles, burst-pulse sounds and multi-component calls of Type B1 killer whales, respectively.

Whistles

Whistles produced by Type B1 killer whales were categorised into 5 groups as a result of the k-means cluster analysis: B1_01, B1_02, B1_03 B1_04 and B1_05. The most common whistle types were B1_05, B1_03 and B1_04 (n=367, 34.56%; n=336, 31.64%; n=207, 19.49%), while the other 2 whistle types comprised the remaining whistles analysed (n=152, 14.31%). Table 4.5 summarises the measurements of whistles for each group and displays measured parameters.

Table 4.5 Summary of measurements for categorised whistles produced by Type B1 killer whales recorded off the Antarctic Peninsula.

Call Group	*n*		Duration [s]	Fmin [Hz]	Fmax [Hz]	Fdelta [Hz]	Fstart [Hz]	Fend [Hz]	Ext	Infl	FM [1/s]	Steps
TYPEB1_01	81	**Mean**	1.0	3895	7268	3373	4341	6196	6	7	7	0
		SD	0.4	2179	2410	1627	2544	2366	4	5	4	1
		Range: minimum	0.4	678	2766	1070	678	1357	0	0	0	0
		Range: maximum	2.2	10157	13059	8073	10751	13059	23	24	17	7
TYPEB1_02	71	**Mean**	0.4	10914	16704	5790	11892	16481	2	3	8	0
		SD	0.3	2020	2062	1618	2408	2145	2	2	7	0
		Range: minimum	0.1	5093	12445	3782	5093	10243	0	0	0	0
		Range: maximum	1.6	18174	22050	10333	20263	21921	9	10	33	2
TYPEB1_03	336	**Mean**	0.3	2589	4226	1637	2882	3740	1	2	7	0
		SD	0.2	1171	1350	900	1344	1338	1	2	10	0
		Range: minimum	0.0	51	428	250	186	155	0	0	0	0
		Range: maximum	1.0	5399	8073	5654	6450	6262	8	9	55	9
TYPEB1_04	207	**Mean**	0.3	12218	14097	1879	12842	13643	1	2	9	0
		SD	0.2	1816	1904	764	1904	2185	2	2	12	0
		Range: minimum	0.0	8053	10886	572	8981	1520	0	0	0	0
		Range: maximum	0.9	20526	22050	3604	21467	21206	9	10	67	1
TYPEB1_05	367	**Mean**	0.2	5703	8531	2828	6705	7396	1	2	10	0
		SD	0.2	1631	1389	1560	1954	1825	1	1	12	0
		Range: minimum	0.0	1246	5542	429	1246	1979	0	0	0	0
		Range: maximum	1.0	10003	14436	8830	13001	11978	6	7	61	3

Group TypeB1_01. These whistles exhibited the highest numbers of extrema and inflection points along with the longest duration. Most whistles had harmonics. This group comprised 81 whistles (Figure 4.6).

Group TypeB1_02. This group comprised 71 whistles. These whistles were high in frequency with a high frequency-modulation rate. They also showed the highest bandwidth (Fdelta) amongst all whistle groups (Figure 4.6).

Group TypeB1_03. These whistles had the lowest frequencies and a low number of local extrema and inflection points. They were also short in duration. There were a total of 336 whistles in this group (Figure 4.6).

Group TypeB1_04. This group of whistles had the highest frequency, highest frequency-modulation rate and shortest duration. It also had the lowest frequency range. There were a total of 207 whistles categorised in this group (Figure 4.6).

Group TypeB1_05. These whistles were short in duration and had the lowest numbers of extrema and inflections, although a high frequency-modulation rate, which is representative of the short duration of each call. There were a total of 367 whistles categorised in this group (Figure 4.6).

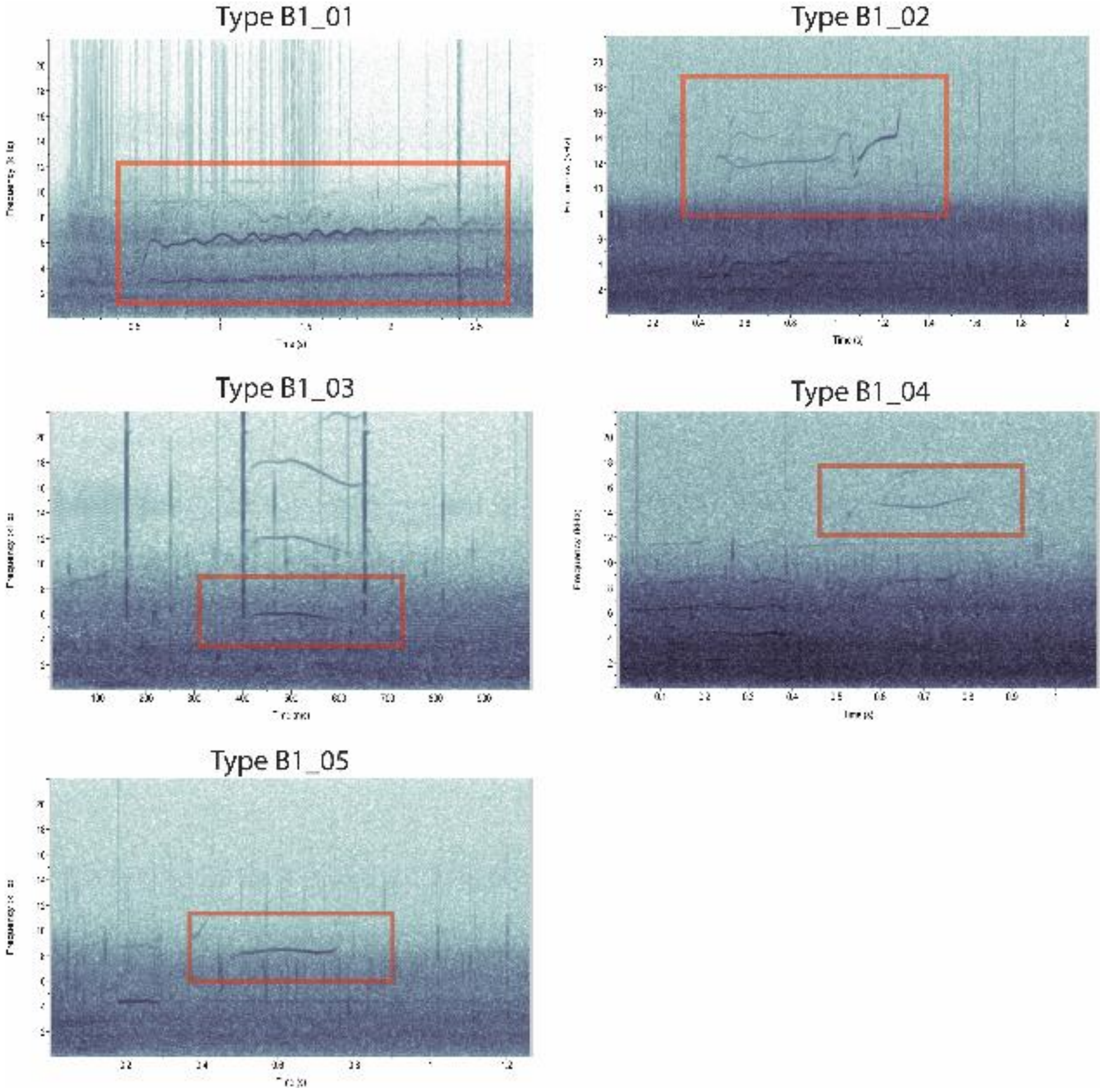

Figure 4.6 Spectrograms of five whistles representing call types B1_01, B1_02, B1_03, B1_04 and B1_05 recorded from Type B1 killer whales off the Antarctic Peninsula (fs = 48 kHz, NFFT = 512, 90% overlap, Hann window).

Burst-pulse Sounds

Burst-pulse sounds produced by Type B1 killer whales were categorised into 4 groups as a result of the k-means cluster analysis: B1_06, B1_07, B1_08 and B1_09. The most common burst-pulse sound groups were B1_09, B1_06 and B1_07 (n=290, 53.50%; n=124, 22.88%; n=124, 22.88%), while the burst-pulse sound group type B1_08 comprised the remaining burst-pulse sounds analysed (n=4, 0.74%). Table 4.6 summarises the measurements of burst-pulse sounds and multi-component calls for each group and displays measured parameters.

Table 4.6 Summary of measurements for burst-pulse sounds and multi-component calls produced by Type B1 killer whales off the Antarctic Peninsula.

Call Group	*n*		Duration [s]	Dur90% [s]	Fmin [Hz]	Fmax [Hz]	Q1Freq [Hz]	Q3Freq [Hz]	Fpeak [Hz]	BW 90% [Hz]	Fcentre [Hz]	Fdelta [Hz]	Min Entropy [bits]	Max Entropy [bits]	Avg Entropy [bits]
TYPEB1_06	**124**	**Mean**	1.3	1.1	807	18457	2358	4077	3204	5031	3135	17650	4	6	5
		SD	0.4	0.3	683	5690	896	1184	1475	1871	1026	5774	1	1	1
		Range: minimum	0.6	0.8	37	1867	281	633	188	961	398	1593	2	5	3
		Range: maximum	2.6	2.2	3653	24000	5814	7106	7090	19664	6675	23830	7	10	8
TYPEB1_07	**124**	**Mean**	0.6	0.4	446	14886	1125	2422	1325	3613	1597	14440	3	6	5
		SD	0.2	0.2	349	7279	698	1195	963	1976	899	7334	1	1	1
		Range: minimum	0.0	0.1	31	1375	94	94	94	47	94	1079	0	2	1
		Range: maximum	1.3	0.8	1577	24000	3015	4828	4031	13078	4031	23897	6	10	7
TYPEB1_08	**4**	**Mean**	0.9	0.6	6268	23507	8354	15543	9629	12534	11306	17239	6	8	8
		SD	0.9	0.5	3935	971	4581	4026	7758	2769	4637	4376	2	1	1
		Range: minimum	0.1	0.1	1263	22050	2718	11953	2719	9776	5953	13681	4	8	6
		Range: maximum	2.1	1.2	10248	24000	13664	20180	20602	15563	17273	22736	8	10	9
TYPEB1_09	**290**	**Mean**	0.5	0.4	1388	18583	2900	4906	3715	5074	3763	17195	4	7	5
		SD	0.2	0.2	1245	5367	1089	1167	1470	1635	1072	5817	1	1	1
		Range: minimum	0.0	0.1	37	5856	603	2906	328	1034	1453	3574	1	4	3
		Range: maximum	1.0	0.8	8159	24000	8355	8953	8441	14438	8441	23767	8	9	9
TYPEB1_10*	**61**	**Mean**	1.2	0.9	655	21619	2633	4391	3542	5574	3475	20964	4	8	6
		SD	0.3	0.2	512	1845	508	1028	1195	1417	788	2072	1	0	0
		Range: minimum	0.8	0.5	58	11732	1809	2110	1787	3187	1917	10127	3	6	5
		Range: maximum	2.0	1.4	2541	22050	3747	6740	6503	9668	5814	22050	7	8	7
TYPEB1_11*	**28**	**Mean**	1.1	0.7	354	22619	1764	4999	2392	6481	3127	22265	4	7	5
		SD	0.5	0.4	130	2265	1155	4082	1859	4156	2032	2222	1	1	1
		Range: minimum	0.4	0.2	128	15048	141	141	141	2063	141	14776	0	4	2
		Range: maximum	3.2	2.2	709	24000	3984	19547	7969	20953	10641	23773	7	9	7
TYPEB1_12*	**1**	**Measurements**	1.1	0.9	2826	22050	4070	5233	4070	8204	4436	19224	3	7	5

***All multi-component calls are presented as an entire call in this table for simplicity. Individual components were measured separately for comparative analysis.**

Group TypeB1_06. These 124 burst-pulse sounds had a long duration with the 1st quartile frequency at 2.3 kHz and the 3rd quartile frequency at 4.1 kHz (Figure 4.7).

Group TypeB1_07. These 124 burst-pulse sounds were short in duration and exhibited both the lowest frequencies and highest frequencies, resulting in the largest bandwidth (Fdelta). These burst-pulse sounds had the lowest range of peak frequency at 0.94 kHz (Figure 4.7).

Group TypeB1_08. These burst-pulse sounds were long in duration and highest in frequency. This category had the highest peak frequency measured at 20.6 kHz and also the highest 3rd quartile frequency at 20.2 kHz. This group comprised only 4 burst-pulse sounds (Figure 4.7).

Group TypeB1_09. These burst-pulse sounds were the shortest in duration and high in frequency. There were a total of 290 burst-pulse sounds categorised in this group (Figure 4.7).

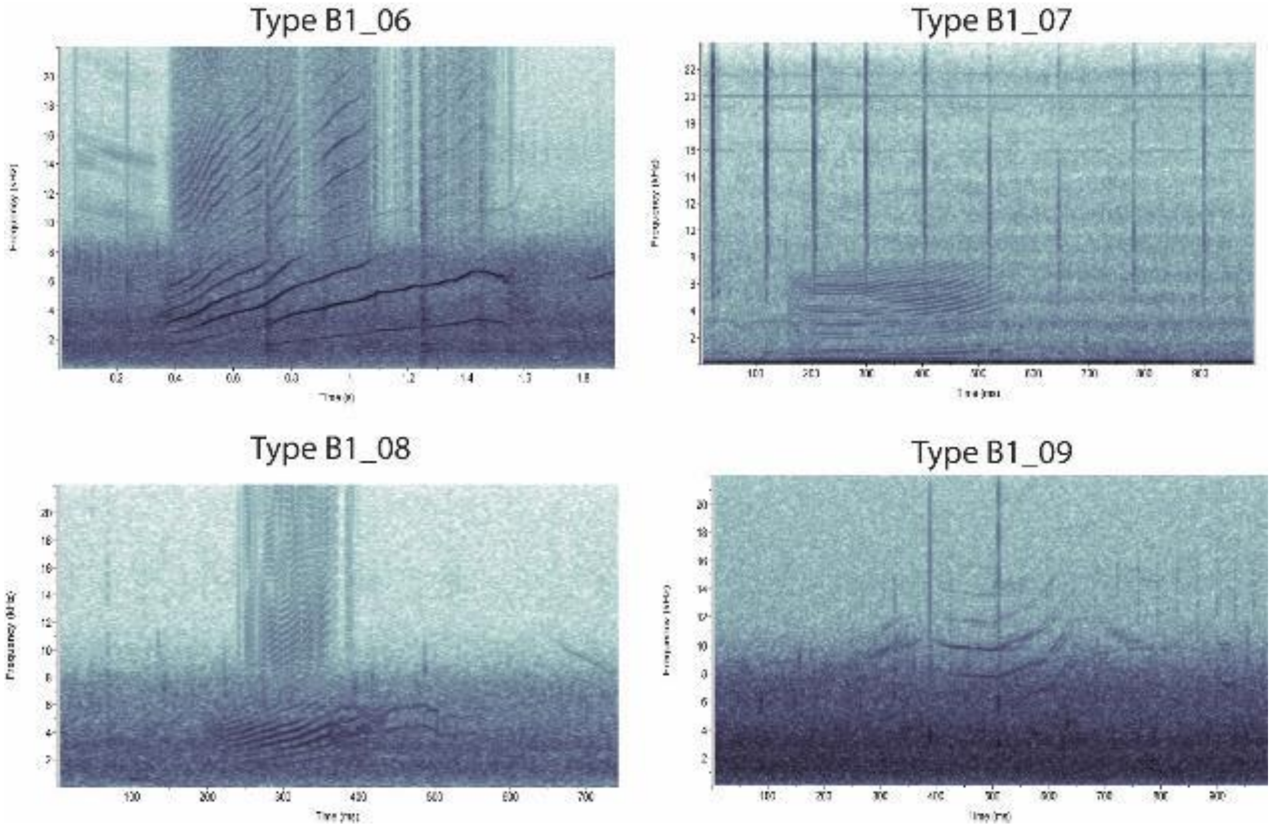

Figure 4.7 Spectrograms of four burst-pulse sound call types recorded from Type B1 killer whales off the Antarctic Peninsula (fs = 48 kHz, NFFT = 512, 90% overlap, Hann window).

Multi-Component Calls

Multi-component calls produced by Type B1 killer whales were categorised into 3 groups as a result of the k-means cluster analysis: B1_10, B1_11 and B1_12. The most common burst-pulse sound groups were B1_10 and B1_11 (n=61, 67.78%; n=28, 31.11%), while the burst-pulse sound group type B1_08 comprised of only 1 call (1.11%). Table 4.6 summarises the measurements of burst-pulse sounds and multi-component calls for each group and displays measured parameters.

Group TypeB1_10. This class comprises only one call: a multi-component call consisting of 3 components. Part 1 is a burst-pulse sound with an approximate 500 Hz sideband spacing (SBS). Part 2 is a burst-pulse sound with a SBS of 1-2 kHz. Part 3 is a whistle, usually demonstrating an inverted-U contour. This call was documented 61 times throughout the analysis, with little variation between calls. Table 4.6 gives measurements for the entire call (i.e., over all 3 components. Individual components were measured separately for comparative analysis (Figure 4.8).

Group TypeB1_11. This is a multi-component call consisting of two burst-pulse components. This call was repeated by Type B1 killer whales 28 times throughout recordings. This call is a burst-pulse sound that starts out with a SBS of approximately 0.1 kHz that increases over time to approximately 1 kHz. The two components were measured as an entire call for Table 4.6. Individual components were measured separately for comparative analysis (Figure 4.8).

Group TypeB1_12. This is a two-component call which was observed once during recordings. Part 1 is a burst-pulse sound with an approximate 500 Hz SBS. The call then transitions into part 2 which is a whistle that is likely slightly amplitude-modulated, as indicated by weak sidebands. The two components were measured as an entire call for Table 4.6. Individual components were measured separately for comparative analysis (Figure 4.8).

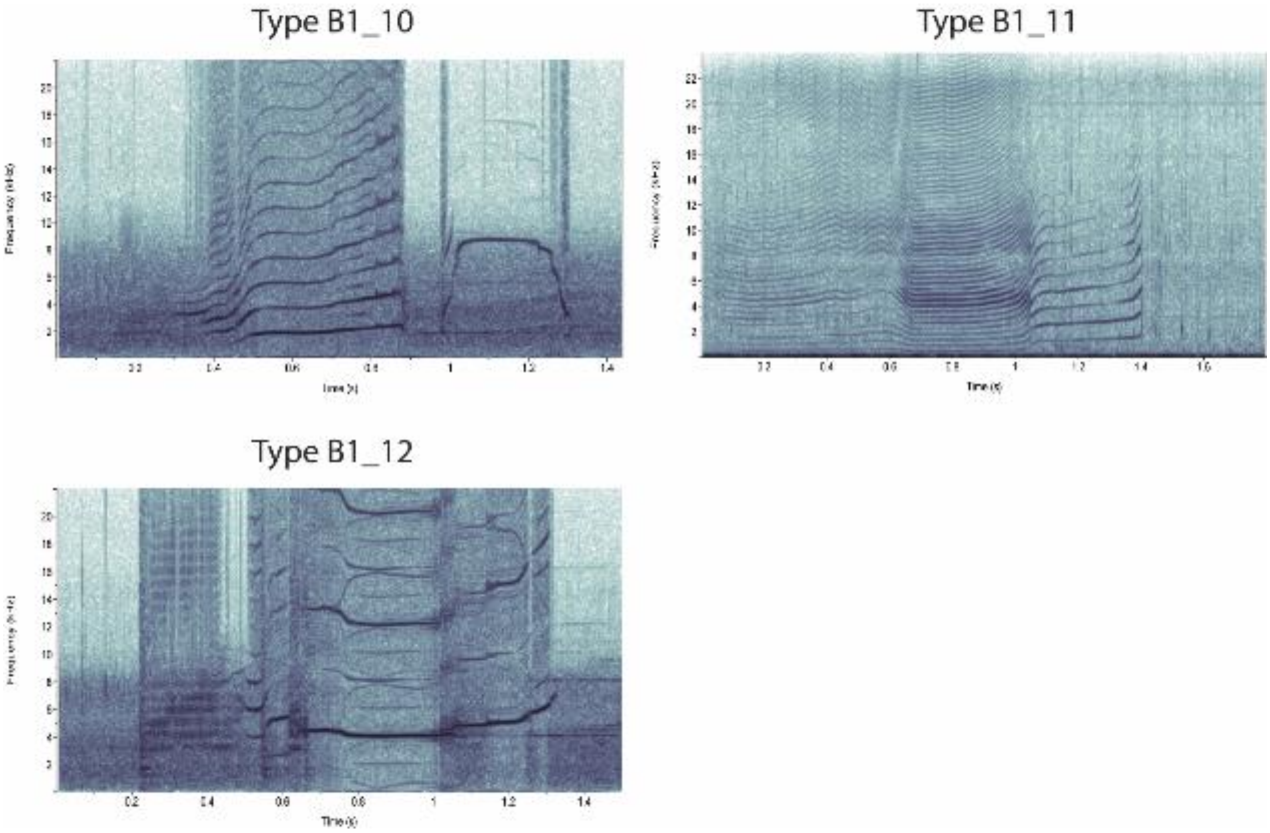

Figure 4.8 Spectrograms of three multi-component call types recorded from Type B1 killer whales off the Antarctic Peninsula (fs = 48 kHz, NFFT = 512, 90% overlap, Hann window). The calls shown for B1_10 and B1_12 have significant energy at high frequencies. The recording system did not include an anti-aliasing filter at the Nyquist frequency of 24 kHz, which is why higher-frequency energy “folds” down, appearing mirror-reflected at the top edge of the spectrogram.

ECOTYPE B2

Calls analysed for Type B2 killer whales were grouped separately for whistles and burst-pulse sounds, with whistles grouped into three categories and burst-pulse sounds grouped into three categories. There were also two categories of calls that contained multiple components. Figure 4.9, Figure 4.10 and Figure 4.11 illustrate spectrographic examples of whistles, burst-pulse sounds and multi-component calls of Type B2 killer whales, respectively.

Whistles

Whistles produced by Type B2 killer whales were categorised into 3 groups as a result of the k-means cluster analysis: B2_01, B2_02 and B2_03. The most common whistle type was B2_01 (n=111, 51.63%) while the other 2 whistle types B2_02 and B2_03 comprised the remaining whistles analysed (n=53, 24.65%; n=51, 23.72%) respectively. Table 4.7 summarises the measurements of whistles for each group and displays measured parameters.

Table 4.7 Summary of measurements for categorised whistles produced by Type B2 killer whales recorded off the Antarctic Peninsula.

Call Group	*n*		Duration [s]	Fmin [Hz]	Fmax [Hz]	Fdelta [Hz]	Fstart [Hz]	Fend [Hz]	Ext	Infl	FM [1/s]	Steps
TYPEB2_01	111	**Mean**	0.4	5510	7984	2474	6648	6791	2	3	9	0
		SD	0.4	1211	1193	1125	1465	1482	3	3	9	0
		Range: minimum	0.1	2923	5795	453	703	3735	0	0	0	0
		Range: maximum	2.7	8690	11863	6316	9844	11098	13	14	33	5
TYPEB2_02	53	**Mean**	0.4	2416	3942	1526	2998	2849	1	2	5	0
		SD	0.3	1508	1917	834	1654	1466	2	2	7	0
		Range: minimum	0.1	97	519	369	242	208	0	0	0	0
		Range: maximum	1.2	7280	8134	4778	5430	5024	8	9	34	1
TYPEB2_03	51	**Mean**	0.6	8083	12116	4034	11037	9379	3	3	7	0
		SD	0.8	2415	2041	2028	2053	2694	6	7	7	0
		Range: minimum	0.1	2856	10227	951	7914	3954	0	0	0	0
		Range: maximum	5.8	16806	20595	9655	19332	17684	39	40	27	2

Group TypeB2_01. These whistles were low in frequency and long in duration, with few extrema and inflection points. This group comprised 111 whistles (Figure 4.9).

Group TypeB1_02. This group comprised 53 whistles. These whistles were the shortest in duration, had the lowest frequency and had the lowest numbers of local extrema and inflection points (Figure 4.9).

Group TypeB2_03. These whistles had the longest duration (5.8 s), the highest frequency (20.1 kHz) and the highest numbers of local extrema and inflection points. A total of 51 whistles were categorised into this group (Figure 4.9).

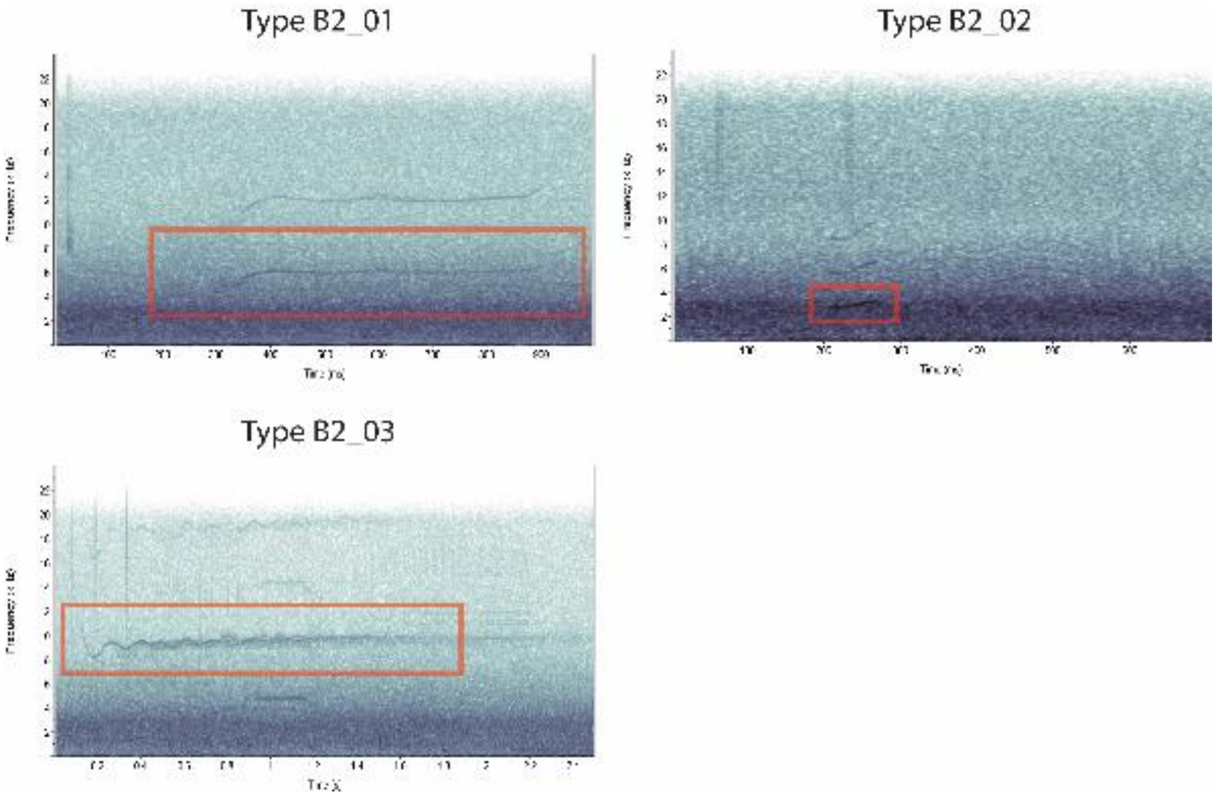

Figure 4.9 Spectrograms of three whistle call types recorded from Type B2 killer whales off the Antarctic Peninsula (fs = 48 kHz, NFFT = 512, 90% overlap, Hann window).

Burst-pulse Sounds

Burst-pulse sounds produced by Type B2 killer whales were categorised into 3 groups as a result of the k-means cluster analysis: B2_04, B2_05 and B2_06. The most common burst-pulse sound groups were B2_05 and B2_04 (n=38, 61.29%; n=19, 30.65%), while the burst-pulse sound group type B2_06 comprised the remaining burst-pulse sounds analysed (n=5, 8.06%). Table 4.8 summarises the measurements of burst-pulse sounds and multi-component calls for each group and displays measured parameters.

Table 4.8 Summary of measurements for categorised burst-pulse sounds and multi-component calls produced by Type B2 killer whales recorded off the Antarctic Peninsula.

Call Group	*n*		Duration [s]	Dur90% [s]	Fmin [Hz]	Fmax [Hz]	Q1Freq [Hz]	Q3Freq [Hz]	Fpeak [Hz]	BW 90% [Hz]	Fcentre [Hz]	Fdelta [Hz]	Min Entropy [bits]	Max Entropy [bits]	Avg Entropy [bits]
TYPEB2_04	19	Mean	0.3	0.2	114	5339	404	1276	431	1688	736	5225	4	6	5
		SD	0.2	0.2	76	5623	285	935	525	1080	609	5619	1	1	1
		Range: minimum	0.1	0.1	24	494	82	258	70	258	152	371	2	5	4
		Range: maximum	0.9	0.6	302	23231	1078	2719	2461	3117	2297	23157	7	8	7
TYPEB2_05	38	Mean	0.7	0.6	987	16461	2048	3072	2561	2898	2556	15474	4	6	5
		SD	0.3	0.2	896	5394	547	553	650	696	444	5791	1	1	1
		Range: minimum	0.2	0.1	136	6865	938	2438	328	1875	1969	6426	2	5	4
		Range: maximum	1.2	1.0	3031	24000	3282	4875	4219	5297	3844	23547	7	8	7
TYPEB2_06	5	Mean	0.2	0.2	3858	15887	4416	7809	4256	8456	5513	12028	3	6	4
		SD	0.1	0.1	775	4011	820	4295	1080	4304	1943	4638	1	1	1
		Range: minimum	0.1	0.1	2964	11556	3141	4078	3000	4594	3469	6503	2	5	3
		Range: maximum	0.4	0.4	5052	20913	5438	14719	5813	14344	8625	17949	4	8	5
TYPEB2_07*	12	Mean	0.6	0.5	1414	14776	2113	3496	2562	3770	2840	13362	4	6	5
		SD	0.2	0.1	904	4826	786	973	1061	1793	894	5070	1	1	1
		Range: minimum	0.4	0.3	565	7680	891	2625	891	2344	2016	6261	2	5	4
		Range: maximum	0.9	0.8	3293	22508	3609	5953	4828	4734	4734	21943	5	8	5
TYPEB2_08**	3	Mean	1.1	1.0	2114	20523	2461	3141	2391	2367	2789	18409	3	5	4
		SD	1.0	0.8	969	783	696	464	862	365	630	186	0	1	0
		Range: minimum	0.4	0.4	1429	19970	1969	2813	1781	2109	2344	18278	3	4	4
		Range: maximum	1.8	1.6	2799	21077	2953	3469	3000	2625	3234	18541	3	6	4

***All multi-components calls are presented as an entire call in this table for simplicity. Individual components were measured separately for comparative analysis.**

Group TypeB2_04. These 19 burst-pulse sounds were the lowest in frequency (0.24 kHz) with the 1st quartile frequency at 0.4 kHz and the 3rd quartile frequency at 1.2 kHz. (Figure 4.10).

Group TypeB2_05. These 38 burst-pulse sounds were the longest in duration (1.2 s) and had the highest frequency (24 kHz) (Figure 4.10).

Group TypeB2_06. These 5 burst-pulse sounds were the shortest in duration (range of 0.1 – 0.4 s) and had the lowest bandwidth (Fdelta) (Figure 4.10).

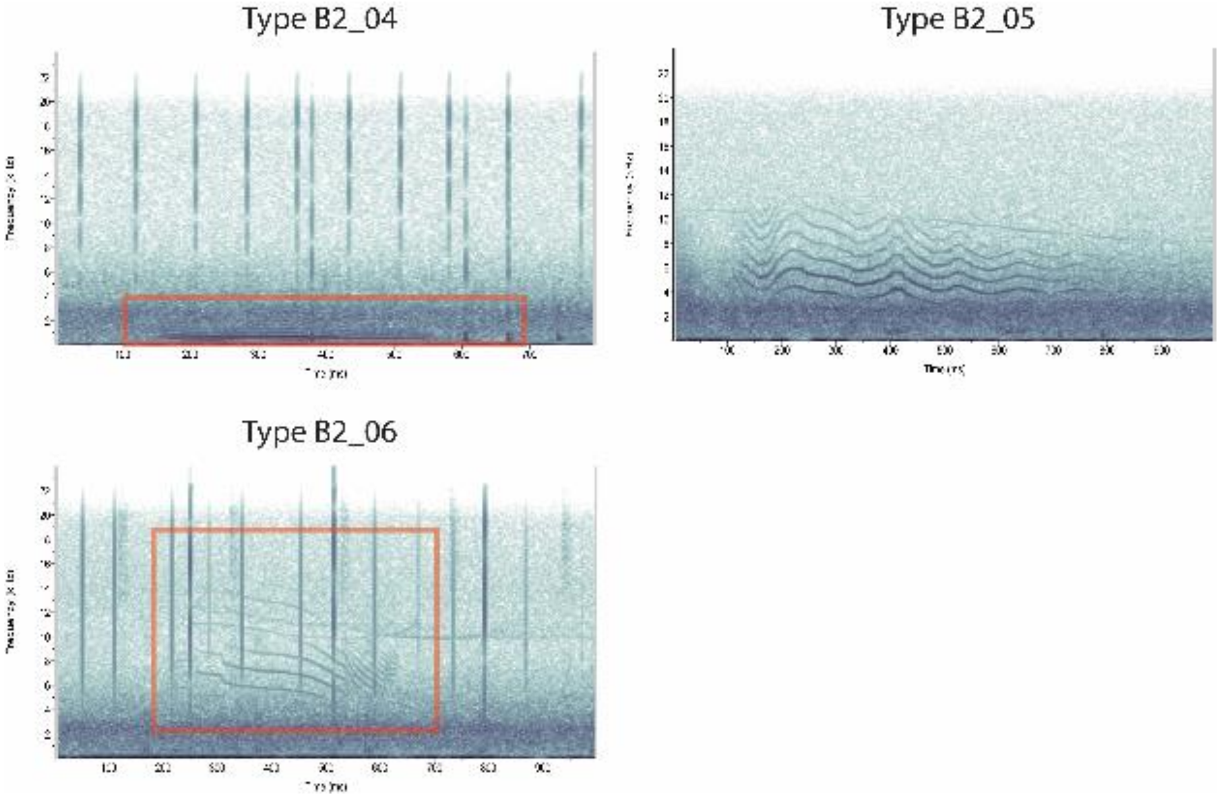

Figure 4.10 Spectrograms of three burst-pulse sound call types recorded from Type B2 killer whales off the Antarctic Peninsula (fs = 48 kHz, NFFT = 512, 90% overlap, Hann window).

Multi-Component and Biphonic Calls

Multi-component and biphonic calls produced by Type B2 killer whales were categorised into 2 groups as a result of the k-means cluster analysis: B2_07 and B2_08. Call type B2_07 was observed 12 times, a total of 4.11% out of the entire observed Type B2 killer whale call repertoire. While call type B2_08 was observed 3 times, a total of 1.03% out of the entire observed Type B2 call repertoire. Table 4.6 summarises the measurements of burst-pulse sounds and multi-component calls for each group and displays measured parameters.

Group TypeB2_07. This is a two-component biphonic call. Part 1 is a burst-pulse sound with an approximate 1 kHz SBS. Part 2 is a biphonic whistle that usually commences and finishes with the burst-pulse, hence having the same approximate duration. This whistle exhibited contours with many local extrema and inflection points. There was a total of 12 calls categorised in this group. The two components were measured as an entire call for Table 4.8. Individual components were measured separately for comparative analysis.

Group TypeB2_08. This is a two-component call that transitions from a whistle to a burst-pulse sound. Part 1 is a whistle with a small number of extrema and inflection points. Part 2 is a burst-pulse sound with SBS between 0.5 – 1 kHz. Calls had a duration of 0.4 to 1.8 s. There was a total of 3 calls categorised in this group. The two components were measured as an entire call as presented in Table 4.8 for simplicity. Individual components were measured separately for comparative analysis.

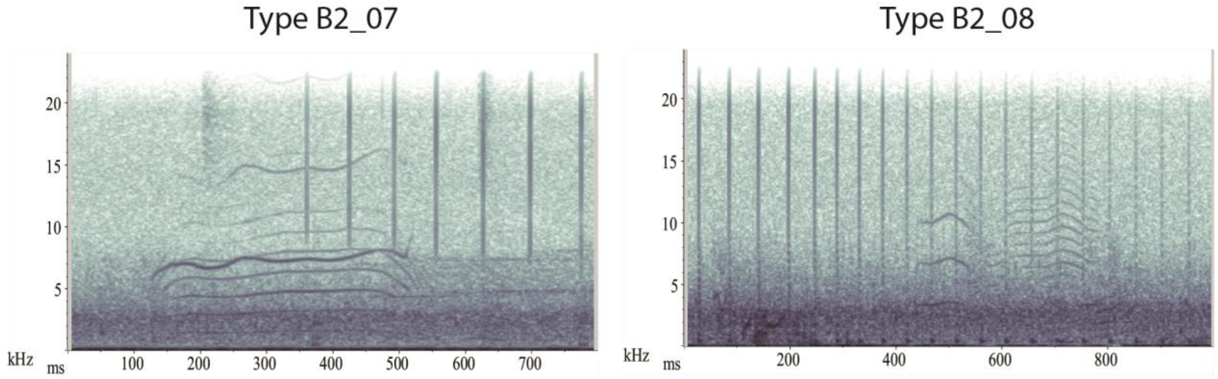

Figure 4.11 Spectrograms of two multi-component and biphonic call types recorded from Type B2 killer whales off the Antarctic Peninsula (fs = 48 kHz, NFFT = 512, 90% overlap, Hann window).

The analysis of calls of Types B1 and B2 detected four different multi-component calls that were repetitive in their repertoire. Calls categorised in group TypeB1_10 and TypeB1_11 were evident 61 and 28 times, respectively (Figure 4.12). Group TypeB1_10 consists of multi-component calls that start as distinct pulses at increasing pulse repetition rate (PRR) and continue as a burst-pulse sound, followed by a distinct inverted-U shaped whistle. Group TypeB1_11 was also seen to be repeated by Type B1 killer whales and contained a burst-pulse sound that starts out with a SBS of approximately 0.1 kHz that increases over time to approximately 1 kHz.

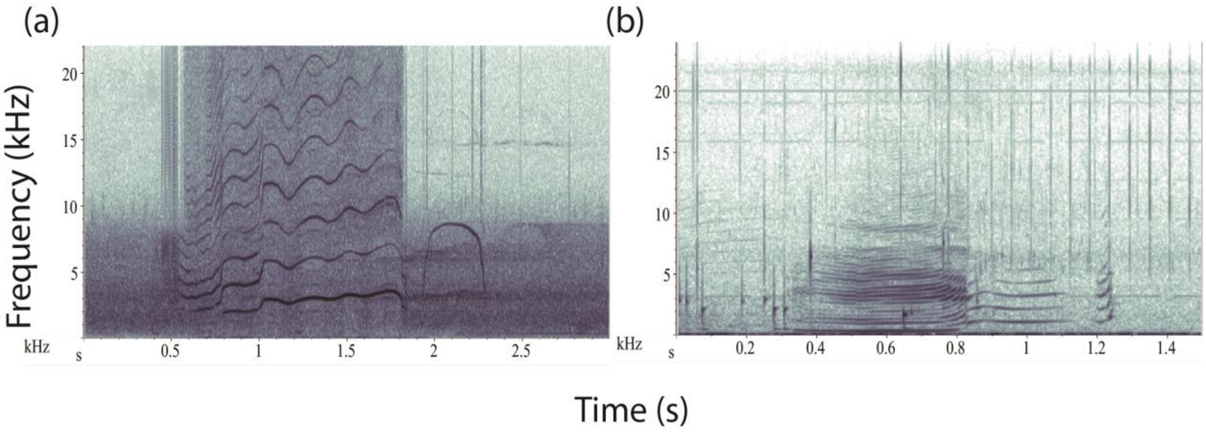

Figure 4.12 Spectrograms of repeated calls from Type B1; (a) Group TypeB1_10 is a multi-component call that was repeated 61 times, this call starts as distinct pulses at increasing pulse repetition rate (PRR) and continues as a burst-pulse sound, followed by a distinct concave-contoured whistle; (b) Group TypeB1_11 that was repeated by Type B1 killer whales 28 times and is a burst-pulse sound that starts out with a side-band spacing (SBS) of approximately 0.1 kHz that increases over time to approximately 1 kHz SBS (fs = 48 kHz, NFFT = 512, 90% overlap, Hann window).

Two multi-component calls were repeated throughout the Type B2 recordings. Calls categorised into Group TypeB2_07 were biphonic calls consisting of a burst-pulse sound with an SBS of approximately 1 kHz with a biphonic whistle that is highly frequency-modulated and starts with an upsweeping contour. These calls were observed 12 times throughout the recordings. A multi-component call was also seen to be repeated three times and was categorised in Group TypeB2_08. This is a two-component call that transitions from a whistle to a burst-pulse sound (Figure 4.13).

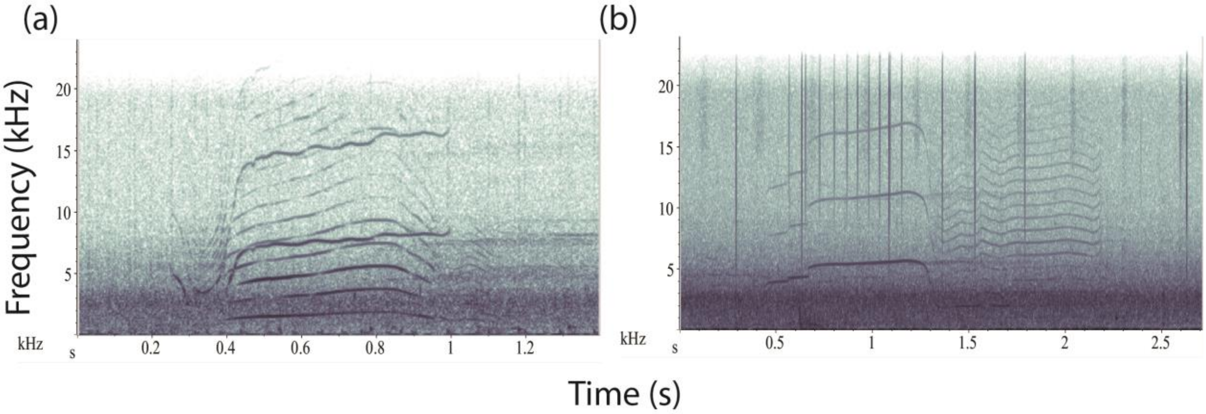

Figure 4.13 Spectrograms of multi-component calls from Type B2; (a) Call TypeB2_07 is a two-component biphonic call; (b) Call TypeB2_08 is a multi-component call, where a whistle transitions into a burst-pulse sound (fs = 48 kHz, NFFT = 512, 90% overlap, Hann window).

4.3.2 Call Comparison with Antarctic Killer Whale Call Repertoires

Whilst comparing calls from different ecotypes and considering each call in its entirety, i.e. all components are measured as one, may be good for qualitative analysis, a segment-based comparison was used for quantitative analysis, where all whistle and burst-pulse components were measured and compared individually, rather than as part of the entire call.

Comparing whistles produced by Type B1, B2 and C killer whales showed a similar frequency range across the 3 ecotypes, with the fMin and fMax fundamentals ranging from 0.51 kHz to 22.06 kHz. The minimum duration of whistles was similar across the three ecotypes, ranging from 0.02 to 0.05 seconds, however, the maximum frequency showed some variation with the longest whistle produced by Type B2 killer whales of 6 seconds, in comparison to 2 and 3 second whistle maximums produced by Type B1 and C, respectively. The FM rate of whistles produced by Type B1 was higher (min=0, max=67) than those of Type B2 and Type C (min=0, max=34; min=0, max=34), respectively. Summary statistics for the acoustic parameters of whistles recorded from Type B1, B2 and C killer whales are listed in Table 4.9.

Table 4.9 Descriptive statistics of whistles recorded from Type B1, Type B2 and Type C killer whales throughout the Antarctic region. Sample sizes for each ecotype are included in the brackets. For each parameter, values given are the range and the mean ± standard deviation.

	Type B1 (*n* = 1123)			**Type B2 (*n* = 229)**			**Type C (*n* = 246)**		
	Minimum	Maximum	Mean ± Standard Deviation	Minimum	Maximum	Mean ± Standard Deviation	Minimum	Maximum	Mean ± Standard Deviation
Minimum Frequency (Hz)	51	20526	6065 ± 3791	97	16806	5266 ± 2533	290	10854	4924 ± 2282
Maximum Frequency (Hz)	428	22050	8774 ± 4311	519	21077	8036 ± 3309	2273	17702	9745 ±3134
Start Frequency (Hz)	186	21467	6753 ± 4176	242	19332	6637 ± 3081	290	17702	7013 ± 4085
End Frequency (Hz)	155	21921	7808 ± 4572	208	21077	6563 ± 3081	941	13802	7017 ± 2651
Bandwidth 90% (Hz)	151	8204	1874 ± 1347	199	6938	1883 ± 1078	194	8391	2901 ± 1861
Delta Frequency (Hz)	250	18215	2708 ± 1882	369	18278	2769 ± 1947	820	11064	4821 ± 2325
Duration (s)	0.02	2	0.3 ± 0.3	0.05	6	0.5 ± 0.5	0.02	3	0.7 ± 0.4
Number of extrema	0	23	1.5 ± 2.1	0	39	2.2 ± 4.4	0	29	3.2 ± 4.2
FM rate (1/s)	0	67	8.8 ± 10.3	0	34	7.3 ± 8.5	0	34	5.7 ± 6

Burst-pulse sounds produced by Type B1, B2 and C killer whales showed a difference in call energy, where the bandwidth containing 90% of the call energy was highest in Type C repertoire (min=0.28 kHz, max=43.83 kHz), in comparison to Type B1 and B2 (min=0.05 kHz, max=20.95 kHz; min=0.26 kHz, max=14.3 kHz), respectively. The MinEnt and MaxEnt showed some variation across the 3 ecotypes, with the MinEnt and MaxEnt ranging from 0.17-9.97 bits, 1.96-7.98 bits, and 1.1-9.94 bits for Type B1, B2 and C killer whale calls, respectively. Summary statistics for the acoustic parameters of burst-pulse sounds recorded from Type B1, B2 and C killer whales are listed in Table 4.10.

Table 4.10 Descriptive statistics of burst-pulse sounds recorded from Type B1, Type B2 and Type C killer whales throughout the Antarctic region. Sample sizes for each ecotype are included in the brackets. For each parameter, values given are the range and the mean + standard deviation.

	Type B1 (*n* = 632)			**Type B2 (*n* = 74)**			**Type C (*n* = 402)**		
	Minimum	Maximum	Mean ± Standard Deviation	Minimum	Maximum	Mean ± Standard Deviation	Minimum	Maximum	Mean ± Standard Deviation
1st Quartile Frequency (Hz)	94	13664	2410 ± 1293	82	5438	1798 ± 1143	948	36188	2932 ± 1975
3rd Quartile Frequency (Hz)	94	20180	4279 ± 1942	258	14719	2996 ± 168	1723	42188	5138 ± 3442
Bandwidth 90% (Hz)	47	20953	4916 ± 2130	258	14344	3086 ± 2138	281	43828	6235 ± 6301
Centre Frequency (Hz)	94	17273	3213 ± 1523	152	8625	2334 ± 1384	1292	38297	3483 ± 2472
Delta Frequency (Hz)	1079	23897	17303 ± 6111	371	23547	12349 ± 6938	4059	47834	17261 ± 10844
Peak Frequency (Hz)	94	20602	3106 ± 1808	70	5813	2126 ± 1296	188	37078	3513 ± 2486
Average Entropy (bits)	0.96	9.39	5.2 ± 1	3.30	7.34	5.1 ± 0.8	2.1	8.7	5.1 ± 1.1
Minimum Entropy (bits)	0.17	7.99	3.8 ± 1.3	1.96	6.89	3.8 ± 1.1	1.1	7.8	3.9 ± 1.2
Maximum Entropy (bits)	2.41	9.97	6.6 ± 0.9	4.43	7.98	6.1 ± 0.9	4.8	9.4	7 ± 0.9
Duration (s)	0.04	3.15	0.7 ± 0.4	0.10	1.23	0.5 ± 0.3	0.01	2.4	0.5 ± 0.4

4.3.3 Comparison of variables between Antarctic ecotypes

A comparison of variables for each type of vocalisation (whistles and burst-pulse sounds) plotted for Antarctic ecotypes Type B1, B2 and C showed clear differences between all Antarctic ecotypes. A comparison of whistles showed a clear distinction between ecotypes when considering the number of components, evident by the distance between clusters and especially evident for Type C killer whales (Figure 4.14). This was the strongest variable supporting acoustic divergence of whistles between ecotypes, followed by delta frequency and duration.

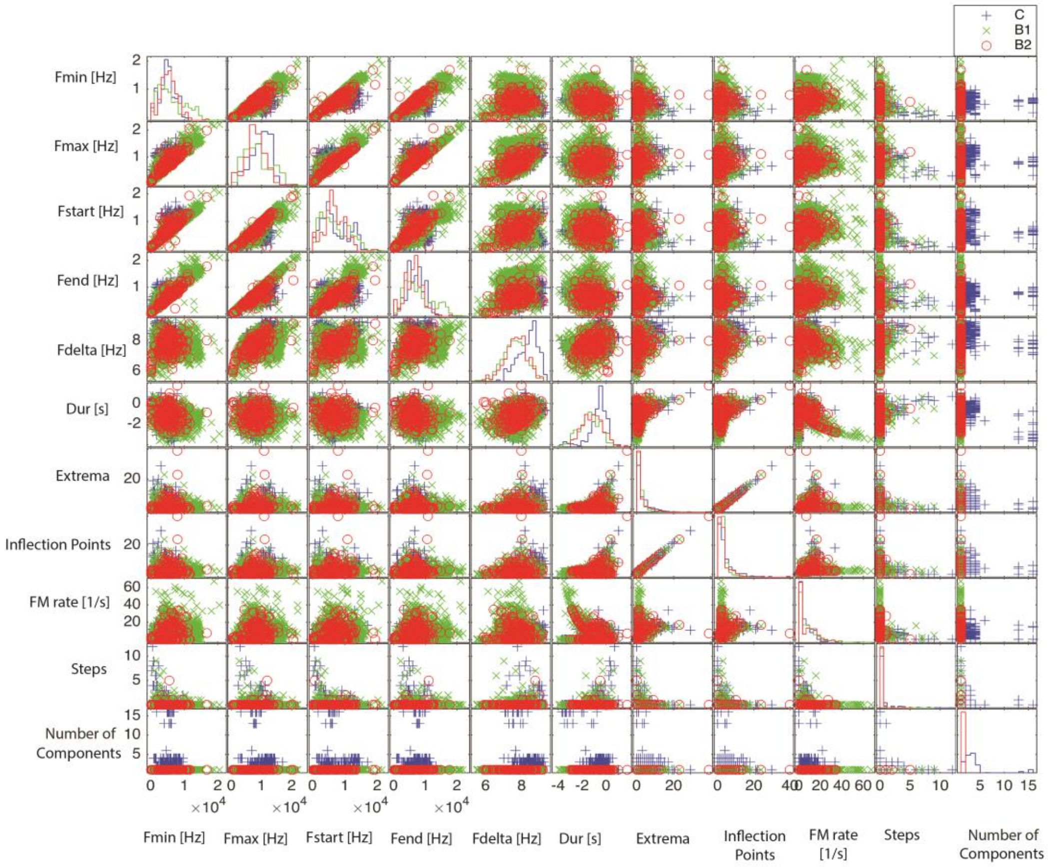

Figure 4.14 Variables of whistle components for Antarctic ecotypes B1, B2 and C plotted against each other in MATLAB (The MathWorks Inc., 2014b, Natick, Massachusetts, United States). Whistle variables plotted include: Fmin, Fmax, Fstart, Fend, Fdelta, Dur, Extrema, Inflection Points, FM rate, Steps and the number of components.

A comparison of burst-pulse sounds showed there was a clear distinction between ecotypes when considering the number of components, evident by the distance between clusters and especially so for Type C killer whales (Figure 4.14). This was the strongest variable supporting acoustic divergence of burst-pulse sounds between ecotypes, followed by bandwidth and duration.

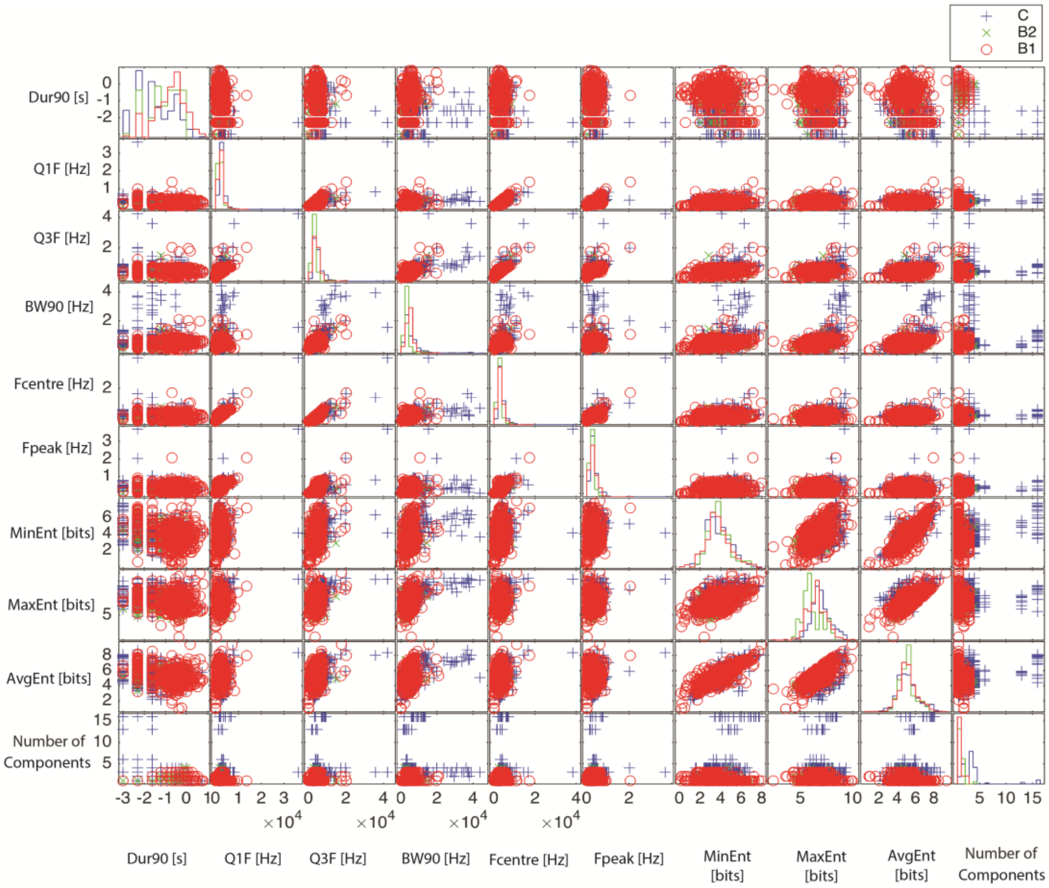

Figure 4.15 Variables of burst-pulse sound components for Antarctic ecotypes B1, B2 and C plotted against each other in MATLAB (The MathWorks Inc., 2014b, Natick, Massachusetts, United States). Variables of burst-pulse sounds plotted include: Dur90%, Q1F, Q3F, BW90%, Fcentre, Fpeak, MinEnt, MaxEnt, AvgEnt, and the number of components.

4.3.4 Multivariate Analysis of Variance (MANOVA)

The MANOVA performed on 11 features of whistles revealed a clear distinction between all 3 ecotypes, with the largest separation between Type C and both Type B's. Types B1 and B2 also showed differentiation, with the plot showing a centralised distribution for both ecotypes B1 and B2 (Figure 4.16).

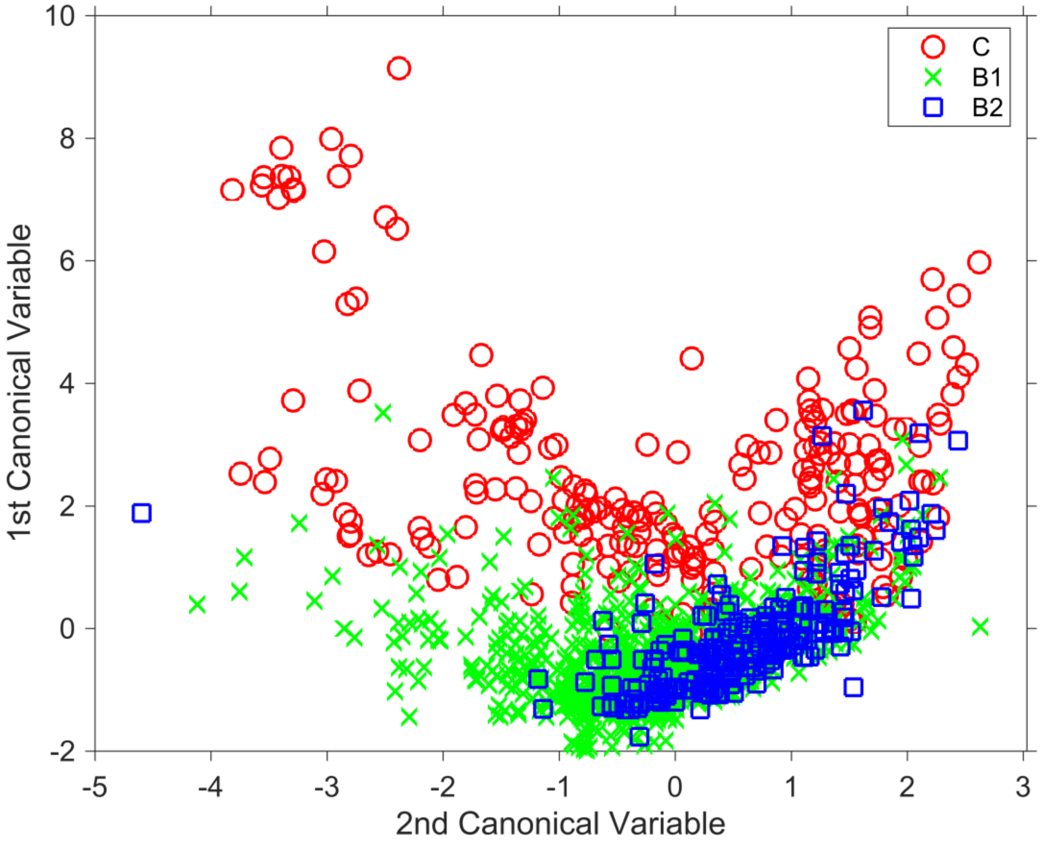

Figure 4.16 Multivariate analysis of variance performed in MATLAB (The MathWorks Inc., 2014b, Natick, Massachusetts, United States) on 11 features of whistles and compared across Antarctic killer whale ecotypes B1, B2 and C.

The MANOVA performed on 10 features of burst-pulse sounds revealed a clear distinction between all 3 ecotypes, and again with the largest separation between Type C and both Type B's. Types B1 and B2 also show minimal differentiation, with the distributions of B1 and B2, but having separate means (Figure 4.17).

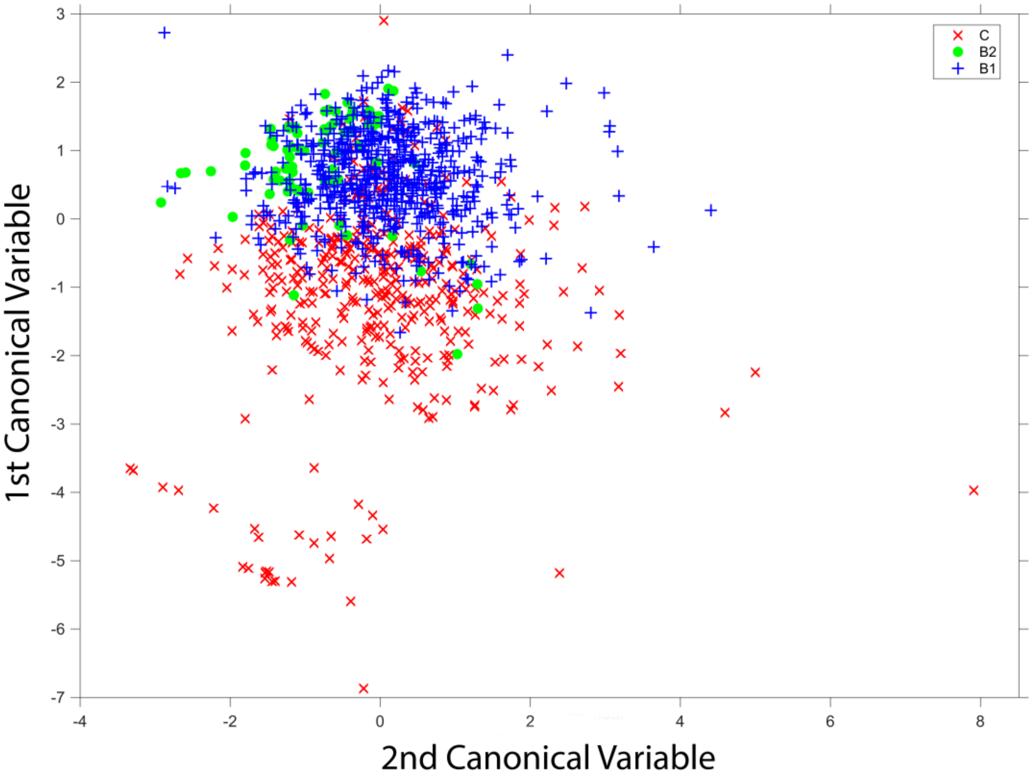

Figure 4.17 Multivariate analysis of variance performed in MATLAB (The MathWorks Inc., 2014b, Natick, Massachusetts, United States)on 10 features of burst-pulse sounds and compared across Antarctic killer whale ecotypes B1, B2 and C.

4.3.5 Analysis of Variance (ANOVA)

The ANOVA results supported both the comparison of whistle and burst-pulse sound variables measured and the MANOVA. Results from the ANOVA for whistle comparison within and between the three ecotypes were statistically significant and showed strong support for three different populations (*F*= 4.12, p= 0.016).

Results from the ANOVA for burst-pulse sound comparison within and between the three ecotypes were statistically significant and showed even stronger support for three different populations (*F*= 35.29, p= 1.3812e-61).

4.3.6 Comparison of Multi-Component and Biphonic Calls

Results showed a clear difference in the number of biphonic calls between ecotypes, with Type C demonstrating a larger repertoire of biphonic calls. The recorded Type C repertoire contained 45% biphonic call types (n=13 call types). This is large in comparison to Type B2 having only 3% of call types with a biphonation and Type B1 displaying no biphonic call types at all in the available recordings.

There is also a clear distinction between single component calls and multi-component calls across Antarctic ecotypes. The Type C repertoire consisted of 71% multi-component call types, compared to only 6.2% of multi-component call types in the Type B1 repertoire, and 1.9% in the Type B2 repertoire. A demonstration of the complexity of Type C calls, containing multiple components and biphonations present, in comparison to Type B1 and B2 calls comprising single component calls with no biphonations, can be seen in Figure 4.18.

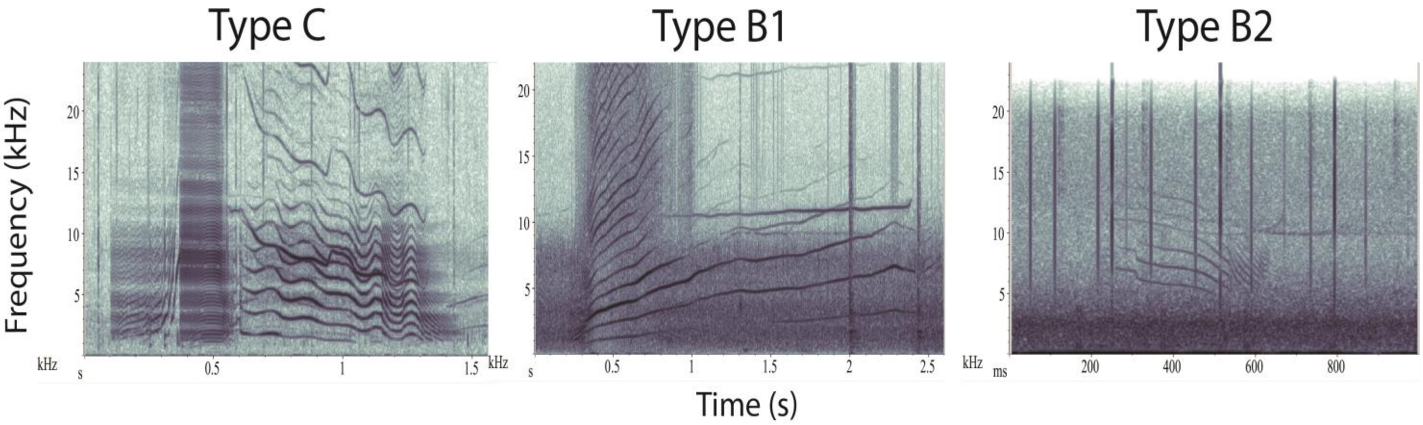

Figure 4.18 Spectrograms of examples of calls of each Antarctic ecotype recorded during this study. Type C calls recorded in McMurdo Sound, Ross Sea, Antarctica 2012-2013, see Chapter 3. Type B1 and Type B2 calls recorded off the Antarctic Peninsula, between 2009 -2018.

4.3.7 Similarity of Call Types Across Antarctic Ecotypes

Acoustic divergence of call repertoires between Antarctic ecotypes B1, B2 and C was evident from quantitative analysis. Following this, similarity in call types of Antarctic ecotypes was examined based on the aural and structural characteristics of calls; i.e., a qualitative analysis. Across Antarctic ecotypes B1, B2 and C a total of 4 call types were found that looked similar in structure and characteristics. Three call types from Type B1 and one call type from Type B2 could be considered similar in structure with calls categorised from Type C killer whales in McMurdo Sound, Ross Sea. Similarities in the call structure amongst these calls included call duration, frequency range, number of components, biphonic calls present, and the rate of frequency modulation (Figure 4.19).

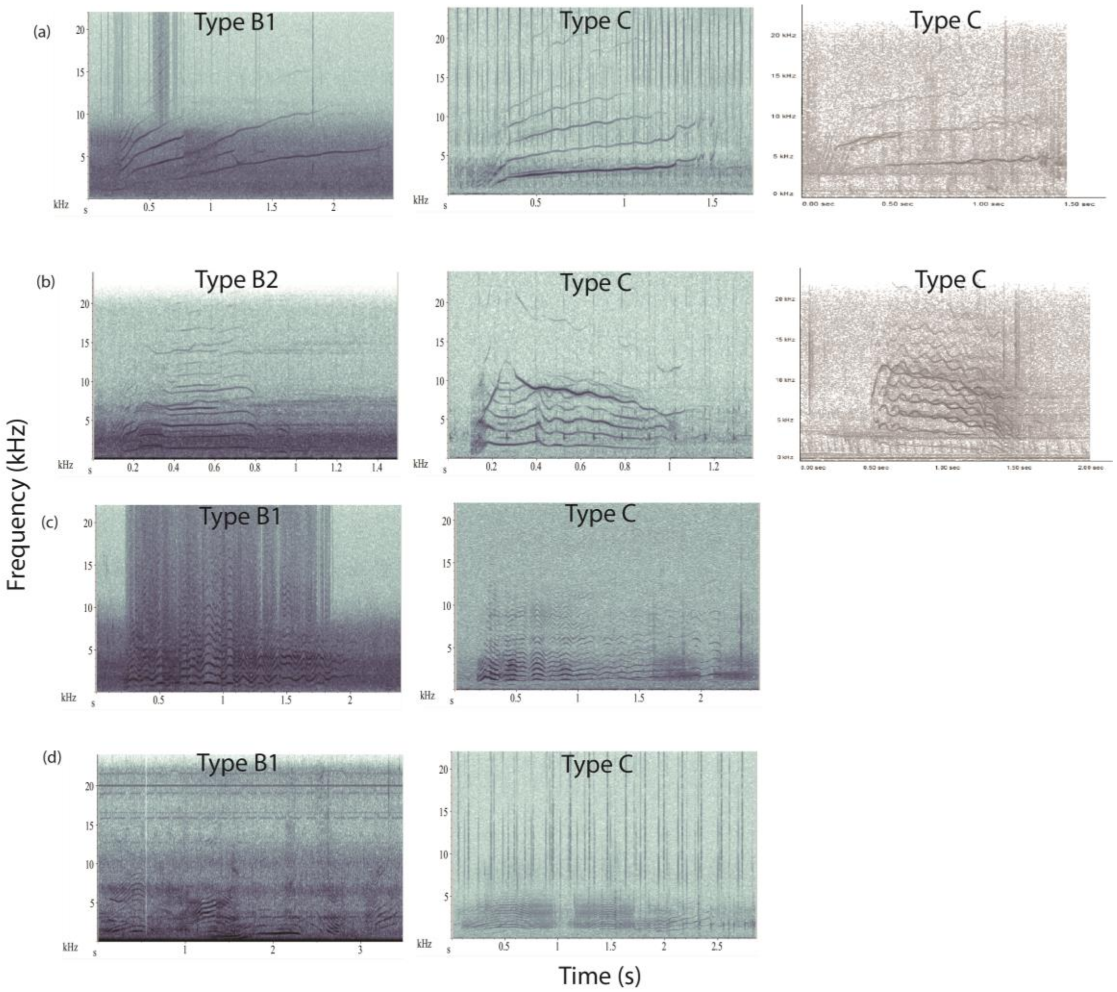

Figure 4.19. Spectrograms of call types recorded from Type B1 and B2 killer whales off the Antarctic Peninsula (*left panel fs = 48 or 44.1 kHz, NFFT = 512, 90% overlap, Hann window*) compared to similar call types recorded from killer whales in Antarctic waters: (a) Call from Type B1 killer whales recorded in Rothera, Antarctic Peninsula compared with (*from left*) call type McM7 from Type C killer whales in McMurdo Sound (Chapter 3) and AM4 call type from Type C killer whales in McMurdo Sound (Richlen & Thomas, 2008); (b) Call from Type B2 killer whales in Gerlache Strait compared with (*from left*) call type McM8 from Type C killer whales in McMurdo Sound (Chapter 3) and AM7 call type from Type C killer whales in McMurdo Sound (Richlen & Thomas, 2008); and (c) Call from Type B1 killer whales in Rothera compared

with (*from left*) McM11 from Type C killer whales in McMurdo Sound (Chapter 3); and (d) Call from Type B1 killer whales in Paradise Bay, Antarctic Peninsula compared with (*from left*) McM12 from Type C killer whales in McMurdo Sound (Chapter 3).

4.4 Discussion

This study presents the first description of the call repertoire of Types B1 and B2 killer whales. Limited dedicated research has been undertaken on Type B killer whales in the Antarctic region, with this study being the first to investigate the acoustic behaviour of this ecotype. This study investigates acoustic divergence amongst Antarctic Type B and Type C killer whales and is the first to examine the use of call repertoire as a diagnostic tool for identifying sympatric ecotypes in Antarctic waters.

4.4.1 Categorising Calls and Vocal Repertoire

The vocal repertoires of Types B1 and B2 killer whales include whistles, burst-pulse sounds and echolocation clicks, similar to those reported from killer whales in other regions. Quantitative analysis was used to delineate call categories, with a k-means cluster analysis. Currently there is no singular method for objectively defining killer whale call types, nor is there a singular method for validating call-type categories. The majority of studies on killer whale repertoire have primarily categorised call types on the aural qualities and structural characteristics examined in spectrograms through human observers (Ford, 1991; Saulitis et al., 2005; Yurk et al., 2002), however this method has its limitations and is inherently subjective, with reduced reproducibility and criteria for categorisation not clearly being defined. Previous studies have applied quantitative techniques to validate these perceptual classification methods (Brown & Miller, 2007; Deecke et al., 1999; Sharpe, Castellote, Wade, & Cornick, 2017), with Wellard et al. (2015) undertaking a quantitative k-means cluster analysis to describe killer whale calls recorded in Australian waters. The repertoire size classified by k-means clustering in this study resulted in 12 and 8 call types defined for Types B1 and B2, respectively. This number of call types in repertoire is similar to what has been reported for other populations of killer whales in the Northern Hemisphere (Ford, 1987; Strager, 1995) but is smaller in comparison to the repertoire described for Type C killer whales in Antarctic waters presented in Chapter 3 of this thesis and also by Schall and Van Opzeeland (2017).

The maximum frequency of whistle fundamentals appears to vary substantially across killer whale populations, in contrast to what is reported for other delphinids (Ding et al., 1995). Whistle fundamental frequencies have been reported up to 36 kHz in the North Pacific region (Filatova, Ford, et al., 2012; Riesch et al., 2006; Simonis et al., 2012; Thomsen et al., 2001) and up to 74 kHz in Norwegian and Icelandic killer whales (Samarra et al., 2010). This study demonstrated that Antarctic Type B killer whales exhibit whistle frequencies well within the range of documented bandwidths across other regions, with whistle fundamental frequencies ranging up to 22 kHz. Although this fundamental frequency may in fact go higher, because 22 kHz was the Nyquist frequency of some of the equipment used throughout this study, higher frequencies could not be recorded.

Most calls documented in the repertoire from Types B1 and B2 were single component calls, with only 6.2% of calls and 1.9% of calls consisting of multi-components for Types B1 and B2, respectively. The rate of biphonic calls was also low, with Type B2 having only 3% calls with a biphonation and Type B1 displaying no biphonic calls. Biphonic calls have been reported in the repertoire of fish-eating killer whales in both the Northwest Pacific (Filatova et al., 2009) and Northeast Pacific (Foote et al., 2008), with these calls more common when animals occurred in mixed groupings consisting of members of different pods. Biphonic calls were only evident in the fish-eating ecotype Type B2 killer whales during this study, whilst no biphonations were recorded from the mammal-eating ecotype Type B1 killer whales. These seemingly 'simple' call repertoires exhibited by Type B1 and B2, with their small number of components and lack of biphonations, may be reflective of prey choice or limited sampling of groups and behaviour.

4.4.2 Call Comparison with Repertoires of Antarctic Killer Whales

A simple qualitative comparison of Antarctic ecotypes based on aural and structural characteristics of calls demonstrated a distinct difference between Types C, B1 and B2 call repertoires. Type C killer whales displayed a more complex call structure with a high number of biphonic and multi-component calls. Type B killer whale calls consisted mostly of single component calls and had a combined low rate of only 0.6% calls containing a biphonation.

Quantitative analysis in this study supported the observed difference in aural and structural characteristics of calls seen between Antarctic ecotypes. An initial comparison examining variables of whistles and burst-pulse sounds, independently plotted against each other across Antarctic ecotypes B1, B2 and C showed a clear distinction between ecotypes, with the largest divergence appearing at the measurement of number of components. Here it was evident that Type C killer whales differ acoustically from B1 and B2 when considering this variable, along with variables such as duration and bandwidth.

The MANOVA performed on the 11 and 10 features of whistles and burst-pulse sounds, respectively, also supported evidence of acoustic divergence across Antarctic ecotypes B1, B2 and C. The largest separation between all the ecotypes was between Type C and both Type B's. Type C was the most acoustically divergent of all 3 ecotypes. Type B1 and B2 calls also showed some differentiation, with the plot showing a centralised distribution for both ecotypes B1 and B2. Lastly, an ANOVA was performed and results were analogous to what had been demonstrated in the previous tests, with strong support for three different populations. All quantitative analyses in this study demonstrated acoustic variation between Antarctic killer whale ecotypes Type B1, B2 and C.

The acoustic differences between Antarctic ecotypes are supported by similar studies from the North Pacific. Three ecotypes of killer whale occur in sympatry in the North Pacific (residents, Bigg's and offshores) based on their morphology, behaviour, and genetic differences. Studies have shown that these ecotypes differ in their vocal behaviour. Resident fish-eating killer whales are highly vocal and use stable, acoustic repertoires that define family groups (Ford, 1991; Ford & Fisher, 1983). Both offshore and resident killer whales have similar echolocation and communicative behaviour while foraging (Dahlheim et al., 2008) whilst mammal-eating Bigg's killer whales produce clicks and whistles infrequently, which is likely due to potential eavesdropping prey and used as a stealth tactic to avoid detection (Barrett-Lennard et al., 1996; Deecke et al., 2005). This clear differentiation of acoustic repertoires between ecotypes and their prey specialisation has also been seen in other regions, such as the southern Indian Ocean. Here mammal-eating killer whales limit their vocal behaviour to just a few, narrowly defined contexts and tend to be silent when hunting southern elephant seals (*Mirounga leonina*) around the Crozet Islands and produce pulsed calls after a successful attack (Guinet, 1992). These previous studies support this study's findings, where fish-eating Type C killer whales in the Antarctic region display more complex and multi-component calls, than the predominantly single component and monophonic calls of Type B1 and B2 killer whales.

Similarities in the vocal repertoires of different populations and ecotypes may also reflect their ancestry (Filatova, Deecke, et al., 2012) and can be used in combination with genetic data to better understand their phylogenetic relationships. It is likely that Type B1 and B2 killer whales are most closely related phylogenetically (Durban et al., 2017), but ecologically, Type B2 and Type C are more closely associated with their dietary behaviour of fish-eating rather than mammal-eating, although B2 killer whales are not exclusive fish-eaters and have also been observed eating penguins. Because prey preference has an impact on the call repertoire of their predator, it would be beneficial to increase the sample size of calls recorded from B2 killer whales and obtain recordings with numerous groups and differing behaviours. The lack of a complex vocal repertoire observed in Type B2 killer whales in this study may not be representative of their entire vocal output.

4.4.3 Implications for Passive Acoustic Monitoring (PAM)

The difficulty of observing killer whales in the Southern Ocean, particularly at higher latitudes in the winter months, means utilising remote listening stations is a viable way to gain distribution and occurrence data. Characterising ecotype-specific call repertoire is crucial when utilising PAM, with both remote listening stations and towed acoustic arrays, in these remote areas and attempting to identify sympatric ecotypes in the same region. Results from this study indicate acoustic differentiation between Antarctic ecotypes B1, B2 and C, with the most noticeable difference in their repertoire being call complexity and number of call components. This study suggests that acoustically identifying Type C in comparison to Type B1 and B2 is achievable, but these results do not allow discriminating between sympatric ecotypes B1 and B2. Further acoustic analysis is needed for Type B2 killer whales to allow for a full representation of the call repertoire over numerous encounters of individuals and behaviours.

4.4.1 Conclusion

This study has provided the first description on the call repertoire of Type B killer whales found in Antarctic waters and performed an acoustic comparison between the call repertoire of Antarctic ecotypes B1, B2 and C killer whales. Future research should focus on describing other Antarctic killer whale ecotypes A and D, and subsequently, investigate ecotype-specific dialect across all Antarctic killer whales.

Future research comparing sympatric Antarctic ecotypes and their vocal repertoires will ultimately allow us to passively monitor their movements, distribution and relative abundance. This is an important step towards understanding more about this species in Antarctic waters and provides valuable information for future protection and management measures.

5 The Social Structure of Killer Whales (*Orcinus orca*) in the Bremer Sub-Basin, Western Australia

Abstract

Sociality within Australian killer whale populations has never been investigated, and the unique aggregation and population in the Bremer Sub-Basin provided a first opportunity to study the social organisation of an offshore Australian killer whale community in a deep canyon environment. Investigating and quantitatively characterising the sociality of a population provides crucial insight into the drivers shaping key population processes. This study combined boat-based surveys, photo-identification and social network analysis to examine the population dynamics of killer whales (*Orcinus orca*) in the Bremer Sub-Basin, Western Australia. Data were collected over a period of 5 years with a total of 131 individual killer whales identified during 146 encounters between 2014 and 2018. Association analyses revealed a well-differentiated society, with non-random associations and some individuals forming strong and persistent associations. Two lagged association rate (LAR) models provided equal support for two association models: (1) rapid disassociations and preferred companions; and (2) preferred companions and casual acquaintances. Implications from this study warrant continuous dedicated effort in the Bremer Sub-Basin to further the understanding of ecological, social and evolutionary factors that shape the social structure of this population of killer whales.

5.1 Introduction

Social structure, defined as the content, quality and patterning of relationships among a population’s members (Hinde, 1976), is a fundamental element of the biology of a population. Social structure can affect population growth rates, distribution and genetic structure, and is often a critical factor considered in management and conservation (Whitehead, 2008a). For long-lived mammals with complex societies, understanding sociality is essential for conservation management. Studies on group stability and social organisation of wild cetaceans have been conducted on several odontocete species, including bottlenose dolphins (*Tursiops* spp.) (Baker et al., 2018; Chabanne et al., 2012; Connor et al., 2001; Gero et al., 2005; Lusseau et al., 2006), pilot whales (*Globicephala melas*) (De Stephanis et al., 2008; Ottensmeyer & Whitehead, 2003), Indo-Pacific humpback dolphins (*Sousa chinensis*), Australian snubfin dolphins (*Orcaella heinsohni*) (Parra, Corkeron, & Arnold, 2011), sperm whales (*Physeter macrocephalus*) (Gero et al., 2008; Whitehead, 2003) and killer whales (*Orcinus orca*) (Baird & Whitehead, 2000; Beck et al., 2011; Esteban et al., 2016; Ivkovich et al., 2010; Parsons et al., 2009; Reisinger et al., 2017).

These studies have shown that marine mammals display highly variable social systems including both fluid and stable societies. An example of a fluid society can be found in bottlenose dolphins, whose social organisation has been described as a fission-fusion society, characterised by rapidly changing associations, but also stable associations than can remain for years between pairs (Mann, Connor, Tyack, & Whitehead, 2000). Stable societies are found in sperm whales and killer whales, where females, and sometimes males, live in stable units of maternally related individuals (Bigg et al., 1990; Christal, Whitehead, & Lettevall, 1998; Gero, Gordon, Carlson, Evans, & Whitehead, 2007).

Most information on killer whale kinship and sociality comes from the Northeast Pacific, where long-term studies have explored association patterns and population dynamics for over three decades (Bigg, 1987; Bigg et al., 1990; Ford et al., 1994). Here, two different ecotypes of killer whales live sympatrically: the resident fish-eating killer whales and the transient mammal-eating killer whales, also referred to as Bigg's killer whales. Resident and Bigg's populations show high levels of philopatry at the population and subpopulation level (Barrett-Lennard, 2000; Hoelzel et al., 1998). Both populations are shaped by matrilineal units, composed of mothers and all of their male and female offspring (Bigg et al., 1990). Some social dispersal is observed in mammal-eating killer whales, whilst there is no dispersal of either sex in the fish-eating population (Baird & Whitehead, 2000). In these populations, associations are based on kinship and the social structure is characterised by stable hierarchically structured social units. However, this is not the universal case for killer whales, with several other studies worldwide describing variation in sociality between and within populations of killer whales (Beck et al., 2011; Reisinger et al., 2017; Tavares, Samarra, & Miller, 2017).

A study by Beck et al. (2011) on a population of Atlantic killer whales suggested that sociality is plastic and can be modified to adapt to local ecological conditions. This comparative study of two North Atlantic populations (Iceland and Scotland), each with common ancestry but contrasting diets, revealed that although for both populations in this study the primary social tier consisted of long-term associations, the second social tier of associations between cohesive groups appeared to be more plastic and influenced by ecological selection. This variation of social structure influenced by ecological selection is likely related to prey preference and has a direct impact on group size and structure. For example, Beck et al. (2011) reported fish-eating killer whales in the North Atlantic had larger group sizes (mean ± SD = 14.8 ± 12.0) than the mammal-eating killer whales (mean ± SD = 5.8 ± 3.0). Similar results have been reported by Zerbini et al. (2007) with larger group sizes for fish-eating resident killer whales (mean ± SD = 16 ± 19.1) observed in the Pacific compared to mammal-eating transient killer whales (mean ± SD = 3.9 ± 1.9). Baird and Dill (1996) suggested that these differences in group size and stability with varying dietary preferences could be due to the fact that larger groups of mammal-hunting killer whales would incur a cost due to an increased probability of detection by prey. A study on the Marion Island mammal-eating killer whales also found variability in sociality within a population, where the social structure was illustrated by small social modules which are stable over the years, but exhibit a level of fluidity over shorter periods (Reisinger et al., 2017).

Such differences in sociality according to prey preferences, in particular between mammal-eating vs. fish-eating killer whales, make this study intriguing. This study assesses the social structure of a population of killer whales found seasonally in the Bremer Sub-Basin, with little known about this population, including their feeding ecology. Evidence thus far suggests these killer whales are generalist feeders, preying on a variety of species ranging from fish to cephalopods and marine mammals (Wellard et al., 2016), suggesting that neither model of ‘fish-eating’ or ‘mammal-eating’ population fits the Bremer killer whale community.

The killer whale population in the Bremer Sub-Basin is a relatively recently studied population with a photo-identification (photo-ID) catalogue identifying 140 individuals to date (Wellard & Erbe, 2017). Killer whales are known to occur in high numbers throughout the months of January to April every year, although no dedicated effort has occurred outside these months in this region (Bouchet et al., 2018; Wellard et al., 2016). The area the killer whales have been known to occupy makes logistics and fieldwork challenging, with the animals observed approximately 50 km offshore and with predominantly inclement weather outside of the austral summer and autumn. Legislation in 2017 declared a section of the known aggregation area as a marine park. The Bremer Marine Park covers an area of 4472 km² and water depths from 15 m to 5000 m. The Marine Park is assigned IUCN category II and comprises two zones assigned under this plan: National Park Zone and Special Purpose Zone (Director of National Parks, 2018). However, this newly declared marine park does not encompass the entire range the killer whales have been observed occupying, which leaves a wide range of habitat open to potential detrimental activities, such as oil and gas exploration, increased boat traffic and habitat degradation through commercial fishing operations. The study of association patterns with respect to geographical use is valuable because differences in spatial use do not automatically lead to differences in association patterns and *vice versa*. However, if the social organisation of a population is linked to spatial use in a particular region then this has important implications for population management (Lusseau et al., 2006). This is especially relevant to geographical use of designated marine park and protected areas, such as the Bremer Marine Park.

Assessing the social structure is important, as population characteristics could lead to considerable conservation risk due to anthropogenic impacts. For example, a geographically closed population (no emigration or immigration) could be more susceptible to unexpected changes compared to an open population. Additionally, an open population with a fission-fusion society may be more adaptable to changing circumstances compared to a society characterised by discrete social clusters of strong and long-term associations, which in turn could lead to social segregation and eventual genetic differentiation. Therefore, understanding association patterns and population dynamics of the Bremer killer whale population is an important first step towards understanding the ecological, social and evolutionary factors that shape the social structure of this population, and will be beneficial in assisting future management and conservation decisions.

This study is the first to examine the social structure and association patterns in a population of killer whales found in Australian waters, using identification photographs collected over a 5-year period in the Bremer Sub-Basin. This study will further enhance our understanding of mechanisms that drive the social structure in these killer whales and will contribute to the management and conservation of this important killer whale population in Australian waters.

5.1.1 Objectives

This objectives of this study were to: (1) collect identification photographs of killer whales observed seasonally in the Bremer Sub-Basin, (2) grade photograph quality and identify individuals, (3) determine association patterns between and within the population, (3) conduct a cluster analysis to examine relationships between individual killer whales and any grouping within the population, (4) determine the number of social modules within the population, and (5) investigate temporal stability of associations in the population.

5.2 Methods

5.2.1 Study Area

The Bremer Sub-Basin is located off the southwest continental shelf of Australia and extends over an area of 11,500 km^2 in water depths of 100 to 4500 m (Exon et al., 2005) and contains numerous submarine canyons that form part of the Albany Canyons group (Figure 5.1). The Bremer Sub-Basin region is recognised as a biologically important and productive marine ecosystem, with a large number of megafaunal species using this area, including a large number of odontocetes such as killer whales (Bouchet et al., 2018; Department of Environment, 2012). Killer whales may occupy the area at any time of the year, but have been found in high numbers during the months of January to April (Wellard et al., 2015; Wellard et al., 2016).

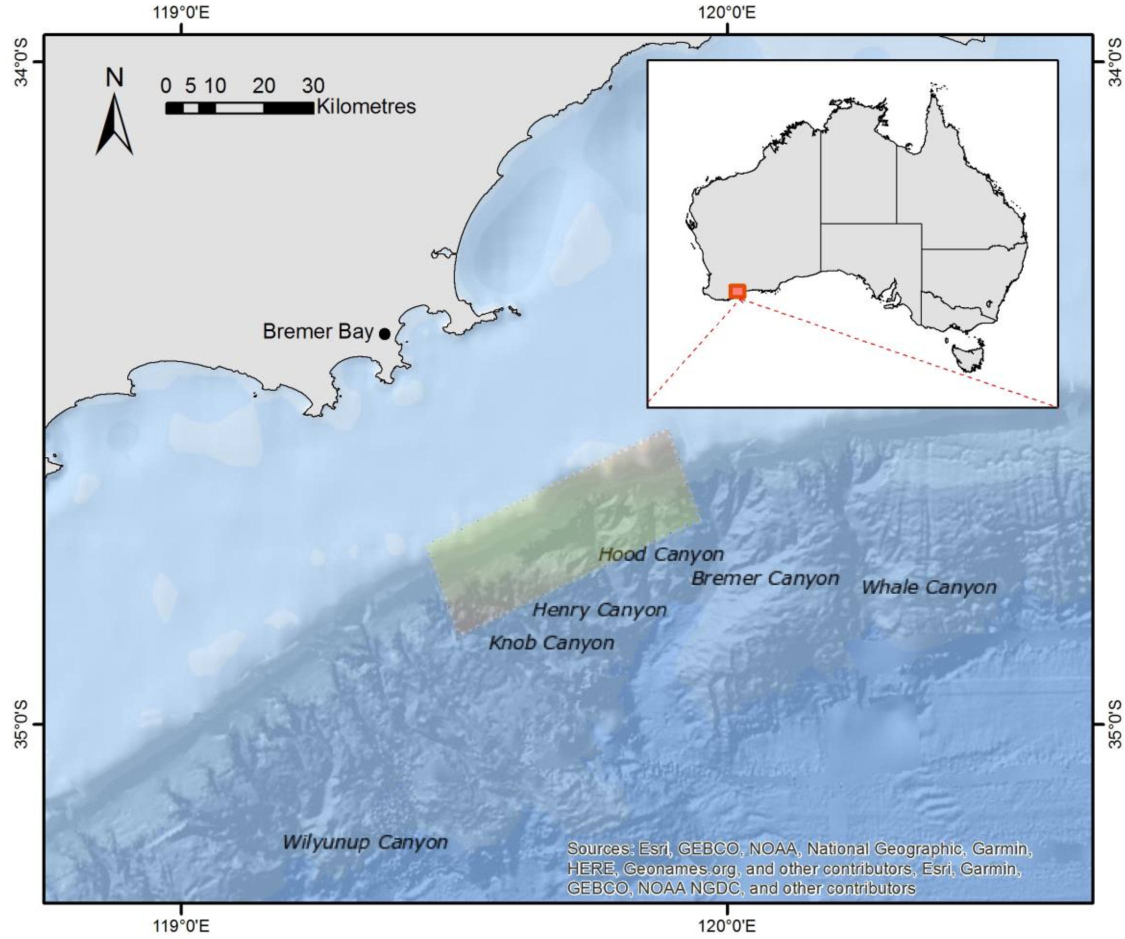

Figure 5.1 Map of the south coast of Western Australia. Area of survey effort undertaken in the Bremer Sub-Basin from 2014-2018 is highlighted. The location of Bremer Bay is indicated in the inset. Map produced using ArcMap GIS software and ESRI World Ocean Base data (ArcGIS, 2012, Redlands, California, United States).

5.2.1 Data Collection

Identification photographs data were taken during opportunistic, non-systematic vessel surveys conducted on two tourist vessels and three dedicated research vessels (Table 5.1). Surveys were focused on a 20 nautical mile radius around a point in the canyon system, centred at 34°44.30'S latitude and 119°35.55'E longitude where predictable killer whale aggregations are known to occur (Figure 5.1). Data were collected during the months of January to April each year from 2014-2018 as these months permitted the best weather for surveys.

Surveys departed from Bremer Bay, southern Western Australia and headed offshore, approximately 50 km south-east. Upon departure, the date, start time and observers for that survey day were recorded and the vessel track was recorded on a Holux RCV-3000 wireless Global Positioning System (GPS) receiver. Environmental conditions were recorded at the beginning of the survey and as conditions changed. Conditions included Beaufort Sea State (BSS; 0-12), swell height (estimated), visibility (up to 10 km), cloud cover (okta scale), glare (intensity from 0 to 3), and wind direction and velocity (estimated). Observations were conducted during daylight hours in good visibility (≥1.0 km) with an average BSS ranging from 2 to 3, and at times the BSS could reach up to 4. At least 2 experienced observers undertook continuous scanning 360° around the vessel throughout the survey. Observers were positioned at the highest vantage point on the vessel, usually the flybridge, for greatest visibility.

Table 5.1 Summary of all vessels used during surveys undertaken in the Bremer Sub-Basin between 2014 and 2018.

YEAR	VESSEL NAME	TYPE OF VESSEL	LENGTH OF VESSEL (m)	VESSEL HULL AND ENGINE
2014	*Southern Conquest*	Research Vessel	18.2	Monohull with single 1000-hp diesel engine
2015, 2016	*Cetacean Explorer*	Tourist Vessel	17	Catamaran with twin 500-hp diesel engines
2015, 2016, 2018	*Due Force*	Research Vessel	18	Monohull with single 840-hp diesel engine
2017	*Big Dreams*	Research Vessel	16.6	Monohull with single 1050-hp diesel engine
2018	*Steep Point*	Tourist Vessel	25	Catamaran with twin 1200-hp diesel engines

When a group of killer whales was detected, the GPS position of the vessel, group size and behaviour state were noted, the vessel would then move slowly towards the animals (~5.0 knots) to within 50 m where GPS position, group size and composition, behaviour state and identification photographs were taken. Behaviour was assigned to one of four behavioural states: (1) travelling, (2) foraging, (3) milling/resting or (4) socialising (Table 5.2). Group size was estimated by counting the number of individuals observed throughout the encounter, and then confirmed later during photographic analysis. Group size was recorded for three categories: the *minimum* number of killer whales counted; the *maximum* number of killer whales estimated to be in the group, and the *best estimate* for the most likely number of killer whales in the group following methodology by Kiszka, Macleod, Van Canneyt, Walker, and Ridoux (2007). The *best estimate* was used to determine group size. If the same group of killer whales was encountered more than once within a day, the observation was noted as a repeat sighting. If the group could not be confirmed as a resight, it was considered a new group. During every encounter, effort was directed towards photographing both sides of all group members using a Canon EOS 7D Mark II digital SLR camera fitted with a Canon 100 - 400mm zoom lens.

Table 5.2 Definition of killer whale behavioural states modified from Ford (1989) and Baird and Dill (1995).

Behavioural State	Definition
Travelling (T)	Killer whales moving steadily in a constant direction, respirations usually synchronous, swimming with short relatively constant dive intervals. Group spacing varies.
Foraging (F)	Killer whales seen with direct evidence of feeding, i.e. prey seen in mouths or in the water. Other indications of feeding and foraging include changes in direction, high-speed swimming with direction, and erratic swimming and diving. Large numbers of birds may also be observed either diving or with food in their mouths.
Milling (M)/ Resting (R)	Killer whales engaged in slow movements or 'logging' at the surface. There is little surface-active behaviour (e.g. breaching or tail-slapping) observed during this behavioural state. Both milling and resting are included in this category.
Socialising (S)	Killer whales engaged in a variety of interactive behavioural events, including body contact, sexual interactions, chasing, breaching or hitting the water surface with body parts.

5.2.2 Photo-identification and Photo Grading

Individuals were identified using natural markings on the dorsal fin, saddle patch and eye patch (see Figure 5.2), a proven and robust method used by numerous killer whale population studies developed by Bigg (1982). The first step taken to identify individual killer whales used features of the dorsal fin. Along the trailing edge of the dorsal fin is an area that abrades and tatters easily, resulting in identifiable tears, notches and nicks (Würsig & Jefferson, 1990). Other features on the dorsal fin that previous killer whale studies have used to help identify individuals include: shape of the dorsal fin, scrapes, scratches and wound marks, and pigment patterns (Bigg, 1982; Dahlheim, Ellifrit, & Swenson, 1997; Ellis, Ford, & Towers, 2007; Ellis, Towers, & Ford, 2008; Ford et al., 1994; Jourdain & Karoliussen, 2018; Samarra, Tavares, Miller, & Vikingsson, 2017; Tixier, Gasco, & Guinet, 2014; Towers, Ellis, & Ford, 2012; Würsig & Jefferson, 1990).

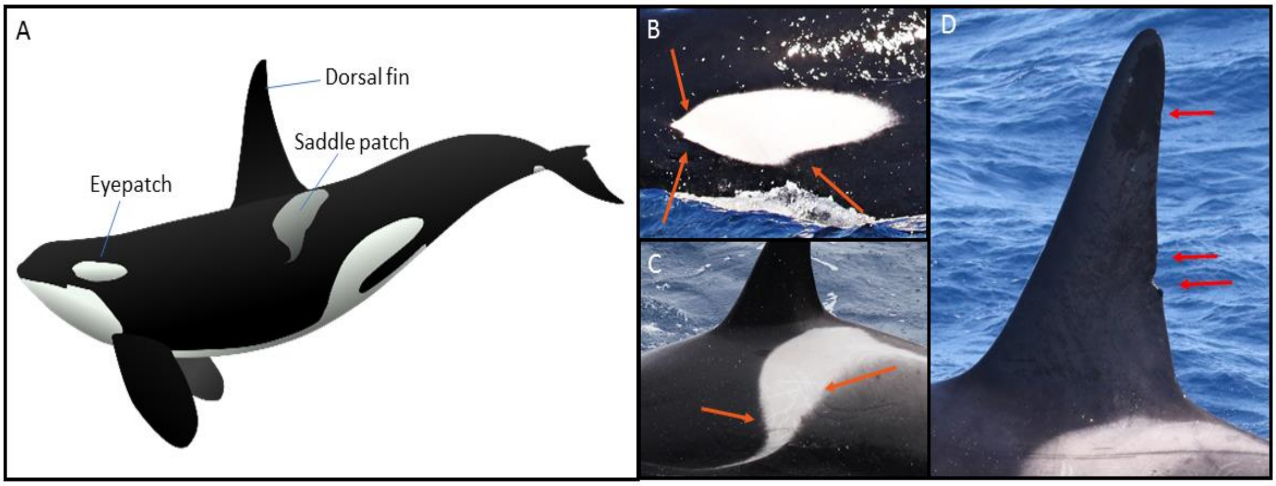

Figure 5.2 Identification photographs and drawing showing diagnostic features used to identify killer whales: (a) Drawing showing the location of identification features on the body of a killer whale (Source: Shutterstock); (b) eyepatch with arrows indicating the unique shape, (c) saddle patch with arrows showing scarring and shape, (d) dorsal fin with arrows indicating notches and nicks along the trailing edge.

Dorsal fin tears and nicks are reliable characteristics that can be used for identification of killer whales for decades (Bigg, 1987), however new additions of marks and any changing of previous marks require consideration during the identification process (see Figure 5.3). The saddle patch is the bilateral grey-white patch posterior and below to the dorsal fin and was also used as a feature for identification. The shape, scarring and degree of shading on the saddle patch can vary from animal to animal, with some individuals having a very faint patch while others are clear enough to see unique contrasting scars. The saddle patch has proven to be a key in identifying individuals in previous killer whale studies (Baird & Stacey, 1988). The white eyepatch found behind the eye was also used for identification purposes in this study. Historically, the eyepatch has not been considered an identification characteristic in killer whale studies, however variations in pigmentation, scarring and the shape of the eyepatch can distinguish between individuals (Visser & Mäkeläinen, 2000). Recent studies of killer whale photo-ID have included the eyepatch as an additional identification characteristic with it proving to be a reliable identification tool (Donnelly et al., 2016; Totterdell, 2015; Towers et al., 2019; Van Twillert, 2014; Wellard & Erbe, 2017).

Figure 5.3 Photographs of individual killer whales from Bremer Sub-Basin showing diagnostic features used for identification purposes: dorsal fin and saddle patch. Individuals pictured here: (a) WA009 "Razor" seen with distinct and persistent nicks on dorsal fin, (b) WA056 "Billie" seen with a new notch on dorsal fin in 2018, however still identifiable with two permanent nicks observed since 2015.

All photographs were examined and assigned a quality score from Q1 (unusable) to Q5 (excellent) depending on focus, lighting, relative angle to the animal, contrast between the dorsal fin and background, proportion of the dorsal fin obscured by water, and the size of the dorsal fin relative to the frame (see Table 5.4). Only photographs rated Q3 and better were considered for further analyses. This grading system was adapted from protocols used in previous cetacean photo-ID studies (Reisinger, De Bruyn, & Bester, 2011; Tosh, De Bruyn, &

Bester, 2008; Urian et al., 2015; Urian, Hohn, & Hansen, 1999). Photo-identification of each individual was undertaken by an experienced individual to ensure correct identification. If any uncertainty existed, a second examiner reviewed the image and if there was still uncertainty then the photograph was rejected. Identification photographs taken during an encounter were then compared to an existing photo-ID catalogue comprised of 140 individuals (Wellard & Erbe, 2017). Animals that could not be matched but were positively identified on more than two Q3-Q5 photographs were given a new alpha-numeric code and added to the catalogue.

Table 5.3 Photographic scoring categories (Q) used to grade killer whale images in the Bremer Sub-Basin. Images were scored from Q1 – Q5 dependent on focus, lighting, contrast between the dorsal fin and background, angle of the animal and proportion and size of the dorsal fin in the frame. Here are examples of photo scores from images of numerous individual killer whales observed in the Bremer Sub-Basin.

QUALITY SCORE	EXAMPLE
Q1	
Q2	

QUALITY SCORE	EXAMPLE
Q3	
Q4	
Q5	

For some individuals the stage of maturity and sex class could be determined. The occurrence of secondary sexual characteristics could be used to identify males and the development of these characteristics during the study period could be used to identify subadult males. Subadult males were identified by the dorsal fin 'sprouting' – a term used when the dorsal fin grows and begins to straighten and lose its curve (see Figure 5.4), with the height/width ratio exceeding 1.4 (Olesiuk et al., 1990). This typically occurs around 15 years of age (Heimlich-Boran, 1986; Matkin, Ward Testa, Ellis, & Saulitis, 2014; Olesiuk et al., 1990; Olesiuk, Ellis, & Ford, 2005). Males were considered to reach physical maturity when the dorsal fin height/width ratio equalled ~1.7, which is typically at about 21 years of age (Olesiuk et al., 1990). The sex of some individuals was verified through observation of either the genital slits or the sex-specific pigmentation. A sexually mature adult female killer whale could also be identified by the consistent close association of a calf, although this is only true for females that have calves. Individuals were classified as adults, subadults (males ca. 15-21 years old), juveniles (ca. 3-14 years old), and calves (ca. 2 years old or younger), adapted from Olesiuk et al. (1990).

Figure 5.4 Identification photographs of catalogued individual WA038 "Nani" from the Bremer Sub-Basin showing evidence of sprouting over the study period.

A discovery curve was plotted to determine photographic coverage of identified population members using cumulative number of identifications for all identified killer whales and year of sampling. This discovery curve was plotted using basic data input and did not account for population parameters, such as birth, death, immigration, or emigration, but instead was plotted for a general observation of the data input.

5.2.3 Social Analyses

Association analyses were conducted using SOCPROG 2.8 (Whitehead, 2009) run in the MATLAB (The MathWorks Inc., 2014b, Natick, Massachusetts, United States) computing environment. Association was defined as presence in the same group. A group was defined as individuals within visual range of the observer (usually within 300 m of each other), travelling in the same direction and usually engaging in the same activity. Individuals photographed in the same group at least once during a single day (the sampling period) were considered associated for the day (Whitehead, 2008a). Only individuals re-sighted at least 3 times were used to analyse the social organisation and stability of relationships. This minimum number of sightings was chosen to ensure that the sightings provide independent associations, which is consistent with several other studies of social structure in cetaceans (Ivkovich et al., 2010; Papale et al., 2017). Restrictions were also set that excluded calves in the analysis due to the tight bond of mother-calf pairs. Calves were not considered associated dyads, but these pairs were treated as a single "individual".

The strength of association between dyads was measured using the half-weight association index (HWI) (Cairns & Schwager, 1987; Whitehead, 2008a). The HWI describes the relation between two animals by indicating the proportion of time a pair of individuals is associated (ranging from 0 to 1: 0 = never and 1 = always). The HWI is calculated as:

$$HWI = \frac{x}{x + y_{AB} + \frac{1}{2}\,(y_A + y_B)}$$

Equation 5.1

Where x is the number of sampling periods in which A and B were observed associated, y_A in which only A was identified, y_B in which only B was identified, and y_{AB} in which A and B were identified but not associated. This index reduces the bias introduced when not all associates of an individual are identified in a sampling period and was best suited to this study.

Permutation tests were performed to determine whether the observed patterns of association were non-random using the method of Bejder, Fletcher, and Bräger (1998) and Whitehead (1999). To measure the quality of the representation of the association pattern and measure the strength between variables and relationships, a Pearson's correlation coefficient (*r*) was used, with *r* ~ 1 an excellent representation; *r* ~ 0.8 a good representation and *r* ~ 0.4 a fair representation.

Pearson's correlation coefficient is calculated as:

$$r = \frac{\sum XY - \frac{(\sum X)(\sum Y)}{n}}{\sqrt{\left(\sum X^2 - \frac{(\sum X)^2}{n}\right)\left(\sum Y^2 - \frac{(\sum Y)^2}{n}\right)}}$$

Equation 5.2

Where *n* is the number of pairs of scores, $\sum XY$ is the sum of the products of paired scores, $\sum X$ is the sum of *X* scores, $\sum Y$ is the sum of *Y* scores, $\sum X^2$ is the sum of squared *X* scores, and $\sum Y^2$ is the sum of squared *Y* scores.

A social differentiation coefficient (*S*) was also used to measure how varied the social system is, with social differentiations <0.3 indicating rather homogeneous societies, >0.5 well socially differentiated populations and >2.0 a population with extreme social differentiation, i.e. generally weak relationships with a few very strong relationships (Whitehead, 2008b).

5.2.4 Network Analysis

Hierarchical cluster analysis and principal coordinates analysis were used to illustrate relationships between individual killer whales and any grouping within the population. This analysis helps to examine the social structure at the community level and examine clusters of associates. In the output dendrogram resulting from the hierarchical cluster analysis, the tree shows the associations among hierarchically formed clusters. The cophenetic correlation coefficient (CCC), the correlation between the actual association indices and the levels of clustering in the diagram, were calculated to indicate the effectiveness of a hierarchical cluster analysis, with values above 0.8 indicating an effective representation (Bridge, 1993) along with a modularity >0.3 indicating that a dendrogram is an acceptable representation of input distances and its division into clusters is appropriate (Whitehead, 2009).

5.2.5 Clusters and Modality

Identifying local structure within a population may improve the understanding of the dynamics of individual affiliations and the establishment of clusters of individuals that might correspond to social units. The eigenvector-based algorithm defined by Newman (2006) was used for maximising modularity (*Q*) to detect the number of social modules within the association network. When applied to association indices, modularity is the difference between the proportion of the total association within clusters and the expected proportion. The formula for modularity is:

$$Q = \frac{\sum_{i,j} \alpha_{ij}\delta(C_i, C_j)}{\sum_{i,j} \alpha_{ij}} - \frac{\sum_{i,j} \hat{\alpha}_{ij}\delta(C_i, C_j)}{\sum_{i,j} \hat{\alpha}_{ij}}$$

Equation 5.3

where a_{ij} is the association index between individual *i* and *j*, $\hat{a}_{ij}$ is the expected value of a_{ij} assuming random associations, $\delta(C_i, C_j) = 1$ if individuals *i* and *j* are members of the same cluster, and $\delta(C_i, C_j) = 0$ if *i* and *j* are members of different clusters.

The modularity value *Q* represents how distinct the units within the community are, taking into account the difference between the proportion of expected non-random associations and the total proportion of association of clusters (Whitehead, 2008a). Modularity values (*Q*) of 0 indicate that the community structure is no stronger than would be expected by chance and values larger than zero represent deviations from randomness. A *Q* value > 0.3 indicates splits in subdivisions or clusters in the dendrogram (Newman, 2006).

Any modules identified signify strongly connected subgroups within the association network, i.e. groups of killer whales that are more highly associated with each other than with others in the population. The observed *Q* value was compared to a distribution of values from 1000 permutations of the observed data, and a Mantel matrix correlation test (1000 permutations) was used to test whether intra-social module association indices were higher than those between social modules.

5.2.6 Lagged Association Rates

Temporal trends in association were examined by plotting the changes in average association rate against time lag, termed the lagged association rate (LAR), which is useful when investigating the type of social bond (permanent, temporary, long- or short-term) present within a society (Whitehead, 2008a). LAR is an estimate of the probability that if two animals are associating at τ_0, they will also be associated at τ_1, τ_2, τ_3, etc. Standard errors were estimated by jackknife methods (Efron & Gong, 1983). Mathematical models representing simulated social structures (Whitehead, 1995) were fitted to the LAR. Model selection was carried out using the quasi-Akaike information criterion (QAIC) which compensates for over-dispersed count data and performs better for LAR. The best-fit model was chosen as that which minimised the quasi Akaike's information criterion (Burnham & Anderson, 2002). The number of bootstrap replications was set to 1,000 to calculate bootstrap-estimated standard errors of the LAR, and the final model selected was plotted against the null association rate, which is the LAR where killer whales associate randomly over time (Whitehead, 2008a).

5.3 Results

5.3.1 Survey Effort and Sightings

A total of 146 groups of killer whales were visually encountered on 91 days during more than 737 h of effort from 2014 to 2018 (Table 5.4, Figure 5.5). Group size ranged from 1 to 20 individuals, with a mean group size of 7.7 ± 5.0 *(*n=146). Behaviours observed included foraging, socialising and travelling. A total number of 71,608 photographs were analysed in this study, from which 22,196 (31%) photographs were rated Q3 and above and used in analysis.

Table 5.4 Summary of the survey effort included in the analysis of the association study of killer whales in the Bremer Sub-Basin.

Year	Survey Effort		Sampling periods (days)	Encounters	Group size (mean ± SD)
	Distance covered (nm)	Survey time (h)			
2014	427.2	51:03:00	6	11	11.4 ± 6.1
2015	1993.6	227:15:00	28	57	6.9 ± 4.5
2016	2347.7	277:45:00	36	62	6.7 ± 4.3
2017	577.2	65:27:00	7	4	12.3 ± 6.8
2018	1121.2	115:58:00	14	12	11.7 ± 5.3
Total	**6466.9**	**737:28:00**	**91**	**146**	**7.7 ± 5.0**

Subsequent to restrictions applied to association analyses mentioned previously, this resulted in a total of 73 individual killer whales sampled. Of these, 33 were of known sex, with 16 females and 17 males, with the remaining 40 individuals of unknown sex. Identified individuals included 49 adults, 14 subadults and 10 juveniles (calves were excluded as part of the restrictions set).

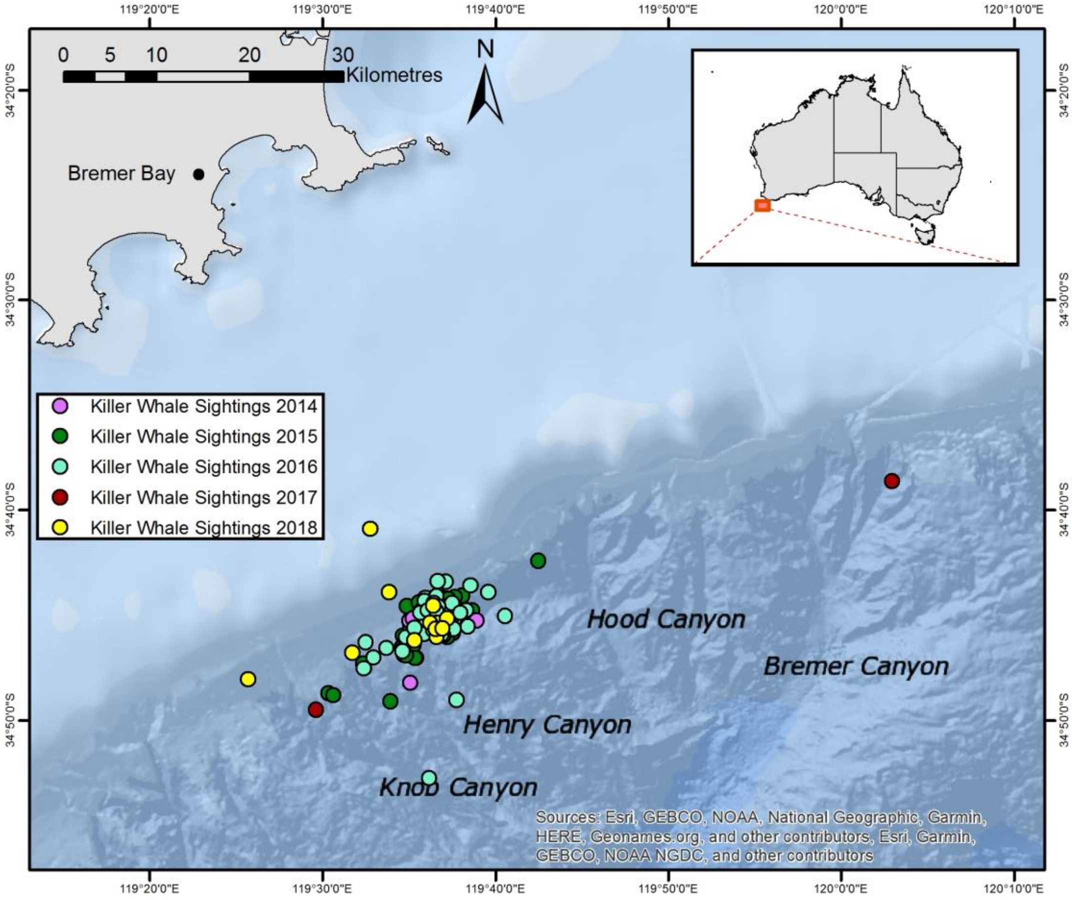

Figure 5.5 Map of the south coast of Western Australia showing killer whale sightings from 2014 – 2018 in the Bremer Sub-Basin that were included in the association analysis. Map produced using ArcMap GIS software and ESRI World Ocean Base data (ArcGIS, 2012, Redlands, California, United States).

A discovery curve was plotted with the basic data function in SOCPROG to assess photographic coverage of identified individuals using cumulative number of identifications and year of sampling (Figure 5.6). There was no clear plateau, signifying that new individuals were identified continuously throughout the survey effort (Figure 5.6). Analyses of the rate at which new individuals enter the data set suggest a population size >140 individuals, with an expectation for more individuals to be identified with continuous effort (Figure 5.6).

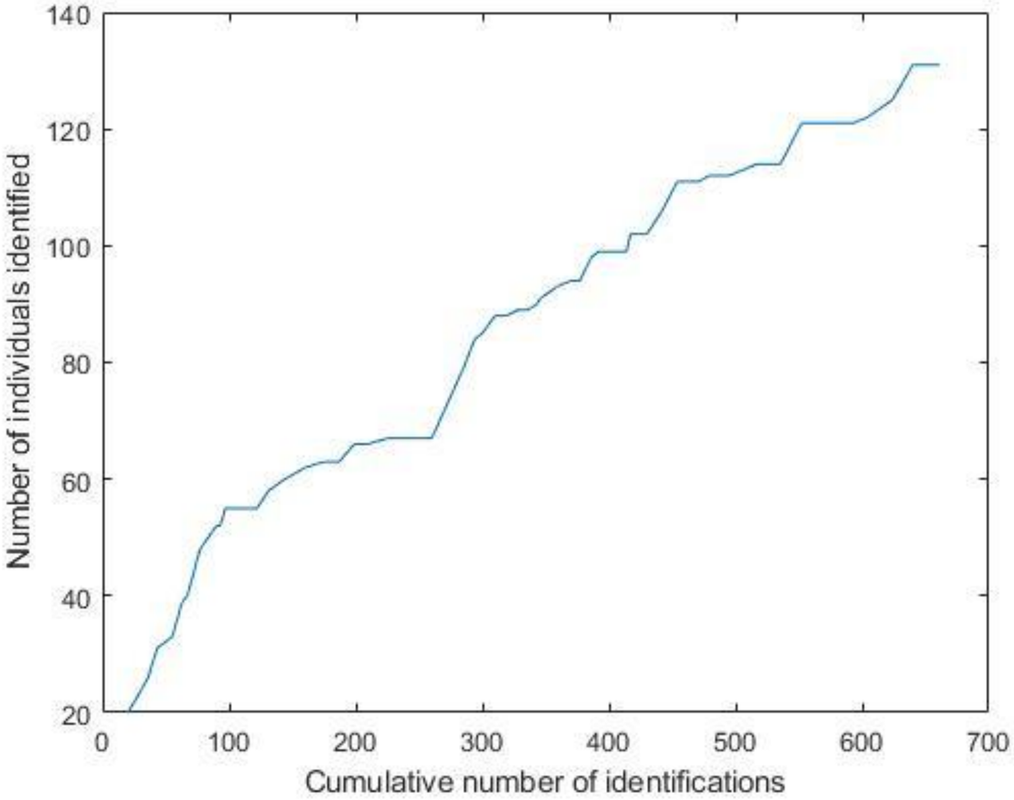

Figure 5.6 Number of identified individuals as a function of the cumulative number of identifications for all identified individual killer whales over the entire study period.

5.3.2 Association Patterns

A total of 73 individual killer whales over 67 sampling periods (days) were analysed. The mean number of individuals per sampling period was 10.12, and the mean number of individuals that could be identified per sampling period was 8.67. The strength of the analyses to detect true social organisation was considered adequate based on Pearson’s correlation coefficient, where the estimate of correlation between true and estimated association indices using the likelihood method was *r* = 0.503 (SE =0.023). Quantification of social differentiation using the likelihood method indicated a well-differentiated society (*S* ± SE= 1.041 ± 0.025) with some strong associations between individuals.

5.3.3 Network Analysis

The average linkage cluster analysis (Figure 5.7) had a high CCC (0.917) indicating that it was a good representation of social structure (Whitehead, 2009). The null hypothesis of random association among individuals was rejected with the SD of calculated pairwise association indices being significantly higher for the real data set than for the random data set (SD_{Real} = 0.17536, SD_{Random} = 0.15627, p = 0.0010) indicating that individuals do not associate at random.

5.3.4 Clusters and Modality

A total of 9 social modules were detected within the network by a modularity value demonstrating a meaningful community division (*Q*= 0.511; (Newman, 2006). With a Q value >0.3 required to identify separate clusters within a community, the Q value of 0.511 indicates important divisions (Figure 5.8). The Mantel matrix correlation test examining inter- and intra-social module association showed significantly higher association indices within social modules (t = 35.398, p<0.0001). The 9 social modules within the network were plotted in a network diagram, with individuals represented by nodes and associations by lines between nodes (Figure 5.9). The social network diagram shows that the modules in each cluster ranged from 2-18 individuals with 68% (n=50) of the entire community contained in 3 main cluster groups.

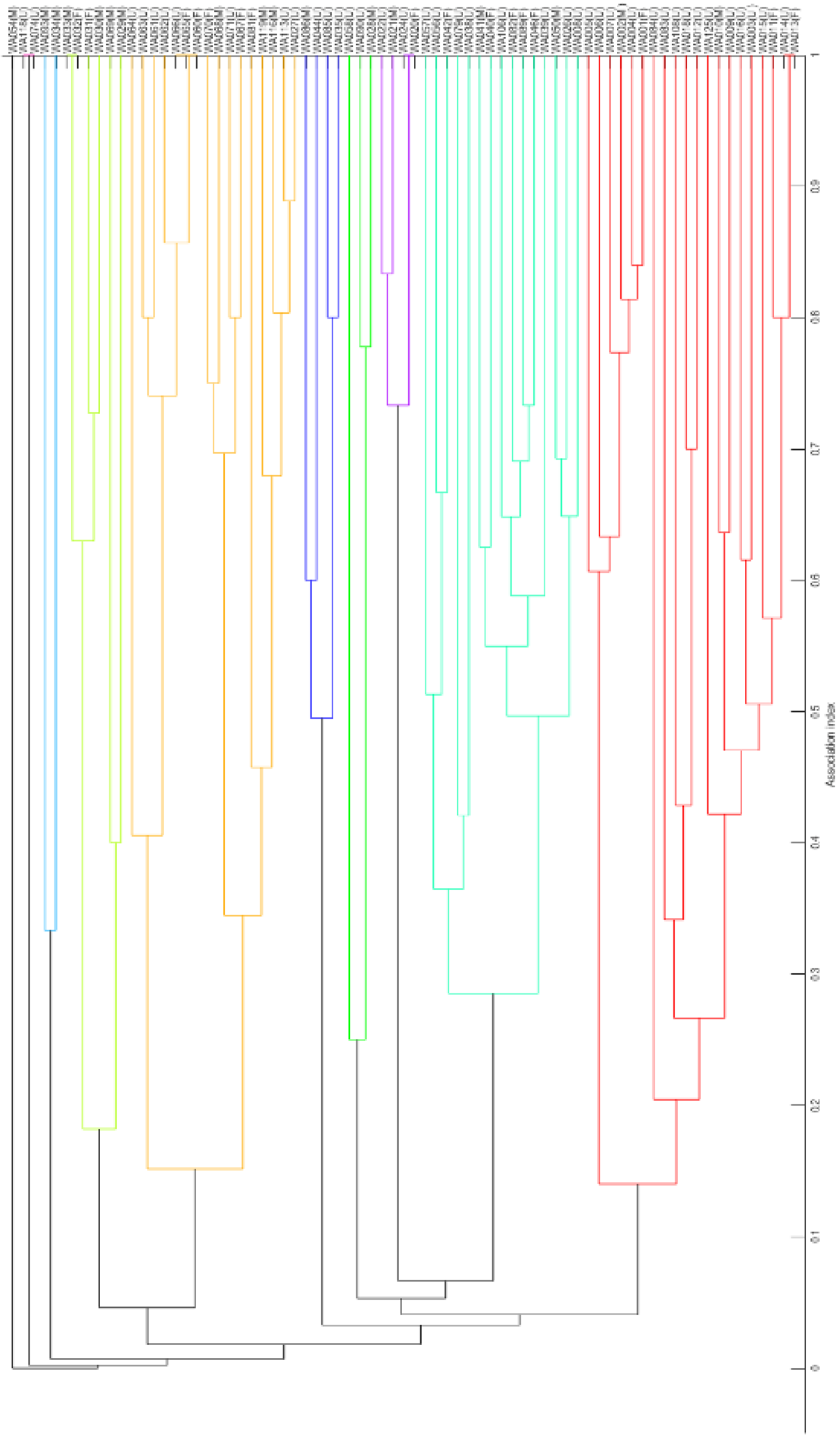

Figure 5.7 Dendrogram showing the results of a hierarchical cluster analysis of association patterns of 73 killer whales in the Bremer Sub-Basin, Western Australia. Individuals are arranged on one axis and their degree of association on the other. The alphanumeric code represents individual killer whales, along with the sex of the individual (Male/Female/Unknown).

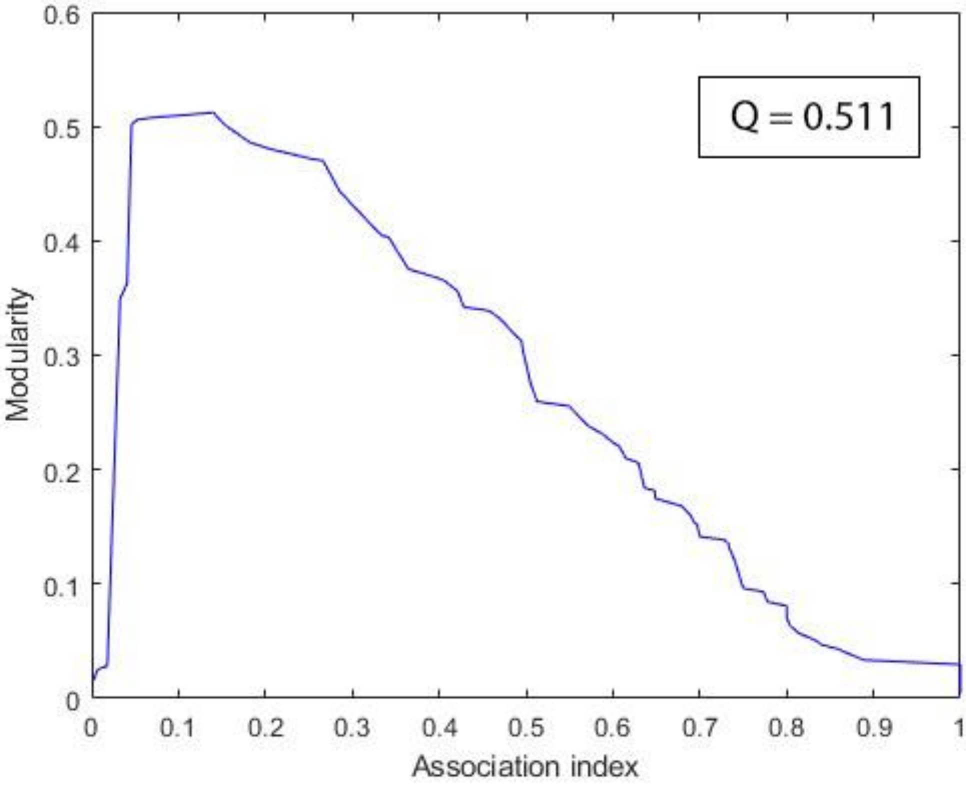

Figure 5.8 Modularity plot for killer whales in the Bremer Sub-Basin, Western Australia. A modularity (*Q*) > 0.3 is required to identify separate clusters. The *Q* value for this community was 0.511 demonstrating a useful division of the data and indicating important divisions.

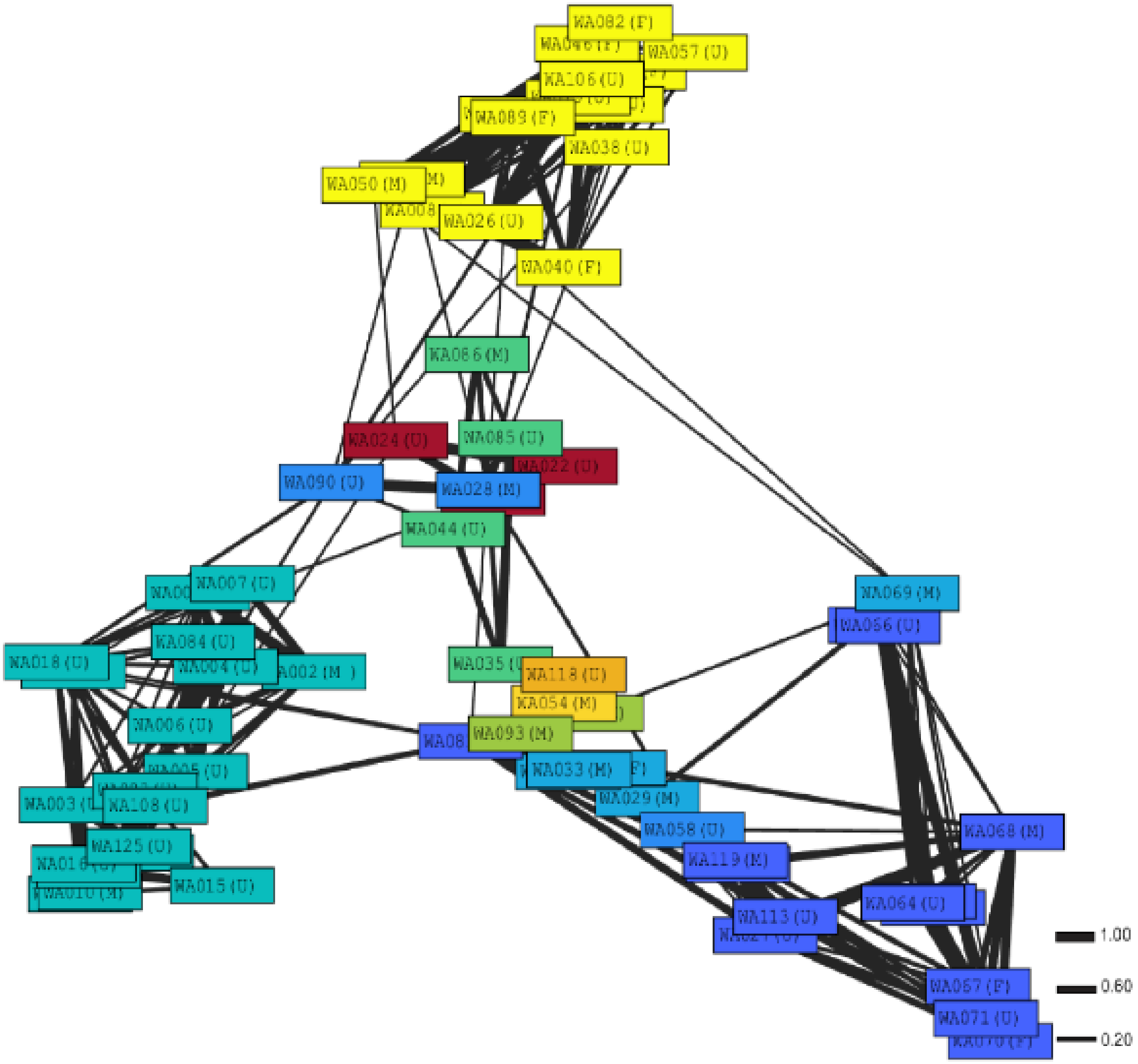

Figure 5.9 Network diagram showing the associations among killer whales in the Bremer Sub-Basin, Western Australia. Individuals are represented by nodes and associations by lines between nodes. Node colour represents the clusters identified by the modularity coefficient (Newman, 2006). Line thickness represents association strength. Alphanumeric codes within each node designate individual killer whales.

5.3.5 Lagged Association Rates

Lagged association rates (LARs) and null association rates were plotted for all killer whales in the Bremer Sub-Basin, excluding calves. Of the eight models initially fitted to the LAR, four were included in the model set fitted to LARs. The excluded models were removed because they had confounded parameters, and the remaining models were fitted. All LARs remained consistently higher than the null association rate.

Table 5.5 Mathematical models fitted to lagged association rates (LARs) describing the temporal stability of associations in the killer whale population in the Bremer Sub-Basin. Bold text indicates the model with the lowest QAIC, and thus was identified as the preferred model.

Model	Model formula	No of parameters	Start parameters	Estimates of parameters (±SE)	QAIC
Rapid disassociations + preferred companions	**a1**	**1**	**a1=0.5**	**a1 = 0.3573 (± 0.0441)**	**4286.12**
Preferred companions + casual acquaintances	a2+(1-a2)*exp(-a1*td)	2	a1=0.5 a2=0.5	a1 = 29.2093 (± 27.681) a2 = 0.3573 (± 0.044)	4288.12
Casual acquaintances	exp(-a1*td)	1	a1=0.5	a1 = 0.0022 (± 0.0939)	8242.03
Closed units	1	0	0	0	77837.38

The most parsimonious LAR model was 'rapid disassociations and preferred companions' (Table 5.5). The model 'preferred companions and casual acquaintances' also had good support from the data, with a QAIC value close in number. This was verified by plotting both models fitted to LARs and with models shown to overlap each other (Figure 5.10). Both of these models indicate there are 'preferred companions' in this community, which indicates some pairs of individuals have a preference for associating, which is constant over time. They also denote some 'rapid disassociation', which indicates some associates disassociate very quickly within one time period; and also 'casual acquaintance', who associate for some time, disassociate, and then may reassociate.

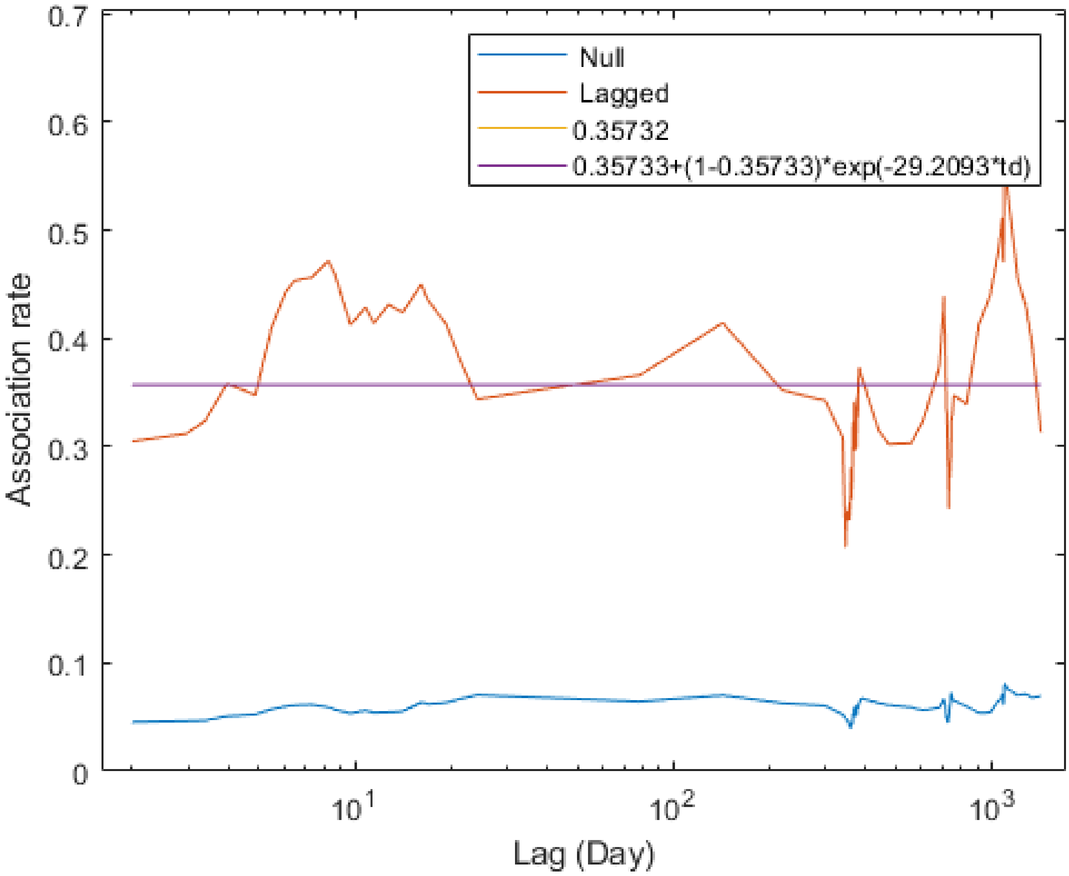

Figure 5.10 The lagged association rates (LARs) and null association rate plotted against time lag with the two best fit exponential models for the population of killer whales in the Bremer Sub-Basin, Western Australia. Both models 'rapid disassociations and preferred companions' and 'preferred companions and casual acquaintances' fit the data well and are shown to overlap on this plot. LAR curves were smoothed with moving averages of 1000 associations.

5.4 Discussion

This study was the first to investigate the social structure of killer whales in Australian waters. The analysis of association patterns between individuals showed that killer whales in the Bremer Sub-Basin do not associate randomly, but rather tend to associate with specific individuals. Evidence also suggests some fluid-fission with some individuals disassociating very quickly, within one time period, and also some casual acquaintances, who associate for some time, disassociate, and then may reassociate. This illustrates the social organisation of killer whales in the Bremer Sub-Basin is characterised by close-knit social modules of mixed sex class composition which are stable over the years, but have a degree of fluidity, i.e. fission-fusion, over shorter times. Killer whales form groups that illustrate temporally stable associations, as well as more fluid and temporally variable associations.

Living in groups is often thought to be the consequence of a trade-off between prey resource availability and predation risk, with both intrinsic (e.g. sex, relatedness) and extrinsic (e.g. resource distribution, predation risk) factors affecting sociality. In group-living mammals with reasonably low levels of predation risk, i.e. top predators such as killer whales, degrees of fission-fusion signify a strategy for managing temporally and spatially varying prey sources (Baird & Whitehead, 2000; Janson & Goldsmith, 1995). This is evident in the sociality of mammal-eating killer whales in the Northeast Pacific, i.e. Bigg's or 'transient' killer whales, with groups occurring in small numbers (~ 1-10 individuals) and members of both sexes dispersing from their natal group (Baird & Dill, 1996; Baird & Whitehead, 2000; Ford & Ellis, 1999). These mammal-eating killer whales have greater prey consumption rates in small groups than in larger groups, therefore dispersal from natal groups may occur as a response to decreased energetic intake related with foraging in larger groups, along with the suggestion that as group size increases, the likelihood of being detected by prey also increases (Baird & Dill, 1996). In comparison, the resident fish-eating killer whales in the Northeast Pacific show the most extreme form of restricted dispersal, with long-term studies revealing a multi-level social structure with matrilineal units at the core and natal philopatry of both sexes to these units, resulting in highly stable, multigeneration matrilines that are closed to immigration (Bigg, 1987; Bigg et al., 1990).

The social structure of killer whales in the Bremer Sub-Basin appears to be most similar to those of Bigg's mammal-eating killer whales, rather than the resident fish-eating killer whales but is still not a perfect fit to either model. Moreover, comparisons of social structure of the Bremer Sub-Basin killer whale population should not be restricted to just these two populations. The feeding ecology and prey preferences of the Bremer Sub-Basin killer whales are still understudied, and at present knowledge is based on opportunistic observations in the field. Killer whales in the Bremer Sub-Basin are generalists feeding fish, cephalopods and occasionally cetaceans (Wellard et al., 2016). However, future studies into their feeding ecology and the use of isotope analysis and dietary markers would be informative.

Outside the Northeast Pacific, quantitative descriptions of social structure in killer whales have shown a variation in group size and sociality. Studies in the North Atlantic, Gibraltar, Russia, Norway and the Southern Indian Ocean (Beck et al., 2011; Esteban et al., 2016; Ivkovich et al., 2010; Jourdain et al., 2017; Reisinger et al., 2017) documented a variety of social structures, ranging from communities similar to those of the Northeast Pacific, both fish-eating and mammal-eating, to other communities, showing diversification and being neither a match for either the 'resident' or the 'Bigg's' model.

5.4.1 Sighting Rate and Association Rates

The cumulative number of identified individuals did not plateau over the study period suggesting that new individuals continued to be identified throughout the study (Figure 5.6). However, it is possible this cumulative number may overestimate the population size, as animals leaving the population through emigration, mortality or possibly misidentifications have not been accounted for. Future research should use mark-recapture methods to investigate these parameters. This result implies that future effort at this study site will most likely identify multiple new individuals indicating that dedicated sampling over sufficient temporal and relevant spatial scales will provide a clearer picture of the Bremer Sub-Basin killer whales population.

Of the total 73 killer whales included for the association analysis, approximately half were of unknown sex. Important social functions and intrinsic factors such as alloparental care, social learning, and mating strategies, together with ecological pressures and other extrinsic factors, would most likely play an important role in the development of non-random and long-term associations among individuals in the Bremer population, something that has been demonstrated before in other studies of killer whale social structure (Baird, 2000; Baird & Dill, 1996). A limitation of this study is the lack of knowledge of sex and genetic relationships of over half of the individuals in this population. However, this study provides a baseline dataset for future investigations, (such as molecular techniques) to investigate the effects of sex-specific relationships and kinship on the sociality of this population.

5.4.2 High Rates of Association and Adult Females

Like other cetaceans, the mother-calf bond in killer whales is very strong and forms the base of female social organisation (Mann et al., 2000; Whitehead, 1995). This study identified pairs of individuals with an association index of 1.0. As calves had previously been removed by the restrictions, these dyads were further investigated. Three of these pairs were thought to be mother-offspring, where the calf had been seen in close association with the adult female over the years of the study period and had since grown beyond 2 years of age and was now categorised as “juvenile” (Individuals: WA013, WA014; WA020, WA024; WA065, WA066). Through visual observations during the study period, these calves had already been deduced to be the offspring of these adult female killer whales. Though no genetic testing has yet been published, this high association rate confirmed the visual observation suppositions. One pair of individuals that had an association index of 1.0 was not a juvenile-adult female pair. Rather it was an adult female and adult male (Individuals: WA032, WA033). During the study period, these individuals have been consistently seen together, along with two other individuals. It is thought that this is a family unit, with possibly WA032 being the matriarch, which could account for WA033 being her adult male offspring. Further genetic analysis not only on these individuals, but on the entire population, will be beneficial and provide a clearer picture of social structure within this population.

5.4.3 Low Rates of Association and Adult Males

No females were documented travelling alone in this study, however males were observed spending part of their time alone. Consistent with Baird (2000), these individuals were termed “roving” males, not because they were observed to move more geographically, but because they appeared to have no strong or enduring associations with other individuals. When roving males associated with other groups, these associations were relatively short periods (e.g. hours or days). For example roving male WA054 was seen with little to no association rates with other individuals. Whilst only a few roving males were documented throughout the study period, studies on the Bigg's killer whales (Baird & Whitehead, 2000; Bigg et al., 1990) support this trend.

5.4.4 Strength of Associations and Distribution

Association analyses indicate a well-differentiated society with some individuals forming strong and persistent associations. Two LAR models were equally well supported: (1) rapid disassociations and preferred companions; and (2) preferred companions and casual acquaintances. Like other killer whale societies, those in the Bremer Sub-Basin exhibited preferential patterns of association with specific individuals throughout the entire length of the study. These non-random associations, coupled with the persistence of these associations, illustrate the occurrence of stable and long-term social bonds among killer whales in the Bremer Sub-Basin.

Along with this preferred companionship, there was also evidence of rapid disassociations and casual acquaintances in the Bremer killer whale sociality. This fluidity may result from a variety of factors: aggregation of individuals at a highly localised resource centre, temporary associations for social reasons, i.e. mating or alloparental care, a multi-level social structure with associations among social modules, or necessity or benefits of cooperative foraging. The aggregation of killer whales in the Bremer Sub-Basin is not yet fully understood. Killer whale occurrence in the Bremer Sub-Basin is most likely connected to high seasonal productivity and prey abundance, however, the environmental features accountable for driving productivity, prey abundance and ultimately killer whale habitat use, remain undetermined. This fluidity in the Bremer killer whales' social structure could in fact be governed by high productivity and prey abundance. This finding further highlights the need for continued dedicated survey effort in this region to allow accurate correlation of ecological data with distribution on the individual and group level.

5.4.5 Implications for Management

It is important to understand the use of the Bremer Sub-Basin region for this population and individual social modules as it has implications for future management and conservation decisions. Currently the Bremer Marine Park covers an area of 4472 km² and has two zones assigned under this plan: National Park Zone and Special Purpose Zone (Director of National

Parks, 2018). However, this 5-year study showed that killer whales only partly use the region within the boundaries of the Marine Park, with most sightings occurring to the West and outside of this declared protected region (see Figure 5.11).

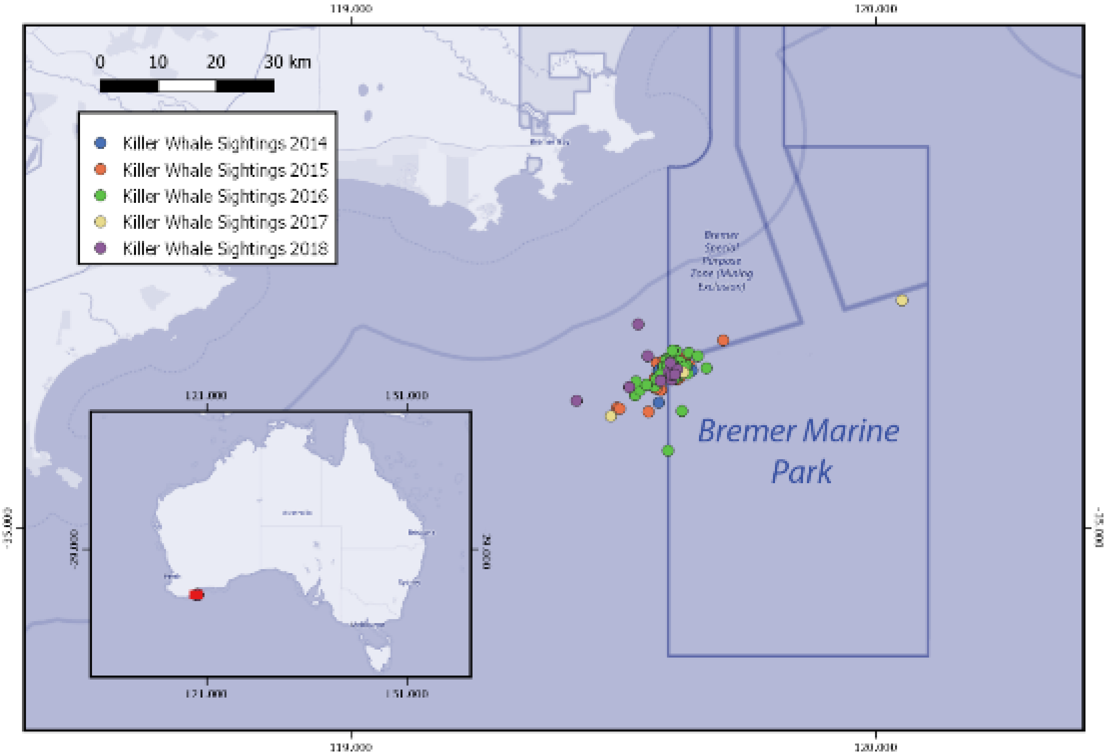

Figure 5.11 Map of killer whale sightings documented during survey effort 2014-2018 overlayed with the recently designated Bremer Marine Park, Western Australia. Maps produced using QGIS mapping software and plugin ESRI World Ocean Base 2018 (QGIS Develpment Team, 2018, Open Source Geospatial Foundation Project, Boston, Massachusetts, United States).

Marine protected areas (MPAs) in Australia are committed to the protection and conservation of biodiversity, and the protection of natural and associated cultural resources (Kenchington, Ward, & Hegerl, 2003). Declaring MPAs involves large amounts of organisation and administration from government authorities, as such, a growing trend is toward the establishment of marine sanctuaries based on their abundance of marine megafauna, with much attention being paid to desirable attributes of protected areas for marine megafauna conservation (Hooker & Gerber, 2004). The design of ecological networks of MPAs is generally based on the identification of high abundance of species of conservation concern or focal biodiversity targets. Killer whales have been declared 'Data Deficient' in Australia (Department Of Environment, 2014; Woinarski et al., 2014), and play an important ecological role as apex predators. This puts this population in high regard for consideration when declaring and defining MPAs. Threats to pelagic organisms are often site-specific or cumulative and can be lessened through spatial protection (Hooker & Gerber, 2004). This indicates that the spatial distribution and sociality of the killer whales needs to be considered. The need for quantitative objectives in the establishment of MPAs is paramount (Roff, 2009). It remains extremely difficult to quantify the proportion of a region that requires protection, especially where the aim is to protect highly mobile and wide-ranging animals like killer whales. For top marine predators, the design and implementation of MPAs needs to consider potential threats together with analyses of population viability. Incorporating behavioural data and life-history into the development of predictive habitat models can help implement more effective MPAs. This emphasises the importance of this study and the need for long-term monitoring of this population.

5.4.6 **Conclusion**

This study has provided the first quantitative examination of association patterns in a killer whale population in Australian waters. Assessing the social structure and delineating the long-term social dynamics of this killer whale community delivers an initial and crucial step towards delineating connections between the extrinsic factors shaping sociality. This study therefore provides a baseline for monitoring the future of the Bremer Sub-Basin killer whale population.

6 Killer Whale (*Orcinus orca*) Predation on Beaked Whales (*Mesoplodon* spp.) in the Bremer Sub-Basin, Western Australia

Abstract

Observations of killer whales (*Orcinus orca*) feeding on the remains of beaked whales have been previously documented; however, to date, there has been no published account of killer whales actively predating on beaked whales. Non-systematic surveys were conducted in the Bremer Sub-Basin during the months of January to April in 2014, 2015 and 2016 onboard commercial ecotourism vessels during daylight hours and variable weather conditions. Whale-watching vessels departed from Bremer Bay, southern Western Australia and headed offshore, approximately 50 km south-east of Bremer Bay. This study describes the first field observations of killer whales interacting with, hunting and predating on beaked whales (*Mesoplodon* spp.) on four occasions during 2014, 2015 and 2016 in the Bremer Sub-Basin, off the south coast of Western Australia.

6.1 Introduction

The killer whale (*Orcinus orca*) is a global species, occurring from shallow coastal waters to deep offshore waters (Forney & Wade, 2006). They are the oceanic apex predator, feeding on a variety of vertebrate and invertebrate species, including other marine mammals, seabirds, bony fishes, sharks, squid and turtles (Jefferson et al., 1991). Prey specialisation of killer whale communities in the Northern Hemisphere has been well documented over the last four decades and can be used to distinguish between sympatric non-interbreeding populations. For example, the Northeast Pacific is home to three ecotypes: sympatric resident and Bigg's (formerly transient) communities, as well as offshore killer whales (Barrett-Lennard & Ellis, 2001; Ford et al., 1994; Ford et al., 1998). Resident and offshore ecotypes feed on fish, in the case of resident killer whales, is predominantly Chinook salmon (*Oncorhynchus tshawytscha*) (Fearnbach, Durban, Ellifrit, & Balcomb, 2011; Ford et al., 1998; Ford et al., 2010), whereas Bigg's killer whales consume almost exclusively marine mammals, with their diet including cetaceans and pinnipeds, and some seabirds and squid (Bigg, 1987; Dahlheim et al., 2008; Ford et al., 1998; Hanson & Walker, 2014).

The North Atlantic is home to three killer whale populations, referred to as population A, B and C. Population A eats predominantly fish, mainly herring (*Clupea harengus*), however has been often observed switching between fish and marine mammals — being indicative of a more generalist predator (Bisther & Vongraven, 2001; Cosentino, 2015; Foote et al., 2009; Vongraven & Bisther, 2014). Population B lives sympatrically with Population A and contains two subpopulations: a generalist feeding on fish and mammals and a specialist feeding on mammals (Beck et al., 2011; Foote et al., 2009; Foote, Similä, Víkingsson, & Stevick, 2010; Foote et al., 2011). Whereas Population C has been reported to eat fish, including bluefin tuna (*Thunnus thynnus*) (Cosentino, 2015; De Bruyn et al., 2013; Foote et al., 2011; McCordic, Todd, & Stevick, 2014; Vongraven & Bisther, 2014).

In Antarctic waters, killer whales have been split into five ecotypes: Type A, Type B1 (pack ice killer whale), Type B2 (Gerlache killer whale), Type C and Type D (Durban et al., 2017; Pitman et al., 2011). These four ecotypes appear to have specialised diets. Types A and B1 have been reported to eat other cetaceans and pinnipeds (Durban et al., 2017; Pitman & Durban, 2010, 2012; Pitman et al., 2011; Pitman & Ensor, 2003), and Type B2 have been recorded to eat penguins (Pitman & Durban, 2010). Type C has been observed to eat fish, while the diet of Type D is virtually unknown, apart from the consumption of Patagonian toothfish (*Dissostichus eleginoides*) observed during longline interactions (De Bruyn et al., 2013; Pitman & Durban, 2010; Pitman et al., 2011; Pitman & Ensor, 2003).

Research on killer whales in Australian waters has been limited. Killer whales have been recorded in all state and territory waters with higher concentrations reported off southern Australia- from southern New South Wales to western Victoria (Morrice, 2004; Mustoe, 2008), and off Western Australia, from the far south-east to mid-north coast (Pitman et al., 2015; Wellard et al., 2015). Seasonal trends in sightings in some locations may suggest fairly consistent occupancy that may coincide with aggregations of prey (Morrice, 2004).

Despite killer whales being sighted in all Australian waters, most sighting data are incidentally collected during ecotourism encounters and from commercial fishers, with limited dedicated field research. Furthermore, only one account of killer whales feeding in Australian waters has been published to date. Pitman et al. (2015) observed killer whales off Western Australia preying on neonatal humpback whales (*Megaptera novaeangliae*) during their northern migration to calving grounds. Beyond this, there have only been reports that killer whales in southern Western Australia potentially feed on the Southern Ocean sunfish (*Mola ramsayi*) (DR personal observation, unpublished) and possibly an unidentified large squid (MB and DR personal observations, unpublished). This study describes, for the first time, field observations of killer whales preying on beaked whales (*Mesoplodon* spp.) in the Bremer Sub-Basin, Western Australia, on four separate occasions during the months of February and March in 2014, 2015 and 2016.

6.2 Methods

6.2.1 Study Area and Data Collection

The Bremer Sub-Basin is an area of approximately 11,500 km^2, off the continental shelf of southwestern Australia, extending from Albany east towards Esperance. This sub-basin contains a complex system of submarine canyons with water depths ranging from 100 to 4500 m (Exon et al., 2005) (Figure 6.1). It is considered a biologically important area that attracts a myriad of species including fish, sharks, and deep-diving whales such as sperm whales (*Physeter macrocephalus*) (Department of Environment, 2012). The wider south-west marine region is further thought to be an important migratory area for humpback whales, and closer to shore, a calving area for Southern right whales (*Eubalaena australis*) (Department of Environment, 2012).

Observations were made onboard commercial ecotourism vessels during daylight hours and variable weather conditions, between January and April in 2014, 2015 and 2016. Surveys were conducted during the months of January to April each year as these months have the most favourable weather for surveys. Whale-watching vessels departed from Bremer Bay, southern Western Australia and headed offshore, approximately 50 km south-east of Bremer Bay. Vessels, *Cetacean Explorer* and *The Southern Conquest*, were operated by Naturaliste Charters and Riggs Australia, respectively (Table 6.1). A total of 141 field trips were conducted over the three field seasons in 2014, 2015 and 2016. All observations occurred in the months of February and March of these years.

Table 6.1 Summary of all vessels used during surveys undertaken in the Bremer Sub-Basin between 2014 and 2016.

YEAR	VESSEL NAME	TYPE OF VESSEL	LENGTH OF VESSEL (m)	VESSEL HULL AND ENGINE
2014	*Southern Conquest*	Research Vessel	18.2	Monohull with single 1000-hp diesel engine
2015, 2016	*Cetacean Explorer*	Tourist Vessel	17	Catamaran with twin 500-hp diesel engines

For each encounter, attempts to photograph all of the killer whales present were made using a Canon EOS 7D Mark II digital SLR camera fitted with a Canon 100 - 400mm zoom lens, following established protocols for killer whale photo-identification (Barrett-Lennard, Matkin, Durban, Saulitis, & Ellifrit, 2011; Bigg, 1982, 1987). Individual animals were identified by a combination of features, including notches on the dorsal fin and fin shape, and differences in the eye patch and saddle patch pigmentation and shape. Species identification of beaked whales observed during encounters used feature characteristics such as beak length and shape, location and size of teeth, colouration and scarring patterns and overall size. Expert opinions were also sought on species identification of beaked whales. Figure 6.1 illustrates the area where observations were made on four separate occasions in 2014 (1 observation), 2015 (2 observations) and 2016 (1 observation).

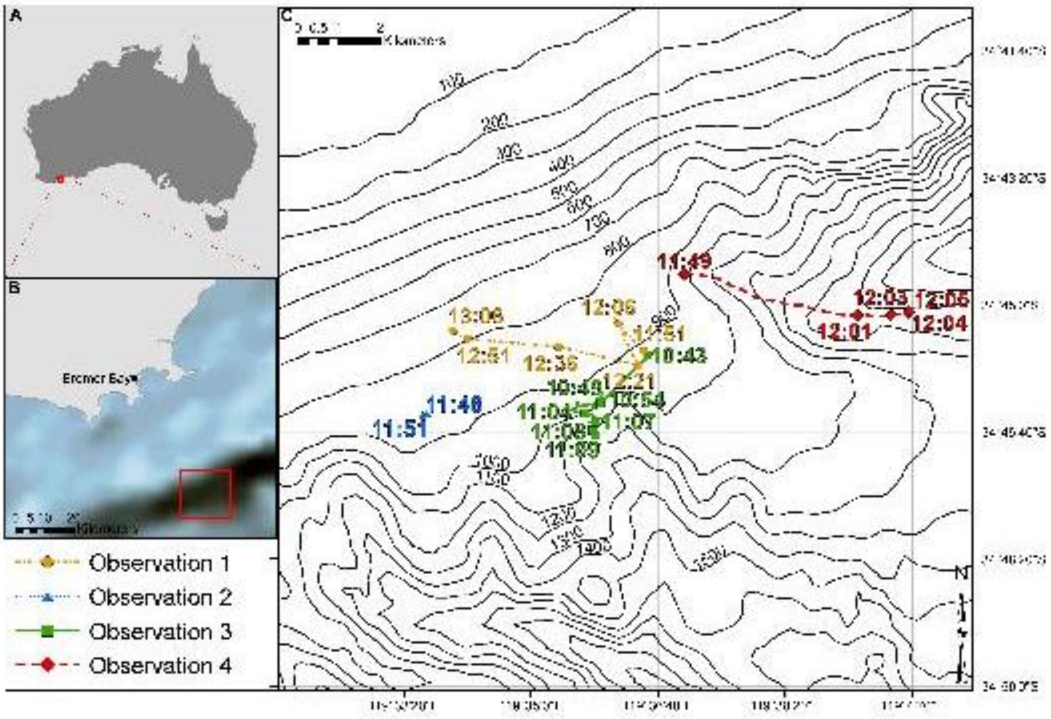

Figure 6.1 Map of the study area offshore of Bremer Bay, Western Australia indicating the locations where four separate predation events of killer whales on beaked whales occurred. Map of Australia (A) shows the location of the canyon complex in the south-west. The box in (A) is expanded in (B) presenting this region in more detail. The box in (B) surrounds the locations where predations were observed and is expanded in (C). Map produced using Natural Earth. Free vector and raster map data sourced from: naturalearthdata.com.

6.3 Results

A total of 141 field trips were conducted over the three field seasons in 2014, 2015 and 2016 with a killer whale sighting rate of 91.5%. During this survey effort, a total of four observations of killer whales interacting with, hunting and predating on beaked whales (*Mesoplodon* spp.) were noted. The median group size for killer whales initially involved in each of the four beaked whale interactions in the Bremer Sub-Basin was 10 (range 6-20). Photo-ID analysis across all observations did not identify consistent groups in the four predation events. Four individuals were recorded in multiple predations, with other individuals only recorded once, although it is likely that not all animals were photographed during the events.

6.3.1 Predation Events

Observation 1: 25 February 2014

At 11:57 WST (Australian Western Standard Time), a group of a minimum of 20 killer whales was sighted off Bremer Bay approximately 36 km from shore (34˚45’S, 119˚36’E). Following initial observations, an unidentified cetacean was sighted within 1 - 2 m of the killer whales. After several surfacings, it was identified as a mesoplodont beaked whale (*Mesoplodon* spp., Figure 6.2). Over the next 67 minutes, the beaked whale was flanked by approximately five killer whales within 1 m on each side (Figure 6.3), with a further 10 to 15 killer whales dispersed within 500 m of the group. Two other large adult male killer whales, identified by their tall dorsal fins, stayed approximately 800 m behind.

Figure 6.2 Photographs taken in the Bremer Sub-Basin, Western Australia on 25 February 2014 during observation 1: a single mesoplodont beaked whale sighted in close proximity to the group of killer whales in 2014 in the Bremer Sub-Basin, Western Australia.

Killer whales surrounding the beaked whale were suspected to be adult females or sub-adult males/females, except for one juvenile, due to their size and falcate-shaped dorsal fin. The killer whales continued to flank the beaked whale at a distance of 1 m or less, until at 12:32 WST the beaked whale broke off and headed towards our boat. The beaked whale was quickly intercepted by another killer whale that was previously with the larger, dispersed group. At 12:41 WST the beaked whale was resighted with several animals again flanking it, within 1 - 2 m on both sides. The killer whales continued to travel alongside the beaked whale at close proximity, and at 12:52 WST- one killer whale appeared to be on top of the beaked whale just behind its dorsal fin, apparently pushing the beaked whale below the surface. Upon the next surfacing, the killer whales were again flanking the beaked whale.

Figure 6.3 Photographs taken in the Bremer Sub-Basin, Western Australia on 25 February 2014 during observation 1: the beaked whale being flanked by killer whales closely on each side.

The first attack on the surface was observed at 13:00 WST, one hour after the initial sighting, although it should be noted attacks may have occurred previously underwater and not been observed. Two adult females and the juvenile charged at the flanks and the head of the beaked whale. Blood was visible on the beaked whale's back and in the water. Upon the next surfacing, the beaked whale was surrounded by five killer whales, with the juvenile at the rear. The number of birds increased, particularly flesh-footed shearwaters (*Ardenna carneipes*), with many diving and feeding in the area.

At 13:01 WST, the killer whales launched another attack, with two individuals striking the beaked whale's left flank. It could not be confirmed whether the killer whales had their mouths open or closed (*i.e.*, whether they were they biting or ramming), but blood was immediately visible in the water. During the next two surfacings, the beaked whale was visible from the rostrum to the dorsal fin, but no injuries were detected in the photos. It would appear that any potential injuries were behind the dorsal fin or on the animal's ventral side. This was concurrent with the blood seen in the water near the peduncle of the animal. Upon one of the beaked whale's last surfacings, one killer whale came into contact with the animal's left flank, but again it was unclear whether the killer whale's mouth was open. It appeared that the killer whale was directly over the beaked whale's dorsal fin and trying to submerge it. This occurred once again over the next three minutes, and other killer whales were observed underneath the beaked whale. During this time the amount of blood at the surface increased, along with the number of birds.

The beaked whale was last sighted at 13:04 WST, with the juvenile killer whale at its head and two other killer whales on top of the beaked whale, pushing it below the surface. The killer whales were then observed conducting short dives around the vicinity of where the beaked whale was last seen. An increase in seabird foraging behaviour was noted at the water surface, with at least 70 flesh-footed shearwaters and two shy albatrosses *(Thalassarche cauta)* present. At 13:16 WST, the killer whales engaged in surface-active behaviour, including tail slapping. Bird foraging activity continued on the surface, and blood was evident in the water.

No flesh was observed in the mouths of the killer whales and although blood was seen in the water and on the beaked whale, it is possible that the attack was unsuccessful attack and the beaked whale escaped, undetected by observers on the vessel. It is, however, probable that it was a successful attack, and the killer whales fed on the carcass below the surface undetected. The two adult males remained distant throughout the attack and may not have been a part of the group. The killer whales started to disperse following their bout of social behaviour, and by 13:37 WST they had left the area.

Observation 2: 8 February 2015

At 11:19 WST, a group of at least seven killer whales, consisting of adult females, sub-adult males/females and juveniles, was sighted approximately 35 km from shore (34˚46'S, 119˚33'E). The animals showed an increase in surface activity. At 11:50 WST, the birds in the area, namely Indian yellow-nosed albatross (*Thalassarche carteri*) and flesh-footed shearwaters, were photographed picking up red flesh from the surface of the water (Figure 6.4A). At 12:15 WST, the killer whales increased their travelling speed. At 12:17 WST, an unidentified beaked whale surfaced approximately 1 m from a killer whale (Figure 6.4B). This was the only time the beaked whale was observed at the surface. The beaked whale's head and body forward of the dorsal fin were the only area visible at the surface. At 12:19 WST, immediately after the sighting of the beaked whale, the killer whales porpoised through the water, and exhibited frequent surface activity. At 12:40 WST, the killer whales exhibited social behaviour, including breaching and tail slapping. At 12:44 WST, birds were again noted on the surface diving and feeding.

Figure 6.4 Photographs taken in the Bremer Sub-Basin, Western Australia on 8 February 2015 during observation 2: (a) flesh observed in the beak of an Indian yellow-nosed albatross (*Thalassarche carteri*), (b) a single beaked whale surfacing in very close proximity next to a killer whale.

Circumstantial evidence suggests that a predation event occurred, due to birds picking up flesh and a beaked whale immediately adjacent to the killer whales, although there was no photographic confirmation of flesh or bone inside the killer whale mouths.

Observation 3: 17 February 2015

At 10:40 WST, a group of at least six killer whales, comprising adult females, sub-adult males/females and juveniles, was sighted approximately 36 km from shore (34˚45’S, 119˚36’E). At 10:49 WST, a mesoplodont beaked whale was sighted within 1 m of the killer whales (Figure 6.5A). The killer whales were both alongside and beneath the beaked whale, which was last seen at 10:55 WST. At 11:04 WST, bird activity increased in the immediate area; the species included flesh-footed shearwater, Indian yellow-nosed albatross, wandering albatross (*Diomedea exulans*) and white-faced storm-petrel (*Pelagodroma marina*). At 11:07 WST, 12 minutes after the last sighting of the beaked whale, a killer whale was photographed with a carcass stripped of skin in its mouth (Figure 6.5). At 11:08 WST, the group of killer whales exhibited increased surface-active social behaviour, including breaching.

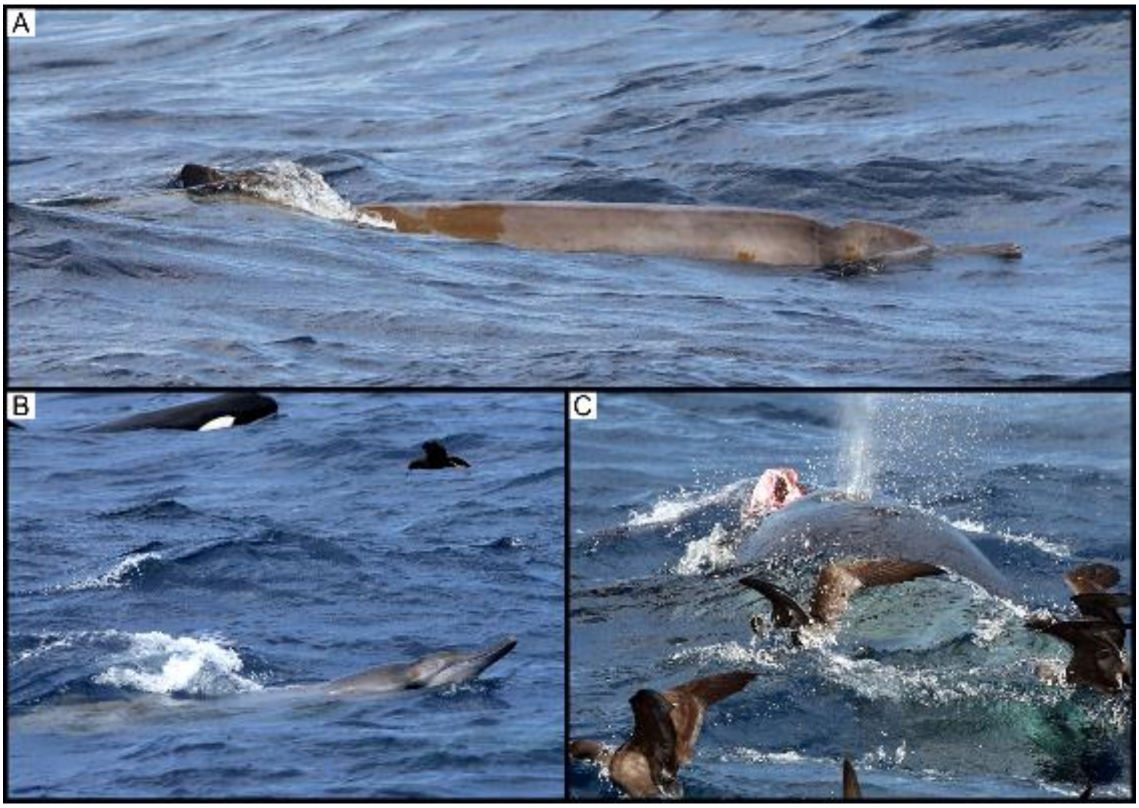

Figure 6.5 Photographs taken in the Bremer Sub-Basin, Western Australia on 17 February 2015 during observation 3: (a) a single beaked whale sighted in close proximity to the group of killer whales, (b) a single beaked whale sighted in close proximity to the group of killer whales, (c) a killer whale observed with flesh and bone in its mouth surrounded by birds foraging on the sea surface.

Observation 4: 18 February 2016

At 11:10 WST, a group of seven killer whales, comprising adult females, one adult male, sub-adult males/females and one calf, was sighted approximately 34 km from shore (34˚43’S, 119˚37’E). Animals were travelling in a south-west direction with consistent surfacing periods. At 11:43 WST, the group suddenly changed direction and headed south-east at increasing speed. At 11:49 WST, the group was traveling at a speed of approximately 18 knots, estimated by the equal speed the vessel was travelling parallel to the killer whales. The first sighting of a beaked whale occurred at 12:03 WST, roughly 5 km south-east (34˚45’S, 119˚39’E) from the original sighting. The beaked whale was porpoising with one killer whale attacking its right flank, resulting in a large bite wound (Figure 6.6). There were repeated attacks on the beaked whale from both sides by at least four killer whales, including a calf, an adult female and male, and a sub-adult male/female. Additional killer whales had now joined this group, with at least three new killer whales taking part in the attack. The beaked whale's head was sometimes out of the water during these attacks allowing for positive identification as a strap-toothed whale (*M. layardii*) based on the pigmentation pattern of the head (Figure 6.7A). The beaked whale was next seen at the surface, with considerable surface activity and splashing, and at least two killer whales alongside it. During this surface period, the killer whales stripped the skin off the body of the beaked whale from the rostrum to the dorsal fin (Figure 6.7B). At 12:04 WST, three killer whales synchronously attacked the beaked whale (Figure 6.8A). Next, the beaked whale's underside was seen completely stripped of skin and at least three killer whales dragged it underwater, leaving a large quantity of blood in the area (Figure 6.8B). This was the last sighting of the beaked whale. A HTI-96-MIN hydrophone (High Tech Inc., Long Beach, MS, USA) with built-in pre-amplifier (flat frequency response of 2 Hz to 30 kHz; sensitivity -164.1 dB re 1 V/µPa) was lowered over the side of the boat and vocalisations were recorded onto a Sound Devices 722 digital recorder (Sound Devices Corp., Reedsburg, WI, USA) sampling at 96 kHz, 24-bit. The calls detected during this recording were mostly whistles of class BC01, BC02, BC04 and transition call BC09 (Wellard et al., 2015).

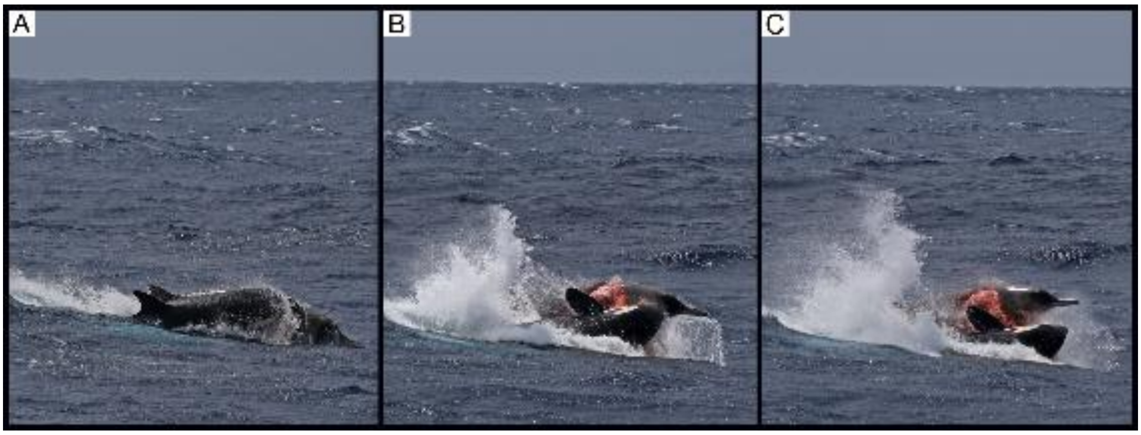

Figure 6.6 Photographs taken in the Bremer Sub-Basin, Western Australia on 18 February 2016 during observation 4: The beaked whale seen porpoising through the water with a killer whale attacking its right flank resulting in a large bite wound.

Birds, including Indian yellow-nosed albatross and flesh-footed shearwaters, were picking flesh from the surface of the water. The total number of killer whales observed in the area had increased to a minimum of 19 animals. Over the next 40 minutes, a large oil slick was seen on the surface and the killer whales slowly dispersed from the area.

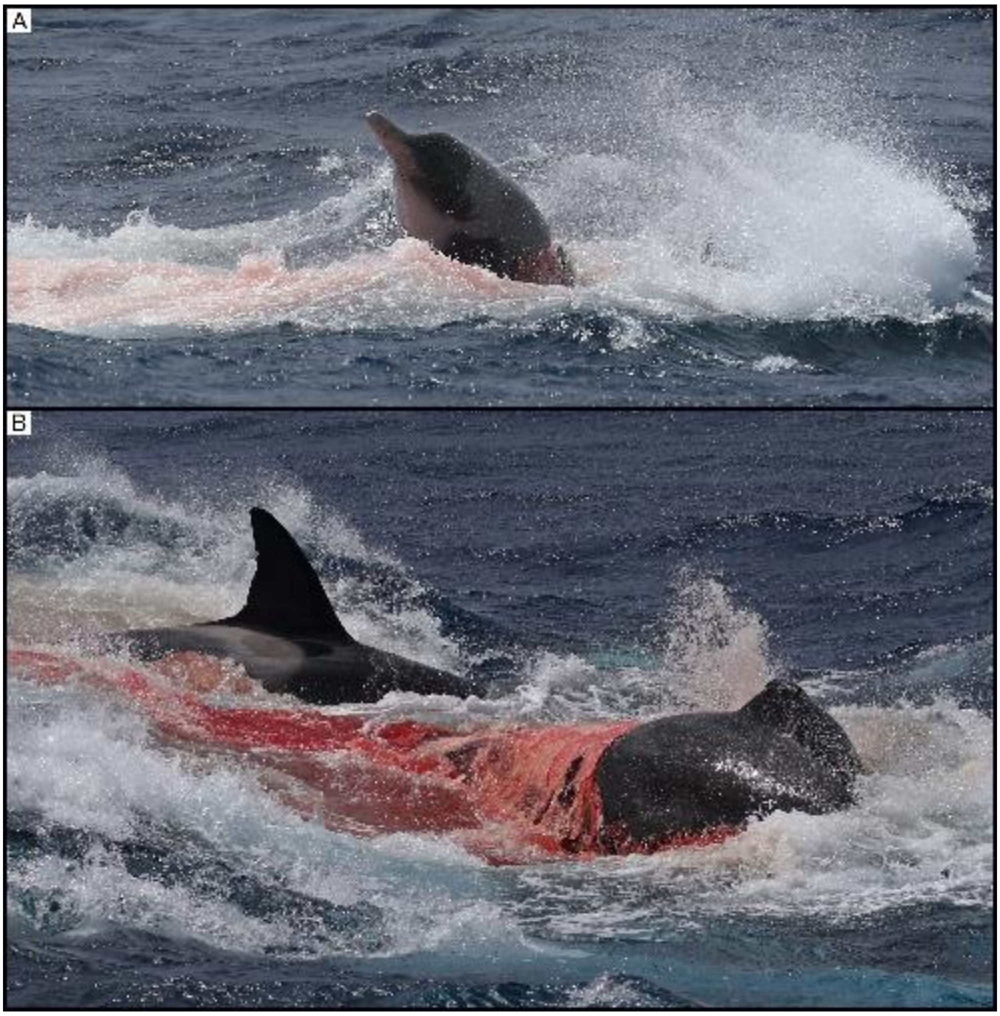

Figure 6.7 Photographs taken in the Bremer Sub-Basin, Western Australia on 18 February 2016 during observation 4: (a) the beaked whale's head clear out of the water allowing for a positive identification of strap-toothed whale (*Mesoplodon layardii),* (b) the beaked whale with its skin stripped off the body from the rostrum to the dorsal fin.

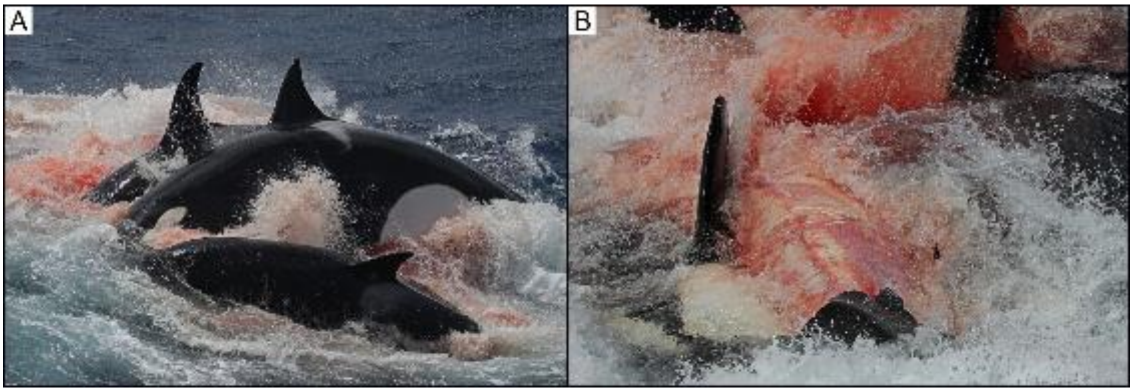

Figure 6.8 Photographs taken in the Bremer Sub-Basin, Western Australia 18 February 2016 during observation 4: (a) three killer whales synchronously attacking the beaked whale, (b) the beaked whale's underside seen completely stripped of skin as the killer whale drag the beaked whale underwater.

6.4 Discussion

Beaked whales (family Ziphiidae) are small to medium sized toothed whales (suborder Odontoceti), which are elusive and rarely sighted in Australian waters. The family Ziphiidae is one of the most wide-ranging families of cetaceans, however, knowledge about distribution and abundance of beaked whale species is limited (MacLeod et al., 2005). Sightings data indicate that they forage in deep water near the continental slope, in subsea canyons, or along steep-sided islands, and are often associated with cold-core eddy intrusions, which promote upwelling of nutrient-rich water (Amico et al., 2003; Cato et al., 2009; Ferguson, Barlow, Reilly, & Gerrodette, 2006; Gannier & Epinat, 2008; MacLeod & Zuur, 2005; Moulins, Rosso, Nani, & Würtz, 2007; Waring, Hamazaki, Sheehan, Wood, & Baker, 2001). In Australian waters, knowledge of their biology and distribution has been a result of intermittent sightings and stranding records (Groom, Coughran, & Smith, 2014; Hamilton & Lindsay, 2014a, 2014b).

The Western Australian coast has the highest species diversity (10) of beaked whale strandings compared to other Australian coasts, with 74 Ziphiidae strandings from 1940 to 2010 (Groom et al., 2014). Gray's beaked whale (*Mesoplodon grayi*) was the most frequently reported stranded species (44%), and has been involved in the largest mass stranding (seven individuals) of all beaked whales stranded in Western Australia (Groom et al., 2014).

Most beaked whales are difficult to detect and identify at sea due to their elusive behaviour, low surfacing profile and preference for deep water. Detailed examination of photographs from observations in 2014 and 2015 suggests that these animals were long-beaked species of *Mesoplodon*; most likely Gray's beaked whale and/or strap-toothed whale (R.Pitman, D.Coughran and C.Kemper, pers. comm.). Due to the absence of an erupted tooth and lack of adult colour patterning, these individuals were likely females or juveniles (Jefferson et al., 2015). The distribution of Gray's and strap-toothed beaked whales supports this identification, with both species previously documented off Western Australia, and Gray's beaked whale being the most commonly recorded species of beaked whales in Western Australian waters (Groom et al., 2014). Photographs from observation 4 show distinct diagnostic features and allow for a positive identification of a strap-toothed whale.

Killer whales feeding on beaked whale carcasses have been previously reported: a *Mesoplodon* sp. off Sri Lanka (Gemmell, McInnes, Heinrichs, & Wijeyeratne, 2015), a Cuvier's beaked whale (*Ziphius cavirostris*) in the Mediterranean (Notarbartolo di Sciara, 1987) and a northern bottlenose whale (*Hyperoodon ampullatus*) in Norway (Jonsgård, 1968). Jonsgård (1968) also reported killer whales depredating harpooned beaked whales that were alive but tied to a vessel by harpoon rope. However, there has not been a documented account of killer whales actively hunting and preying on beaked whales to date.

Additional evidence that killer whales prey on beaked whales is provided by playback experiments where pre-recorded killer whale calls were transmitted in close proximity to a tagged Blainville's beaked whale (*M. densirostris*), which initiated avoidance behaviour at a very low received sound pressure level (98 dB re 1 µPa), barely above the ambient noise level (Allen, Schanze, Solow, & Tyack, 2014; Tyack et al., 2011). This beaked whale exhibited a prolonged avoidance response demonstrated by directed swimming over an extended period of time (Allen et al., 2014; Tyack et al., 2011).

After a successful attack, mammal-eating killer whales are often observed exhibiting active social behaviour at the surface, such as pectoral fin and fluke slapping, breaching, and spyhopping (Baird, 1994; Barrett-Lennard et al., 1996; Cosentino, 2015; Deecke et al., 2005). Similar surface active behaviour was observed at the end of the predation events in the Bremer Sub-Basin. Social behaviour in killer whales is typically accompanied by vocalisations (Deecke et al., 2005; Ford, 1989). The calls detected during observation 4 were mostly whistles from four groups categorised by Wellard et al. (2015) including BC01, BC02, BC04 and transition call BC09. These sounds were recorded during both social and travelling behaviour in 2014 and 2015, however, prior predation events had not been observed, but might have been missed.

These observations indicate that only adult female killer whales, sub-adult male/female killer whales and juvenile killer whales were likely involved in attacks on beaked whales, while adult male killer whales remained at a distance behind. This is consistent with killer whale predations observed elsewhere (Arnbom, Papastavrou, Weilgart, & Whitehead, 1987; Jefferson et al., 1991; Visser et al., 2010), although adult males have been reported to take an active role in some predation events (Gemmell et al., 2015; Hancock, 1965; Pitman, Ballance, Mesnick, & Chivers, 2001; Whitehead & Glass, 1985). In 2016- one adult male was observed participating in the attack. While the role of adult males in predation events seems to vary with prey type or specific feeding events, it appears that females and sub-adults are consistently involved in marine mammal predation. Furthermore, juveniles are frequently seen to remain part of the hunting group, in close association to their mothers (Baird, 1994; Cosentino, 2015; Whitehead & Glass, 1985).

Comparing identification photographs across years did not identify consistent groups in the four predation events. Four individuals were recorded in multiple predations, either 2-3 times, with other individuals only recorded once, although it is likely that not all animals were photographed during the events. The social dynamics of this population have been investigated in this thesis (Chapter 5) but group-specific prey preferences are unknown and beyond the scope of this study, highlighting the need for long-term population monitoring in this region. Whilst the median group size for killer whales involved initially in each of the four beaked whale interactions in the Bremer Sub-Basin was 10 (range 6-20), a larger group of a further 10 or more killer whales either followed in close proximity or appeared shortly after the kill. Interestingly, in observation 4, killer whales that were not in the original sighting also joined in the attack on the beaked whale and in feeding on the carcus. Mammal-eating killer whales have been noted for their small group size, whilst fish-eating killer whales and more generalist feeders have been observed to hunt in larger groups (Baird & Dill, 1996; Beck et al., 2011; Cosentino, 2015; De Bruyn et al., 2013; Ford et al., 1998; Hoelzel, 1991; Olesiuk et al., 1990). Baird and Dill (1996) estimated that the optimal group size for North Pacific mammal-hunting killer whales is three individuals and suggested that larger groups of mammal-hunting killer whales would suffer a cost due to an increased probability of detection by prey. Other marine-mammal-eating killer whales also have been observed in small groups: two individuals for the Punta Norte, Argentina population (Hoelzel, 1991), and five for killer whales in Scottish waters (Beck et al., 2011). However, it would appear that small group size of mammal-eating killer whales is not ubiquitous, with mammal-eating Type A and B Antarctic killer whales appearing in groups of 38 and 24 respectively (Pitman et al., 2011; Pitman & Ensor, 2003), 21 Type A killer whales attacking an Antarctic minke whale (*Balaenoptera bonaerensis*) reported by Pitman and Ensor (2003) and eight killer whales in New Zealand attacking a pod of false killer whales (*Pseudorca crassidens*) reported by Visser et al. (2010).

There are other accounts of Bremer Sub-Basin killer whales potentially feeding on sunfish and an unidentified large species of squid (MB and DR personal observations, unpublished). Both are known prey species of killer whales (Gladstone, 1988; Hanson & Walker, 2014; Nishiwaki & Handa, 1958; Ryan & Holmes, 2012; Weir, Collins, Carvalho, & Rosenbaum, 2010; Yamada et al., 2007). Interestingly, specialised ecotypes, such as the North Pacific Bigg's killer whales, which are known to feed primarily on marine mammals, have been shown to also prey on cephalopods (Hanson & Walker, 2014). It remains to be determined whether the killer whales observed feeding on squid and sunfish are the same population seen feeding on beaked whales, and therefore whether Bremer Sub-Basin killer whales have a broader prey base including non-mammalian prey. If there is an abundant and suitable species of prey, then specialisation may occur, while generalist feeding could be due to the lack of predictability and abundance of any specific prey type (Baird et al., 2006; Pitman et al., 2015).

6.4.1 **Conclusion**

This study provides the first report on the feeding behaviour of the killer whales observed in the Bremer Sub-Basin, Western Australia. Very little is known about killer whales in Australian waters and descriptions of their feeding behaviour and prey preferences is generally lacking, with only one other published account to date (Pitman et al., 2015). Although the entire diet of this killer whale population is yet to be determined, these observations provide insight into what prey species constitute part of their diet. Understanding the feeding ecology of a killer whale population is important. The needs and prey preferences vary across killer whale populations worldwide. The variety of prey preferences and foraging techniques killer whales display need to be considered when implementing protection measures and population management.

7 General Discussion

7.1 Aim and Objectives of Thesis

The aim of this thesis was to increase knowledge and provide new information on the population of killer whales (*Orcinus orca*) in Australian and Antarctic waters. This was achieved through the completion of three main goals:

- Investigate the acoustic behaviour of killer whales found in Australian and Antarctic waters and describe the call repertoire of Antarctic Types B1, B2 and C, and Western Australian killer whales (Chapters 2, 3, and 4).
- Examine and quantitatively characterise the social structure of killer whales observed in the Bremer Sub-Basin, Western Australia (Chapter 5).
- Investigate the feeding behaviour of killer whales observed in the Bremer Sub-Basin and provide insight into the feeding ecology of killer whales found in Western Australian waters (Chapter 6).

To the author’s knowledge, this thesis presents the first quantitative analysis of the acoustic features of killer whale vocalisations in Australian and Antarctic Peninsula waters and presents an acoustic comparison between sympatric ecotypes in Antarctic waters. This study also provides new information on the social structure and feeding behaviour of killer whales in the Australian Bremer Sub-Basin.

7.2 The Call Repertoire of Killer Whales in the Southern Hemisphere

Studies on the vocal behaviour of different killer whale populations in the Northern Hemisphere have identified a mix of unique and shared call types and documented vocal culture, whereby different killer whale groups exhibit distinct call repertoires (Ford, 1991; Strager, 1995; Yurk et al., 2002). In the Southern Hemisphere, there has been considerably less research conducted on the call repertoires of killer whales, with only three studies reporting on killer whale vocal characteristics (Awbrey et al., 1982; Richlen & Thomas, 2008; Schall & Van Opzeeland, 2017) prior to this thesis.

Due to the highly mobile nature of killer whales, along with the large volume of water and open oceans that surround Australia and severe weather of Antarctic waters, traditional (i.e., visual) methods of studying this species are challenging. Passive acoustic monitoring is a technique that can overcome these challenges. Cetaceans are acoustic specialists and rely on sounds for communication and navigation. Visually cryptic species, like killer whales, spend the majority of their lives underwater, which means purely relying on visual methods can be ineffective. Passive acoustic techniques have the advantage that monitoring can continue in poor weather, at night-time, and under other conditions in which visual observations cannot. But for this method to be effective, a detailed description of the acoustic characteristics is necessary. Using autonomous recording systems in remote regions, such as the waters of Antarctica and offshore Australia, allows year-round data collection independent of inclement weather, limited daylight and ice coverage. Quantitatively describing the acoustic repertoire of a species and potentially identifying sympatric populations is important for establishing effective passive acoustic monitoring programmes and essential when using autonomous systems. This thesis presented the first quantitative analysis of the call repertoire of killer whales in Australian waters in the Bremer Sub-Basin, and also described the call repertoire of Type B and Type C killer whales in Antarctic waters.

In Australian waters, this study was only able to collect acoustic recordings from one population of killer whales found in the Bremer Sub-Basin, however, attempts were made to collect in other regions. The vocal repertoire of killer whales recorded in the Bremer Sub-Basin were compared to other reported vocal repertoires of killer whale worldwide (Chapter 2). Calls categorised into call type BC01 and BC02 were most similar to those recorded in Antarctica (Richlen & Thomas, 2008). Other call types, such as the multi-component and transition calls in Group BC09, were homogenous to those of the Northeast Pacific resident killer whales, where calls consist of several parts with different frequency content and modulation (Ford, 1991). This study provides the foundation of understanding the call repertoire of Australian killer whales and described basic signal structure characteristics found in the population of killer whales in the Bremer Sub-Basin.

Future studies investigating the call repertoire of other killer whales observed in Australian waters should focus on investigating population or region-specific dialect. The Bremer Sub-Basin has been identified as the most reliable site for killer whale sightings in Australian waters, with an aggregation documented annually between the months of January to April. One other site found along the Western Australian coastline may also provide potential for acoustic recordings of killer whales. During the austral winter and the humpback whale migration along the coastline of Western Australia, a small group of killer whales are known to feed primarily on neonate humpback whales located off the Ningaloo Reef (Pitman et al., 2015). This study attempted to record vocalisations of this group of killer whales but proved difficult due to the highly mobile nature of killer whales, coinciding with this large area used by this population.

Previous studies of the vocal behaviour of different killer whale populations have revealed quantitative and qualitative differences related to dietary specialisation. Killer whales in the Bremer Sub-Basin have been documented feeding on a variety of prey ranging from fish to squid and marine mammals (Wellard et al., 2016), and are therefore deemed ‘generalists’. This is in stark contrast to this group of killer whales found primarily feeding on humpback whale neonates off the Ningaloo coast. Future effort should be dedicated to collecting acoustic information from this group of killer whales to facilitate a comparison of the call repertoire of these two Western Australian populations, and potentially uncover distinct dialects of each population.

In addition to investigating the vocal repertoire of killer whales in Australian waters, I also examined the vocal repertoire of other killer whale populations in the Southern Hemisphere. This study found the call repertoire of Type C killer whales from McMurdo Sound in the Ross Sea to be complex, with the majority of calls containing multiple components and transitions from distinct pulses to burst-pulse sounds to whistles, along with almost half of all call categories containing biphonations (Chapter 3). This complex and large vocal repertoire likely reflects the feeding ecology of Ecotype C or the behavioural state during the recording, or possibly both. Type C killer whales are known to feed primarily on fish, similar to the resident killer whales in the Northeast Pacific (Ford, 1987). The call repertoire of resident killer whales in the Northeast Pacific includes a large number of call types and a high calling rate and shows distinct acoustic variability in call types. This is similar to the call repertoire of Type C killer whales described, which demonstrated a high number of calls types (29 call categories documented), a high calling rate and a clear distinction of aural and structural characteristics between each call category (see Appendix 3).

The high rate of biphonic calls in this study correlated with encounters of killer whales with larger group sizes, which is supported by studies in the Northwest (Filatova et al., 2009) and Northeast Pacific (Foote et al., 2008) that also showed biphonic calls to be found more common when animals occurred in mixed groupings of different pods. The study site at McMurdo Sound presents a unique habitat, where numerous groups of killer whales congregate at the limited breathing holes, hence resulting in numerous family groups within close vicinity of each other. These large group sizes may explain the prevalence rate of biphonic calls used to locate group members. The high rate of biphonic calls could also be related to the habitat, due in part to the changing ice coverage and closing of breathing holes. Miller (2002) suggested that differences in the directionality of the components in killer whale biphonic calls can provide information on the orientation of a caller relative to a listener. Hence it is possible that killer whales in McMurdo Sound use this directionality feature of biphonic calls to identify signaller orientation and assist in communication and organisation of individuals relative to the shifting location of the ice edge and breathing holes.

Due to the complexity of Type C calls in this study having multiple, successive and simultaneous components, basic quantitative techniques used previously (Wellard et al., 2015) were inapplicable. Qualitative techniques, such as categorising call types based on the aural qualities and structural characteristics examined in the spectrogram, were instead used for categorising calls of Type C. This qualitative methodology has been implemented by the majority of studies on killer whale repertoire (Ford, 1991; Saulitis et al., 2005; Yurk et al., 2002) and has been proven to be effective and reliable (Deecke et al., 1999; Janik, 1999; Yurk et al., 2002). My qualitative method of categorising call types may be biased towards individual perception and can only serve as a description of the vocal repertoire with the functions behind the vocalisations still unknown. However, the qualitative analysis I used to categorise the Type C call repertoire in this study was effective with support from an interobserver reliability test revealing consistent categorisation by four independent observers.

Categorisation of calls demonstrated a large vocal repertoire with 29 call type categories designated for the Type C call repertoire (Appendix 3). This high number of call types and variations categorised, along with the high rate of encounters of individuals during acoustic recordings, suggests a large portion of the repertoire of Type C killer whales from the Ross Sea may have been captured.

This is the first study to describe and report on the repertoire of this ecotype of killer whales in McMurdo Sound. This study indicates that passive acoustic monitoring can be employed to investigate the geographic range and seasonal occurrence of Type C killer whales. With the recent declaration of the Ross Sea Region Marine Protected Area, these findings are valuable and can aid in the future development of policies and management decisions.

Future research should examine the call repertoire of Type C killer whales found in other parts of Antarctic waters to investigate geographic variation in call repertoire. Effort should also be applied in the Ross Sea to record other ecotypes in this region, namely Type B killer whales, to ascertain the call repertoire of sympatric ecotypes and reinforce acoustic identification of ecotypes by characterising ecotype-specific call repertoire – a crucial component required to make passive acoustic monitoring effective.

This study described the vocalisations of Types B1 and B2 killer whales recorded off the Antarctic Peninsula (Chapter 4). Quantitative techniques were applied to categorise calls based on parameters of whistles and burst-pulse sounds rather than qualitative as previously done in Chapter 3. The reason for this was the large number of Type B killer whale vocalisations (n=2469) that were detected and subsequently rated and measured. A k-means cluster analysis grouped these calls, resulting in 20 different call categories (Appendix 4). These call categories do not relate to biological function. A functional call analysis might yield different groupings. Rather, I had thousands of calls and needed a way to summarize their physical features. K-means is a tool that allowed me to group calls based on their physical features, and then describe these features for each category. Currently there is no singular method for objectively defining killer whale call types, nor is there a singular method for validating call-type categories, with the majority of studies on killer whale repertoire primarily categorising call types based on their aural qualities and structural characteristics examined in spectrograms through human observers (Ford, 1991; Saulitis et al., 2005; Yurk et al., 2002). This method of categorising calls may serve purpose when calls are complex and exhibit multi-components but should be used with caution, as it is inherently subjective with reduced reproducibility and criteria for categorisation not clearly being defined. When calls are complex in nature with multi-components and biphonations, such qualitative analysis can be beneficial, but the call categorisations need to be supported. Undertaking an interobserver reliability test, such as the one performed in Chapter 3, can help verify and support the initial classification by human observers. The calls of Type B killer whales exhibited simple structures, with generally only one component and maximally two components. This allowed for a quantitative analysis using segment-based classification.

7.3 A Call Comparison between Antarctic Killer Whale Ecotypes B1, B2 and C

This study demonstrated acoustic variation amongst Antarctic killer whale ecotypes B1, B2 and C (Chapter 4). An initial comparison of variables of whistles and burst-pulse sounds across Antarctic ecotypes showed a clear distinction between ecotypes, with the largest divergence appearing at the measurement of the number of components. This variable where Type C killer whales differed the most from both B1 and B2, supports observations of the complexity of Type C calls, with the majority of call types (71%) being multi-component. This was in stark contrast to the percentages of Types B1 and B2: only 6.2% and 1.9% of calls consisted of multiple components, respectively. Results from a multivariate analysis of variance performed on the features of whistles and burst-pulse sounds further supported this finding by revealing that Type C was the most acoustically distinct of all three ecotypes. The call repertoires of Types B1 and B2 also showed some disparity, although not as strong as the divergence of Type C.

Acoustic variation amongst sympatric killer whale populations has also been observed in the North Pacific, where three ecotypes of killer whale occur in sympatry (residents, Bigg's and offshores) and studies revealing that these ecotypes differ in their vocal behaviour likely due to their prey choice (Deecke et al., 2005; Ford, 1987). Fish-eating killer whales are known to produce sounds prolifically in all behaviour contexts (Barrett-Lennard et al., 1996; Filatova et al., 2013; Holt et al., 2013), possibly because their prey has poor hearing abilities at the frequencies of killer whale calls. By contrast, mammal-eating killer whales prey upon whales, dolphins and pinnipeds, with sensitive underwater hearing abilities within the frequency range of killer whale vocal communication, demonstrating that prey likely shapes the vocal behaviour of the predator

(Deecke et al., 2005). These reports agree with the described call repertoire of the Antarctic Type C and Type B1 killer whales and their prey choice. Fish-eating Type C killer whales display more complex and multi-component calls than mammal-eating Type B1 who have predominantly singular component and monophonic calls. Type B2 killer whales are often seen foraging in relatively ice-free waters where they appear to feed on fish or squid, and occasionally penguins (Jefferson et al., 2015; Pitman & Ensor, 2003). With a diet containing a high proportion of fish and squid, seemingly both with poor hearing abilities at the frequency range of killer whale vocalisations, one would assume that Type B2 killer whales have a higher calling rate and a more complex call repertoire due to the reduced risk of detection by their prey. It is likely Type B1 and B2 killer whales are closely related phylogenetically (Durban et al., 2017), but ecologically, Type B2 and Type C are more similar with their diet dominated by fish rather than mammals. Future research should attempt to capture recordings of numerous groups of Type B2 killer whales in different behavioural states. The lack of complex vocal repertoire observed in Type B2 killer whales in this study may not be representative of their entire vocabulary.

Future effort in the field should focus on obtaining additional acoustic recordings of Type B2 killer whales to allow for a full representation of call repertoire. It would also be advantageous to record the acoustic behaviour of other killer whale ecotypes found in the Antarctic and sub-Antarctic region, such as Type A and Type D killer whales. The logistics of recording these ecotypes in the remote Antarctic region are challenging but obtaining these recordings would then allow a comparison of all five Antarctic killer whale ecotypes and help uncover any ecotype-specific dialect. A detailed knowledge of the call repertoire of each of the Antarctic killer whale ecotypes would help assess the habitat use, seasonal distribution and movement patterns in this remote region for each ecotype. Such data can uncover potential important information, such as critical habitat use or potential anthropogenic threats, that are crucial for conservation management.

7.4 Sociality of Killer Whales in the Bremer Sub-Basin, Western Australia

Investigating the social structure of a population provides valuable insight into the forces shaping key population processes. Prior to this thesis, there had only been one study investigating the social structure of killer whales in the Southern Hemisphere (Reisinger et al., 2017), which means the sociality in killer whale populations is mostly compared with studies conducted in the Northern Hemisphere. This study incorporated boat-based surveys, photo-identification, association analyses and social network techniques to examine the sociality of killer whales in the Bremer Sub-Basin, Western Australia.

This study showed that killer whales in the Bremer Sub-Basin did not associate randomly but preferred to associate with specific individuals (Chapter 5). There was some fluid-fission with some individuals disassociating quickly, and also some casual acquaintances, who associated for some time, disassociated, and then reassociated. This suggests that the social organisation of killer whales in the Bremer Sub-Basin is characterised by close-knit social modules which are stable over the years, but have a degree of fluidity, i.e. fission-fusion, over shorter times.

The social structure of the Bremer Sub-Basin killer whales appears to be most similar to that of Bigg’s mammal-eating killer whales, rather than the resident fish-eating killer whales but is still not a perfect fit to either model. Moreover, comparisons of social structure of the Bremer Sub-Basin killer whale population should not be restricted to just these two populations. The feeding ecology and prey preferences of the Bremer killer whales are still understudied, and at present knowledge is based on opportunistic observations in the field. Killer whales in the Bremer Sub-Basin feed on fish, cephalopods and occasionally cetaceans (Wellard et al., 2016), i.e., they are generalists. However, future studies into their feeding ecology and the use of isotope analysis and dietary markers would be informative.

Association analyses in this study indicated the occurrence of a well-differentiated society with some individuals forming strong and persistent associations. Like other killer whale societies, those in the Bremer Sub-Basin demonstrated preferential patterns of association with specific individuals throughout the entire length of the study. These non-random associations between individuals, coupled with the persistence of these associations, indicated the presence of stable, strong and long-term social relationships among killer whales in the Bremer Sub-Basin.

Along with this preferred companionship, there was also evidence of rapid disassociations and casual acquaintances in the Bremer killer whale sociality. This fluidity may result from a variety of factors: aggregation of individuals at localised resource centres, temporary associations for social reasons, i.e. mating or alloparental care, a multi-level social structure with associations among social modules, or necessity or benefits of cooperative foraging.

The aggregation of killer whales in the Bremer Sub-Basin is not yet fully understood. Killer whale occurrence here is most likely connected to high seasonal productivity and prey abundance, however, the physical and environmental features accountable for driving productivity, prey abundance and ultimately killer whale habitat use, remain undetermined. This fluidity in the killer whales social structure could in fact be governed by high productivity and prey abundance. This finding further highlights the need for continued dedicated effort in this region to allow accurate correlation of ecological data with distribution at the individual and group level.

While this thesis investigated the sociality of the Bremer killer whale population, several questions remain unanswered. Killer whale sightings are known to occur in between the months of January and April, but it remains unclear whether this population of killer whales leaves the Bremer Sub-Basin region or remains throughout the winter months. Year-round surveys have not been undertaken in this area due to restrictive weather conditions and lack of funding. To investigate the distribution of the Bremer Sub-Basin killer whales, aerial surveys and deployment of long-term loggers could overcome problematic inclement weather prohibiting vessel-based surveys. Future research investigating the spatial range of this population could help with assessing the occurrence and distribution in relation to potential anthropogenic activities or threats. It is especially important to understand the use of the region by this population and individual social modules as it has implications for future management and conservation decisions.

7.5 Technologies to Investigate Killer Whale Feeding Preferences in Australian waters

Information on the prey preferences and foraging behaviour of Australian killer whales is lacking, despite killer whales being sighted in all Australian state and territory waters. Prior to the observations by Wellard et al. (2016) (Chapter 6), there was only one published account of feeding in Australian waters. Pitman et al. (2015) observed killer whales off Western Australia preying on neonatal humpback whales (*Megaptera novaeangliae*) during the humpback whale northern migration to calving grounds. Beyond this, there have been anecdotal accounts of differing prey items, but none yet documented or published. This study presented, for the first time, field observations of killer whales preying upon beaked whales (*Mesoplodon* spp.) in the Bremer Sub-Basin, Western Australia, on four separate occasions during the months of February and March in 2014, 2015 and 2016.

Although interesting, these observations do not represent the entire diet of the killer whales observed in the Bremer Sub-Basin. Future research should look at different techniques to investigate the diet preferences of this population. Opportunities to collect fecal samples and investigate stomach contents of deceased killer whales can help to understand the diet of this species, however these opportunities are rare in Australian waters and are limited as they only reveal what the individual has ingested during its last few meals and are not representative of the typical long-term diet. Stomach content analyses are also typically biased as a result of differential rates of digestion of hard parts (Tollit et al., 1997; Yonezaki, Kiyota, Baba, Koido, & Takemura, 2003) and may not signify the diet of healthy individuals when sampled from a small number of stranded animals.

Chemical analyses using biopsy samples can provide information that may better reflect the dietary preferences of killer whales. The most common methods investigating the diet of marine mammals include using the stable isotope signatures of carbon (^{13}C) and nitrogen (^{15}N) in the epidermis and fatty acid signature analysis of blubber (Gendron, Aguiniga, & Carriquiry, 2001; Herman et al., 2005; Iverson, Field, Don Bowen, & Blanchard, 2004; Krahn et al., 2007; Matley, Fisk, & Dick, 2015; Silva et al., 2019). Stable isotope and fatty acid signature analysis are advantageous when investigating the feeding ecology of marine mammals as it is can be difficult to directly observe feeding behaviour, which is especially true of highly mobile cetaceans such as killer whales. Stable isotope analysis of ^{13}C and ^{15}N in the epidermis can be measured to examine the geographical area and trophic position at which marine mammals feed, due to marine predators incorporating chemicals from their prey to reflect the trophic level of the diet and the regions from which the prey were taken (Kelly, 2000; Krahn et al., 2007).

Due to the limited knowledge on the feeding preferences of killer whales found in Australian waters, using dietary biomarkers such as fatty acids and stable isotopes, can yield insights into the diet, the region where this population is feeding and trophic ecology of this species. While encounters with killer whales are typically rare and unpredictable in Australian waters, the area offshore from Bremer Bay appears to support a large number of killer whales during the austral summer and autumn and provides an opportunity for other technologies, such as chemical analyses used on biopsy samples, to take place.

Alongside chemical analyses, continuous survey effort and monitoring is also required to determine if the population of killer whales in the Bremer Sub-Basin employs any specialised foraging techniques and population-specific hunting strategies. Such information can only be collected during visual observations which require extensive vessel-time and financial resources. However, evaluating the trophic position and feeding preferences of apex marine predators, such as the killer whale, is crucial in understanding marine food webs.

7.6 Future Research and Management Implications

This thesis provided new insight into the populations of killer whales in Australian and Antarctic waters and provides baseline information to assist with future management and conservation decisions.

The remoteness of both offshore Australia and the Antarctic region makes access for ecosystem monitoring difficult. The recent creation of marine protected areas at two of the study sites in this research – the Bremer Marine Park and the Ross Sea Marine Region Protected Area – denotes that fundamental baseline data are needed to facilitate proper management of resources, monitor the health of the ecosystem and maintain the ecological integrity of the systems. The utility of upper-trophic-level species, or ‘top predators’, as ecosystem indicators has the potential to assist in management decisions with the results from this study.

Understanding the movements, relative abundance, distribution and habitat usage of top predators such as killer whales can help assess the ecosystem health of marine protected areas and assist the development of policies and management decisions. One method of investigating these is passive acoustic monitoring. Autonomous acoustic recorders are an economical tool for long-term monitoring of habitat usage by vocalising marine species in particular in restricted locations and during prohibitive weather when vessels cannot go to sea – a problem during the austral and Antarctic winter season.

Results from this study delivered acoustic information including the call repertoire of Antarctic killer whale ecotypes Type B1, B2 and C, and the Bremer Sub-Basin killer whales. Future research should apply these results and use the current long-term recorders that are already in place at these sites. Long-term data sets offer insights into distribution, population ecology, and human impacts, which for cryptic or highly mobile species can otherwise be difficult to achieve. By using automated detection software of killer whale calls in these long-term data sets I would be able to assess the presence of killer whales in other regions, and in particular, any marine protected areas or areas under anthropogenic pressures. Although passive acoustic monitoring can be very effective in monitoring marine mammals, there are limitations with this technique. The vocal behaviour of a species is unique and needs to be understood to determine whether acoustic monitoring will be effective. Another important consideration is the acoustic environment. Acoustic masking can occur in noisy environments, such as urban habitats or highly biodiverse regions, and the sounds of the target species can be masked, making monitoring individual species challenging. Passive acoustic approaches have long been applied to studying visually cryptic animals such as cetaceans, and although there are factors that need to be considered when using passive acoustics, such technology in combination with other techniques and emerging technologies, can help us gain a better understanding of this species in these habitats.

Along with implications of future research into the call repertoire of this species, other areas of interest and knowledge gaps that should be explored are sociality and feeding preferences, particularly for the Australian killer whales. This study presented first-time information on the social organisation and feeding behaviour on the killer whale population sighted in the Bremer Sub-Basin.

Association analyses undertaken during this research provide a first step towards understanding the links between the extrinsic factors shaping social structure and the impacts of past and future changes in social and population dynamics. Sociality within Australian killer whale populations has never been investigated, and the unique aggregation and population in the Bremer Sub-Basin allows a first chance to study the social organisation that exists in an offshore Australian killer whale community. Continued effort at this study site will also allow further observations to be obtained on their feeding behaviour and prey preferences. Understanding more about this apex predator, and its role in the marine ecosystem, is critical for the conservation of this species and for the environment in which it resides. Implications from this study warrant continuous dedicated effort at this study site to further our understanding of ecological, social and evolutionary factors that shape the social structure and feeding preferences of this population of killer whales found in the Bremer Sub-Basin.

This thesis highlights the importance of baseline data when studying an apex predator in the marine ecosystem and presents new knowledge of this species in two different regions. This research improves our understanding of vocal behaviour, sociality and feeding behaviour in the Australian and Antarctic region. Information provided by this research can be used to assist future management and conservation initiatives, particularly in relation to the newly designated marine protected areas of the Bremer Marine Park and the Ross Sea Region Marine Protected Area. Understanding the ecological niche killer whales occupy and the impact they have as an apex predator is important to understanding the ecosystem in its entirety. Future research should include continuous effort at both sites to fill knowledge gaps of this iconic species.

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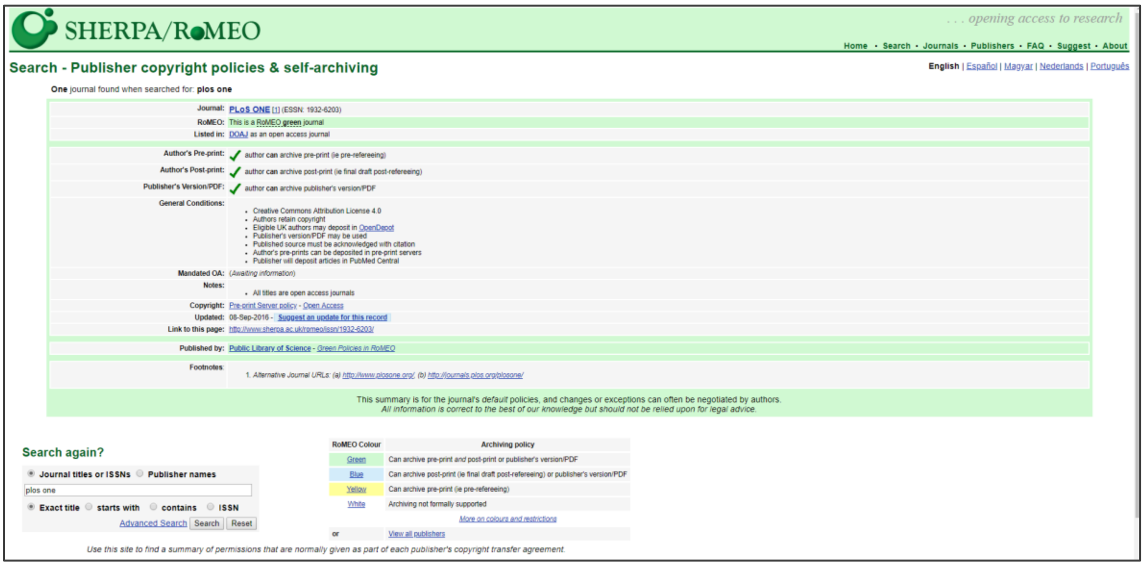

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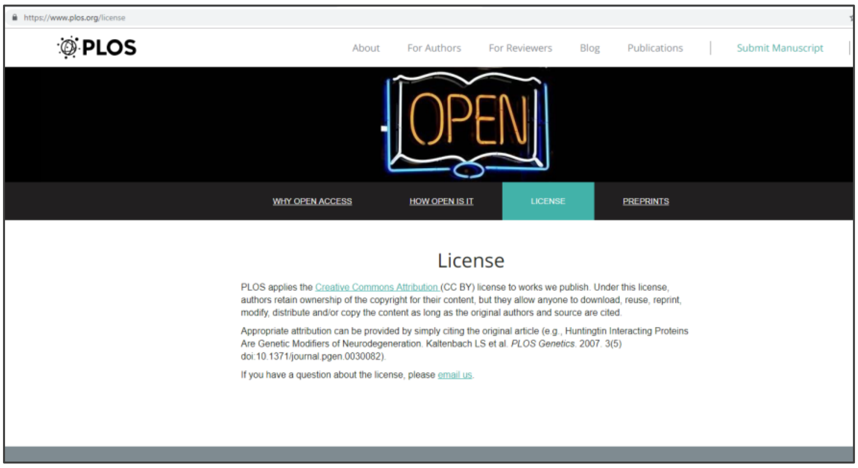

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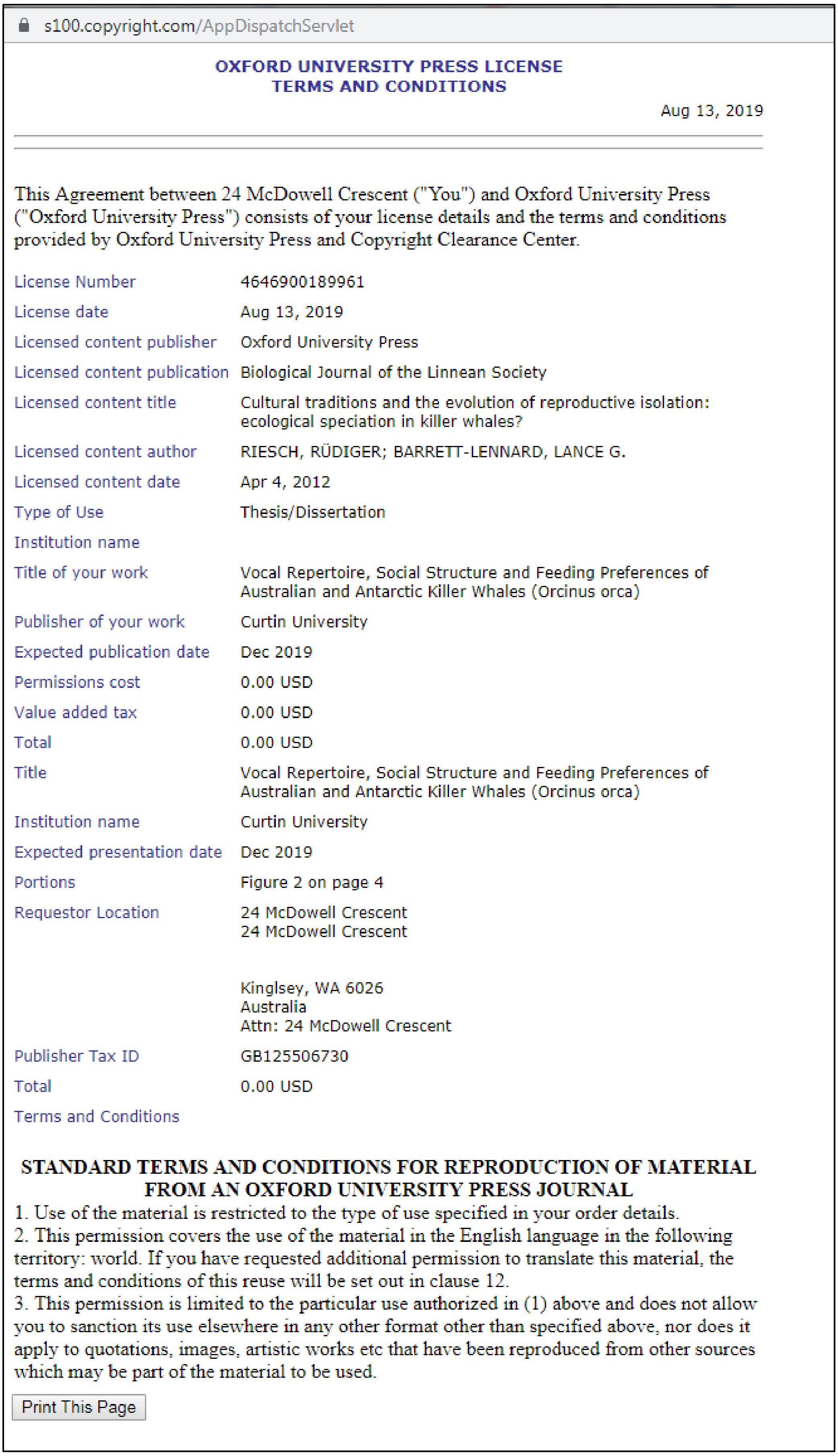

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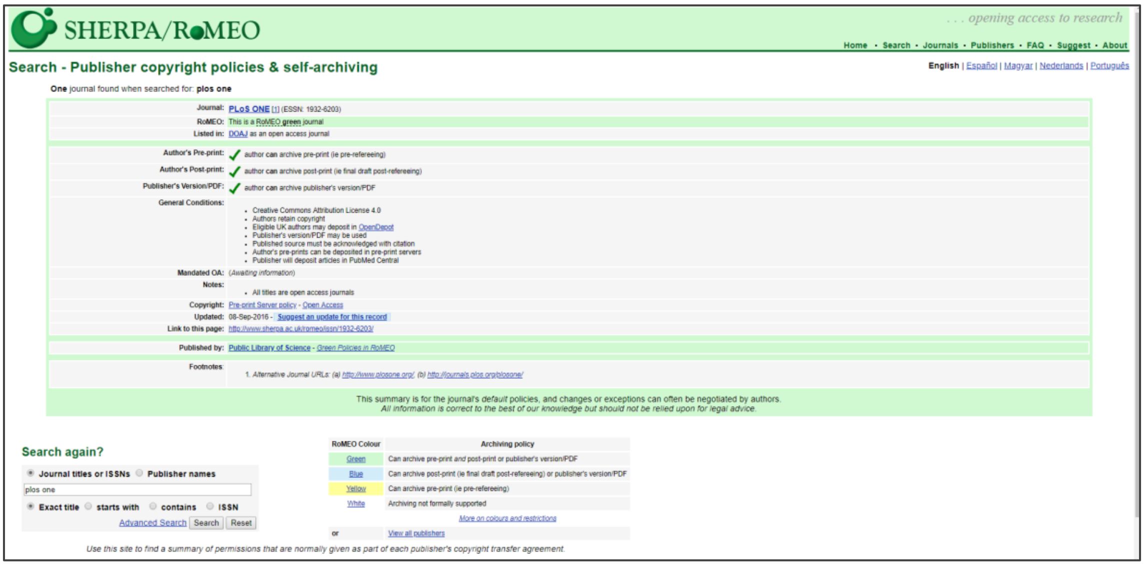
Chapter 6

Wellard, R., Lightbody, K., Riggs, D., Fouda, L., Blewitt, M. & Erbe, C. (2016) Killer whale (*Orcinus orca*) predation on beaked whales (*Ziphiidae* spp.) in the Bremer Sub Basin, Western Australia. PLoS ONE 11(12): e0166670.



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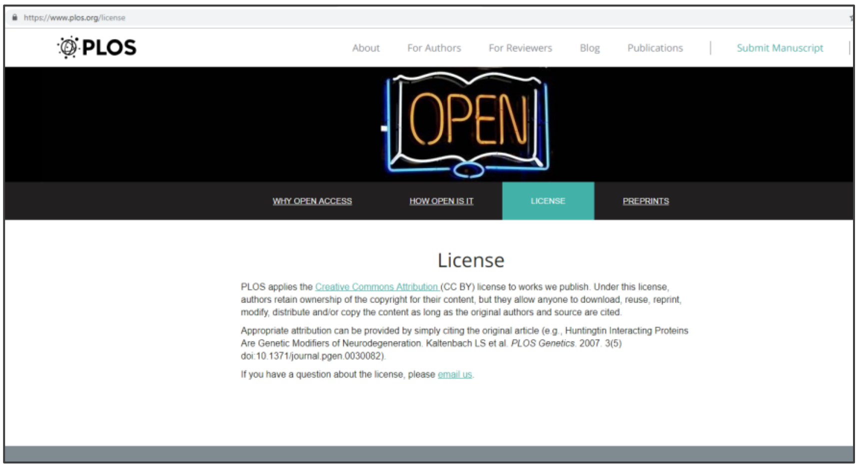

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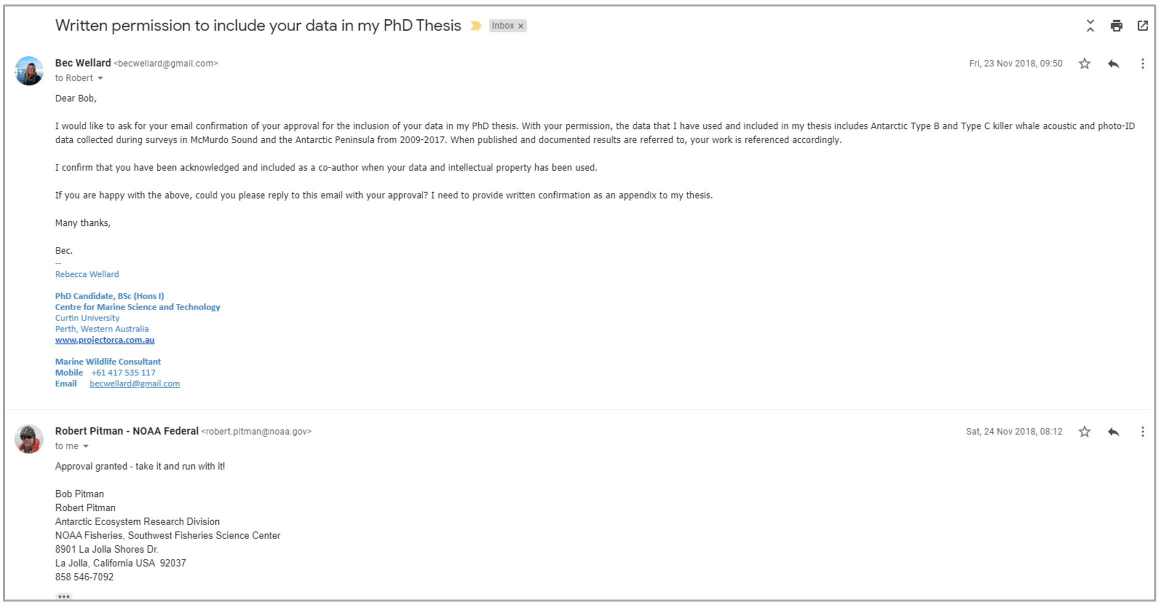

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Many thanks,

Bec.
--
Rebecca Wellard

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Robert Pitman - NOAA Federal <robert.pitman@noaa.gov>
to me
Sat, 24 Nov 2018, 08:12

Approval granted - take it and run with it!

Bob Pitman
Robert Pitman
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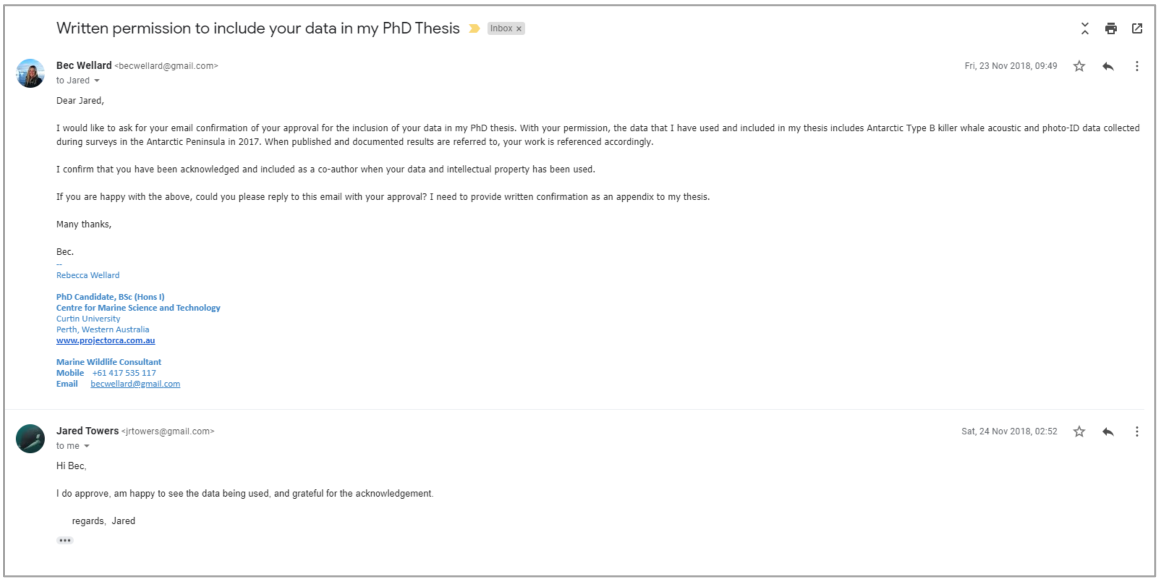

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Bec.
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Rebecca Wellard

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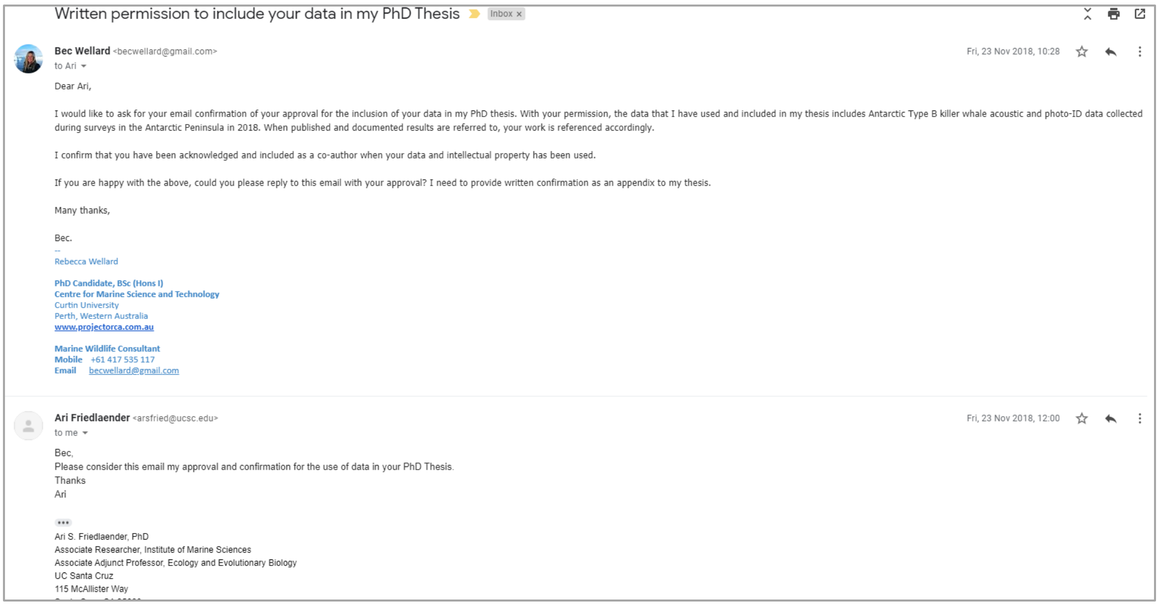
Jared Towers <jrtowers@gmail.com>
to me
Sat, 24 Nov 2018, 02:52

Hi Bec,

I do approve, am happy to see the data being used, and grateful for the acknowledgement.

regards, Jared



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Many thanks,

Bec.
--
Rebecca Wellard

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Ari Friedlaender <arsfried@ucsc.edu>
to me
Fri, 23 Nov 2018, 12:00

Bec,
Please consider this email my approval and confirmation for the use of data in your PhD Thesis.
Thanks
Ari

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Associate Adjunct Professor, Ecology and Evolutionary Biology
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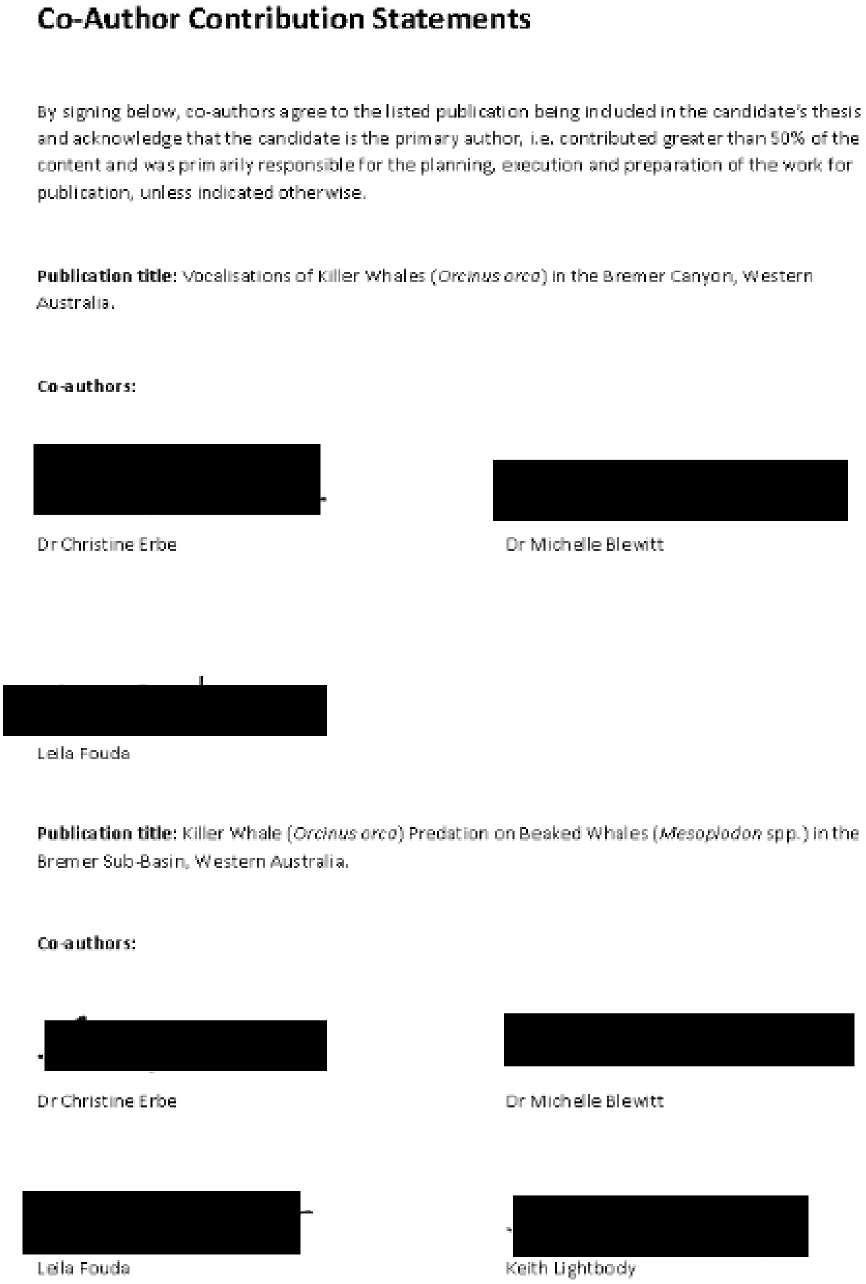
115 McAllister Way



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Co-authors:

[redacted]
Dr Christine Erbe

[redacted]
Dr Michelle Blewitt

[redacted]
Leila Fouda

Publication title: Killer Whale (*Orcinus orca*) Predation on Beaked Whales (*Mesoplodon* spp.) in the Bremer Sub-Basin, Western Australia.

Co-authors:

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Dr Christine Erbe

[redacted]
Dr Michelle Blewitt

[redacted]
Leila Fouda

[redacted]
Keith Lightbody

Appendix 2: Summary statistics of measured acoustic parameters for each call type classified in the Type C killer whale repertoire from McMurdo Sound, Antarctica.

Here I present a table of descriptive statistics (mean ±SD) of catalogued and categorised Type C killer whale calls from McMurdo Sound, Ross Sea relevant to Chapter 3 of this thesis. Listed in this table are measurements of the fundamental frequency for whistle (W) and biphonic whistle (Bi) components and measurements of the entire component for burst-pulse sounds (P). Measurements of individual components are displayed here, along with measurements of the entire call where multiple components are present. Individual measurements for each component are detailed in the Type C Killer Whale Call Catalogue (Appendix 3).

Call Type	Component	Component	Statistic	Dur [s]	Fmin [Hz]	Fmax [Hz]	Fdelta [Hz]	BW 90% [Hz]	Fpeak [Hz]	Fcentre [Hz]	Q1F [Hz]	Q3F [Hz]	MinEnt [bits]	MaxEnt [bits]	AvgEnt [bits]	Dur90% [s]	Fstart [Hz]	Fend [Hz]	Ext	Infl	FM	Steps
1	**P**	**1**	**Mean**	0.21	1007	12988	11981	3612	2791	3021	2588	3790	3.4	6.8	5.0	0.16						
n=101			***SD***	0.09	478	5032	4997	1790	623	858	396	1301	0.5	0.4	0.5	0.06						
	P	**2**	**Mean**	0.18	830	31350	30521	9743	4073	4402	2951	6354	5.1	7.2	6.2	0.14						
			SD	0.03	367	14593	14686	10008	4041	2185	1190	4682	0.7	0.9	0.8	0.05						
	P	**3**	**Mean**	0.85	884	14401	13517	4502	4155	4071	3012	4852	3.6	6.5	4.3	0.54						
			SD	0.23	321	5315	5407	1840	1140	904	794	880	0.9	0.5	0.4	0.12						
	Bi	**4**	**Mean**	0.60	7284	12809	5525	3054	8536	8798	8161	9642	2.8	6.0	3.7	0.44	12492	8893	3	3	5.3	0
			SD	0.12	1289	1084	1181	1228	1893	1597	1572	1556	0.7	0.5	0.5	0.10	1826	1746	3	3	5.3	0
		Entire	**Mean**	1.25	752	30358	29606	5805	4153	4048	2979	4802	3.3	6.9	4.8	0.76						
			SD	0.30	396	13139	13327	3194	1143	952	779	979	0.7	0.8	0.3	0.17						
1a	**P**	**1**	**Mean**	0.22	1634	43989	42355	20361	3188	6352	3609	8824	5.1	8.5	7.2	0.19						
n=40			***SD***	0.04	304	9059	9170	11167	978	4395	1735	4816	1.2	0.6	0.7	0.04						
	P	**2**	**Mean**	0.78	1061	14350	13289	6469	4881	4881	3621	5414	4.1	6.8	4.6	0.60						
			SD	0.14	477	1768	2002	1756	1719	1317	569	1474	0.8	0.4	0.4	0.12						
	Bi	**3**	**Mean**	0.68	7950	13116	5166	2953	9211	9398	8818	10184	2.8	6.0	3.7	0.54	13116	9390	4	4	5.3	0
			SD	0.12	799	1013	934	630	1271	1045	973	898	0.8	0.4	0.3	0.17	1013	1110	3	2	3.5	0
		Entire	**Mean**	0.94	907	43937	43030	14133	4881	4922	3650	6768	3.7	7.2	5.3	0.73						
			SD	0.12	615	8997	9387	9608	1719	1318	711	3702	0.8	0.9	0.6	0.10						
2	**P**	**1**	**Mean**	0.13	1162	14684	13522	3788	3089	3110	2510	3895	4.0	6.7	5.4	0.10						
n=111			***SD***	0.09	472	8727	8833	1826	1098	865	636	1005	0.8	0.9	0.5	0.06						
	P	**2**	**Mean**	0.82	915	16564	15648	5836	3750	3787	3199	4695	3.5	6.7	4.3	0.58						
			SD	0.17	330	8864	8921	2048	1197	1049	953	931	0.8	0.7	0.4	0.12						
	Bi	**3**	**Mean**	0.70	7778	12064	4285	2688	9504	9581	8817	10273	2.5	5.3	3.3	0.51	10227	9207	3	4	5.6	0
			SD	0.14	1226	1545	1195	830	1693	1406	1357	1357	0.6	0.5	0.6	0.13	2579	1591	2	3	4.2	0
		Entire	**Mean**	0.88	986	16115	14924	5878	3766	3769	3183	4685	3.2	6.0	4.2	0.61						
			SD	0.18	420	8783	8178	2006	1211	1047	954	926	0.7	0.6	0.5	0.13						
3	**P**	**1**	**Mean**	0.84	981	17114	16133	7341	3996	4369	3300	6534	3.9	7.2	4.9	0.64						
n=130			***SD***	0.19	376	7939	7963	4150	1857	1913	962	2677	0.9	0.8	0.6	0.14						

Call Type	Component	Component	Statistic	Dur [s]	Fmin [Hz]	Fmax [Hz]	Fdelta [Hz]	BW 90% [Hz]	Fpeak [Hz]	Fcentre [Hz]	Q1F [Hz]	Q3F [Hz]	MinEnt [bits]	MaxEnt [bits]	AvgEnt [bits]	Dur90% [s]	Fstart [Hz]	Fend [Hz]	Ext	Infl	FM	Steps
	Bi	**2**	**Mean**	0.61	3628	10666	7037	4686	5661	6120	5248	7511	3.1	5.9	4.1	0.50	4020	7989	2	3	4.8	1
			SD	0.18	1634	1524	1852	2016	2247	2393	1963	2421	0.6	0.7	0.4	0.18	1569	2883	1	1	2.2	1
		Entire	**Mean**	0.86	987	17328	16341	7425	3984	4373	3308	6533	3.8	7.2	5.0	0.65						
			SD	0.18	388	7674	7723	4044	1867	1911	973	2657	0.9	0.7	0.5	0.14						
3a *n=30*	**P**	**1**	**Mean**	0.98	681	17377	16696	4297	2398	2961	2375	4586	2.9	7.0	4.4	0.45						
			SD	0.10	182	5073	5180	2200	104	1052	125	1933	0.7	0.8	0.3	0.14						
	Bi	**2**	**Mean**	0.45	3178	9832	6654	3742	4250	4898	4102	5656	2.7	6.0	3.6	0.28	3030	7461	2	3	6.8	2
			SD	0.11	1094	1028	1906	2284	1719	1374	1330	1276	0.7	0.3	0.6	0.17	1571	3939	1	1	2.5	1
		Entire	**Mean**	0.98	612	17316	16704	4297	2398	2961	2375	4586	2.9	7.0	4.4	0.45						
			SD	0.10	245	5073	5260	2200	104	1052	125	1933	0.7	0.8	0.3	0.14						
4 *n=59*	**P**	**1**	**Mean**	0.37	1254	26573	25319	17746	3156	4980	3168	8797	5.2	7.8	6.8	0.31						
			SD	0.12	584	15639	15218	12721	1722	3463	1728	8965	0.7	1.0	0.6	0.11						
	P	**2**	**Mean**	1.30	1348	22927	21579	4809	4836	3945	3246	4965	4.3	7.3	4.4	0.82						
			SD	0.12	335	16081	15979	2418	2529	1450	216	2186	0.9	0.9	0.7	0.07						
	Bi	**3**	**Mean**	1.10	5199	10607	5408	4098	6836	7250	6414	8250	3.9	5.3	4.5	0.83	5199	8192	1	2	2.1	0
			SD	0.10	1131	770	1226	1203	1893	1553	1985	673	0.9	0.8	0.6	0.18	1131	790	0	0	0.5	0
		Entire	**Mean**	1.66	1091	26521	25430	7426	4836	3965	3258	5020	4.8	7.4	5.0	1.08						
			SD	0.16	465	15555	15331	8278	2529	1474	239	2217	1.2	1.0	0.5	0.13						
5 *n=84*	**W**	**1**	**Mean**	0.41	4963	10589	5626	2079	6215	6171	5890	6596	2.4	6.1	3.2	0.31	10589	5029	0.4	0.4	1.0	0
			SD	0.09	644	2274	2149	1781	1261	1299	1143	1793	0.2	0.6	0.5	0.10	2274	674	1	1	2.2	0
	P	**2**	**Mean**	0.23	1360	11226	9865	5824	2824	3127	2358	4831	4.5	6.8	5.8	0.18						
			SD	0.13	903	3626	3476	2065	1709	1317	851	1742	0.6	0.4	0.5	0.11						
		Entire	**Mean**	0.66	1365	12255	10890	6416	6356	5950	4693	7006	4.3	6.9	4.6	0.47						
			SD	0.14	897	3299	3169	3040	2974	1083	1648	2612	1.3	0.4	0.5	0.13						
5a *n=43*	**W**	**1**	**Mean**	0.50	5322	9482	4160	2729	6115	6281	5917	6646	2.3	4.6	3.1	0.41	9482	5397	0	0	0.2	0
			SD	0.10	1419	1898	1199	1202	1455	1471	1446	1546	0.9	0.9	0.9	0.09	1898	1629	0	0	0.6	1
6 *n=13*	**P**	**1**	**Mean**	0.10	915	8405	7491	3328	2313	2453	2250	3578	4.0	6.2	5.2	0.10						
			SD	0.03	361	998	1323	1219	72	135	81	1001	0.7	0.2	0.6	0.00						

Call Type	Component	Component	Statistic	Dur [s]	Fmin [Hz]	Fmax [Hz]	Fdelta [Hz]	BW 90% [Hz]	Fpeak [Hz]	Fcentre [Hz]	Q1F [Hz]	Q3F [Hz]	MinEnt [bits]	MaxEnt [bits]	AvgEnt [bits]	Dur90% [s]	Fstart [Hz]	Fend [Hz]	Ext	Infl	FM	Steps
	P	**2**	**Mean**	0.69	956	8877	7921	2922	2688	2578	2016	3094	3.4	6.3	4.3	0.47						
			SD	0.18	395	916	814	665	636	406	447	615	0.5	0.2	0.3	0.15						
		Entire	**Mean**	0.80	746	8974	8228	2969	2688	2578	2031	3156	3.8	6.3	4.4	0.50						
			SD	0.18	67	748	716	728	636	406	420	638	0.7	0.2	0.4	0.20						
7	**W**	**1**	**Mean**	1.38	1309	4714	3406	1990	3188	3094	2734	3542	2.0	4.6	2.9	1.15	1309	4650	7	7	5.4	4
n=88			***SD***	0.54	765	1324	1235	876	991	803	658	932	0.5	0.5	0.6	0.49	765	1331	9	10	6.5	4
8	**P**	**1**	**Mean**	0.81	1511	15779	14268	6181	4540	5826	3917	7232	3.6	6.2	4.6	0.66						
n=36			***SD***	0.08	733	5399	5479	984	1340	930	578	1138	0.4	0.7	0.4	0.05						
	Bi	**2**	**Mean**	0.83	4386	11219	6833	4078	5136	6690	5538	7527	2.8	5.7	3.8	0.64	5016	7204	12	13	15.9	0
			SD	0.09	223	915	1027	725	529	1231	674	1092	0.3	0.5	0.3	0.05	719	983	2	2	2.9	0
		Entire	**Mean**	0.84	1408	15930	14522	6194	4821	5792	3897	7199	3.5	6.5	4.6	0.69						
			SD	0.08	722	5255	5412	972	1030	824	556	1126	0.4	0.5	0.4	0.07						
9	**P**	**1**	**Mean**	0.63	4368	7098	2730	1113	6773	6797	6656	6902	2.6	5.1	2.6	0.50	4461	5501	3	4	5.6	2
n=19			***SD***	0.21	620	654	333	864	814	721	730	709	0.7	0.4	0.2	0.14	635	339	1	2	2.0	1
	Bi	**2**	**Mean**	0.36	915	18218	17303	6773	3457	3562	2941	5016	3.3	7.4	4.7	0.28						
			SD	0.06	445	835	522	3970	234	115	449	2178	0.3	0.5	0.3	0.05						
		Entire	**Mean**	0.99	873	18364	17490	6129	5379	5508	4195	6832	3.4	7.4	3.9	0.78						
			SD	0.25	322	852	570	2729	2404	2028	2094	772	0.7	0.4	0.5	0.21						
10	**P**	**1**	**Mean**	0.07	1905	19587	17681	4084	4932	4805	4321	5401	3.3	7.0	4.9	0.05						
n=95			***SD***	0.02	1081	5445	5655	2212	911	828	842	883	0.6	0.9	0.7	0.05						
	W	**2**	**Mean**	0.25	4402	7544	3142	2258	5526	5724	5281	6304	2.7	5.4	3.5	0.16	4578	5770	2	2	10.1	0
			SD	0.08	685	1230	993	867	924	879	741	1022	0.5	0.7	0.7	0.06	705	1247	2	2	6.7	0
	P	**3**	**Mean**	0.28	955	24704	23749	9025	3027	3586	2406	5303	3.7	7.5	5.4	0.21						
			SD	0.07	522	12452	12721	10074	1787	1557	570	3047	1.2	0.9	0.9	0.05						
		Entire	**Mean**	0.54	843	25262	24420	8663	4465	4705	3585	6570	3.4	7.6	5.0	0.41						
			SD	0.11	523	12178	12504	9681	1631	1412	1137	2408	1.1	0.9	0.8	0.11						
11	**P**	**1**	**Mean**	1.65	413	13998	13585	2894	1690	1892	1548	2678	4.1	7.7	5.4	1.23						
n=36			***SD***	0.38	119	3415	3374	2124	263	188	153	514	1.4	1.0	0.8	0.39						

Call Type	Component	Component	Statistic	Dur [s]	Fmin [Hz]	Fmax [Hz]	Fdelta [Hz]	BW 90% [Hz]	Fpeak [Hz]	Fcentre [Hz]	Q1F [Hz]	Q3F [Hz]	MinEnt [bits]	MaxEnt [bits]	AvgEnt [bits]	Dur90% [s]	Fstart [Hz]	Fend [Hz]	Ext	Infl	FM	Steps
12	**P**	**1**	**Mean**	0.75	271	5824	5553	2531	1504	1910	1451	2629	4.8	7.2	6.1	0.58						
n=65			***SD***	0.19	99	404	380	357	568	319	97	503	0.6	0.1	0.3	0.15						
13	**P**	**1**	**Mean**	0.81	1251	47492	46241	28094	4656	4734	3125	8797	5.9	8.4	7.1	0.60						
n=3			***SD***	0.08	409	544	951	10723	2828	2477	866	4902	0.5	0.9	0.4	0.00						
	W	**2**	**Mean**	0.44	5521	7494	1973	1578	6859	6594	6141	6984	3.6	5.0	4.4	0.40	6269	6745	0	0	0.0	0
			SD	0.01	118	362	250	379	882	420	47	665	0.4	0.1	0.4	0.00	1415	945	0	0	0.0	0
14	**P**	**1**	**Mean**	0.30	278	28188	27910	3636	2745	2842	2001	3516	3.3	7.2	5.0	0.20						
n=16			***SD***	0.10	130	7315	7369	1834	955	496	584	326	0.1	0.2	0.4	0.08						
15	**W**	**1**	**Mean**	0.53	4542	11385	6843	4492	6507	7762	6800	8305	3.1	6.3	4.6	0.45	10905	5022	5	5	9.2	0
n=89			***SD***	0.15	1668	2636	2212	2110	2342	1625	1751	1767	0.5	0.5	0.8	0.15	3335	2258	5	5	9.5	1
	P	**2**	**Mean**	0.15	1065	15129	14064	3896	3394	3463	2881	4144	3.3	6.8	4.9	0.11						
			SD	0.04	550	6644	6822	1226	782	641	547	610	0.6	0.7	0.4	0.04						
	P	**3**	**Mean**	0.33	1835	14652	12817	2639	3408	3560	3298	4095	2.7	7.2	4.2	0.25						
			SD	0.10	729	7203	7272	1571	722	683	566	830	0.4	0.7	0.6	0.09						
		Entire	**Mean**	0.99	960	16666	15706	6480	3215	3596	3080	4754	3.2	7.4	5.0	0.74						
			SD	0.20	484	7170	7276	2998	619	503	494	1306	1.0	0.6	0.5	0.22						
15a	**P**	**1**	**Mean**	0.16	622	21200	20578	4275	3384	3422	2934	3862	2.6	6.5	4.1	0.12						
n=54			***SD***	0.06	211	6329	6357	2131	308	301	451	476	0.5	0.8	0.5	0.04						
	P	**2**	**Mean**	0.35	1879	21000	19121	4144	3234	3183	3000	3956	1.8	6.9	3.1	0.27						
			SD	0.08	532	4795	4644	4465	865	551	444	968	0.5	0.5	0.8	0.07						
		Entire	**Mean**	0.51	599	22273	21674	4486	3422	3347	2873	3914	2.8	6.9	3.5	0.42						
			SD	0.09	229	5076	5109	2813	304	359	326	606	1.7	0.5	0.7	0.08						
16	**P**	**1**	**Mean**	0.42	1193	15750	14557	2652	3134	2826	2451	3502	2.9	6.2	3.7	0.27						
n=7			***SD***	0.07	394	6030	5899	600	1291	855	890	841	1.6	0.4	0.9	0.10						
17	**P**	**1**	**Mean**	0.65	857	25578	24721	6078	2109	2844	2156	4359	3.6	6.2	4.3	0.50						
n=3			***SD***	0.12	166	1091	1251	3342	366	1382	430	2268	0.8	0.1	0.8	0.10						
	Bi	**2**	**Mean**	0.59	5540	13063	7523	3313	6016	6656	6125	7547	2.7	5.8	4.1	0.43	7977	8831	7	8	14.0	0
			SD	0.18	3289	1090	3069	985	3382	3851	3484	4357	0.2	0.5	0.5	0.06	6141	2165	3	3	1.1	0

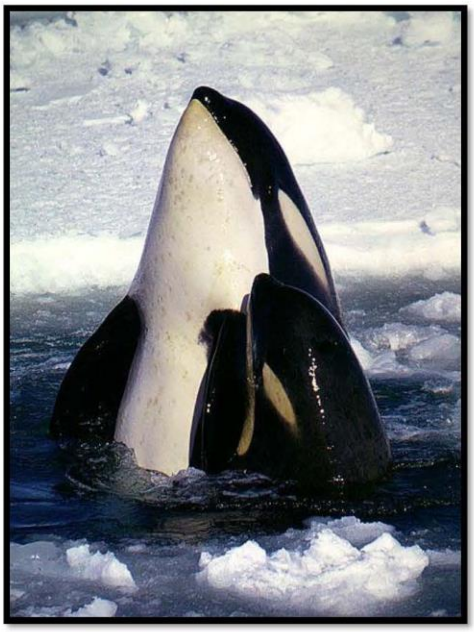
Call Type	Component	Component	Statistic	Dur [s]	Fmin [Hz]	Fmax [Hz]	Fdelta [Hz]	BW 90% [Hz]	Fpeak [Hz]	Fcentre [Hz]	Q1F [Hz]	Q3F [Hz]	MinEnt [bits]	MaxEnt [bits]	AvgEnt [bits]	Dur90% [s]	Fstart [Hz]	Fend [Hz]	Ext	Infl	FM	Steps
		Entire	**Mean**	0.66	880	25615	24735	6078	2109	2844	2156	4359	3.5	6.2	4.3	0.50						
			SD	0.13	186	1078	1255	3342	366	1382	430	2268	0.8	0.1	0.8	0.10						
18	**P**	**1**	**Mean**	0.26	1821	29203	27382	9125	14359	16047	13969	18313	3.6	7.5	6.4	0.20						
n=3			***SD***	0.10	790	16317	15705	6100	19677	19374	19252	20831	0.5	1.5	1.7	0.10						
	P	**2**	**Mean**	1.22	1305	11467	10161	6875	4469	5125	2969	6313	3.8	5.9	4.6	1.00						
			SD	0.04	222	2361	2162	4441	2907	3357	871	3217	1.2	0.9	1.1	0.10						
	Bi	**3**	**Mean**	1.09	6163	12938	6775	5500	8516	9078	8313	10844	3.2	5.7	4.0	0.87	7050	9404	12	12	11.1	0
			SD	0.21	1275	523	1530	1597	683	404	423	1172	0.8	0.8	0.7	0.21	2351	801	3	4	3.6	0
		Entire	**Mean**	1.48	1305	29175	27870	16531	14234	14703	12531	17484	4.0	6.9	5.3	1.00						
			SD	0.06	247	16269	16091	18337	19789	19703	17321	20664	1.7	1.4	1.6	0.26						
19	**P**	**1**	**Mean**	0.64	531	14492	13960	2390	3058	2885	2369	3467	3.1	6.2	4.2	0.45						
n=2			***SD***	0.21	26	2047	2021	213	670	61	305	213	0.9	0.1	0.7	0.07						
	P	**2**	**Mean**	0.36	715	22050	21336	7171	3402	3424	2649	3919	3.6	6.9	4.6	0.30						
			SD	0.06	130	0	130	1492	731	579	396	1096	1.7	0.4	1.2	0.00						
	P	**3**	**Mean**	0.17	1044	12293	11249	4113	3187	2972	2153	3596	4.7	6.3	5.7	0.15						
			SD	0.10	26	648	674	1431	853	244	365	274	0.5	0.0	0.3	0.07						
	P	**4**	**Mean**	0.19	898	9307	8409	1873	1916	2606	2196	3424	3.5	6.3	4.2	0.10						
			SD	0.01	78	52	26	1370	944	30	548	274	1.2	0.3	1.2	0.00						
		Entire	**Mean**	1.62	513	22017	21504	2842	1916	2885	2304	3488	3.5	6.8	4.8	1.35						
			SD	0.37	52	46	98	914	944	61	396	305	1.2	0.8	0.6	0.21						
20	**P**	**1**	**Mean**	0.33	1668	36294	34626	19723	3820	5496	4184	9410	4.5	7.8	6.5	0.28						
n=4			***SD***	0.10	992	7897	8299	12658	4389	3067	2463	3355	1.0	1.0	0.9	0.05						
	P	**2**	**Mean**	0.93	1406	9125	7720	6668	4711	4629	3023	6152	2.9	5.4	4.2	0.63						
			SD	0.18	349	2138	1890	1174	3014	2996	1786	3062	1.0	0.5	0.8	0.15						
	Bi	**3**	**Mean**	0.78	7907	11747	3840	1523	8883	9141	8883	9633	2.1	4.9	2.5	0.58	9792	8635	3	4	4.5	0
			SD	0.14	1725	2072	2181	1472	835	532	811	673	0.7	1.2	0.9	0.10	3922	753	1	1	1.8	1
		Entire	**Mean**	1.24	830	36215	35385	11742	5496	7277	4242	9176	3.3	6.4	4.9	0.85						
			SD	0.23	492	7880	8171	4006	4161	2703	3239	1010	1.4	1.1	0.9	0.06						

Call Type	Component	Component	Statistic	Dur [s]	Fmin [Hz]	Fmax [Hz]	Fdelta [Hz]	BW 90% [Hz]	Fpeak [Hz]	Fcentre [Hz]	Q1F [Hz]	Q3F [Hz]	MinEnt [bits]	MaxEnt [bits]	AvgEnt [bits]	Dur90% [s]	Fstart [Hz]	Fend [Hz]	Ext	Infl	FM	Steps
21	**W**	**1**	**Mean**	1.24	3863	6054	2190	1602	4534	4640	4372	5060	2.8	4.7	3.4	0.96	5166	4480	2	2	1.3	0
n=42			***SD***	0.60	2518	3587	1150	1065	2855	2909	2696	3207	0.8	0.9	1.1	0.49	3292	2681	3	3	1.9	0
22	**W**	**1**	**Mean**	0.19	5456	7773	2317	1120	5830	5960	5829	6206	2.3	4.8	3.0	0.14	7459	6972	1	1	7.3	0
n=52			***SD***	0.08	3241	4166	1436	1056	3211	3261	3206	3398	0.6	1.0	0.8	0.08	4232	4044	1	0	7.5	0
23	**P**	**1**	**Mean**	0.28	904	32617	31714	3906	2570	2805	2258	3336	3.7	6.9	5.1	0.20						
n=6			***SD***	0.10	411	16560	16402	1722	418	283	323	359	0.8	1.1	0.9	0.09						
	W	**2**	**Mean**	0.97	1284	3190	1906	953	2547	2687	2438	2898	1.6	3.8	2.1	0.75	2032	1339	8	9	10.9	0
			SD	0.41	233	447	535	343	378	348	275	361	0.6	0.7	0.6	0.34	464	311	4	4	5.0	0
	P	**3**	**Mean**	0.56	1175	11143	9967	3016	2648	2859	2508	3305	2.7	5.8	4.0	0.43						
			SD	0.32	349	5582	5484	1794	418	284	368	523	0.9	0.8	0.9	0.31						
	Bi	**4**	**Mean**	1.08	2978	10481	7502	3875	4219	4977	4188	6070	2.4	5.0	3.3	0.80	3067	8088	4	5	5.2	0
			SD	0.34	1407	1175	1859	2408	2303	2490	2262	3205	0.9	1.2	0.9	0.28	1469	1178	3	3	4.2	0
		Entire	**Mean**	1.81	890	32566	31675	4172	2625	2789	2516	3141	2.8	6.3	3.7	1.25						
			SD	0.64	412	15192	15066	2640	267	227	121	222	0.8	1.0	1.0	0.57						
24	**P**	**1**	**Mean**	0.79	1528	11513	9985	7398	4578	5898	3859	7398	3.4	6.3	5.1	0.62						
n=6			***SD***	0.16	321	2403	2485	2130	2278	2659	1946	2466	0.5	0.3	0.5	0.13						
	Bi	**2**	**Mean**	0.79	4562	12581	8019	5930	6680	7047	6477	9062	2.9	5.9	4.8	0.62	4610	10515	7	8	9.6	0
			SD	0.15	1184	497	1030	1007	2018	1811	1711	1717	0.4	0.6	0.4	0.04	1253	2130	2	2	2.2	0
		Entire	**Mean**	0.82	1543	13276	11733	8406	4516	6008	3953	7641	3.6	6.4	5.3	0.65						
			SD	0.16	330	1613	1664	2127	2198	2580	2020	2345	0.9	0.3	0.5	0.10						
25	**Pulse**	**1**	**Mean**	1.04	350	9552	9202	4422	1177	1450	1077	2383	2.9	6.6	4.5	0.77						
n=15			***SD***	0.33	149	2575	2713	3024	436	174	224	717	0.4	0.6	0.5	0.31						

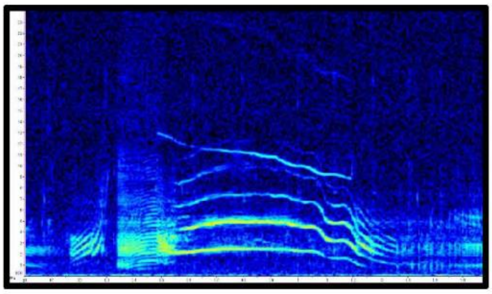
** Due to a large number of multi-components, Call Type 10a have measurements for the entire call , rather than individual call components. For full description its call components, please refer to the Type C Call Catalogue, Appendix 3.

Appendix 3: Antarctic Type C Killer Whale Acoustic Call Catalogue from McMurdo Sound, Ross Sea

This Appendix includes the Call Type Catalogue as referred to in Chapter 3 of this thesis.



Antarctic Type C Killer Whale Acoustic Call Catalogue from McMurdo Sound, Ross Sea



ABSTRACT

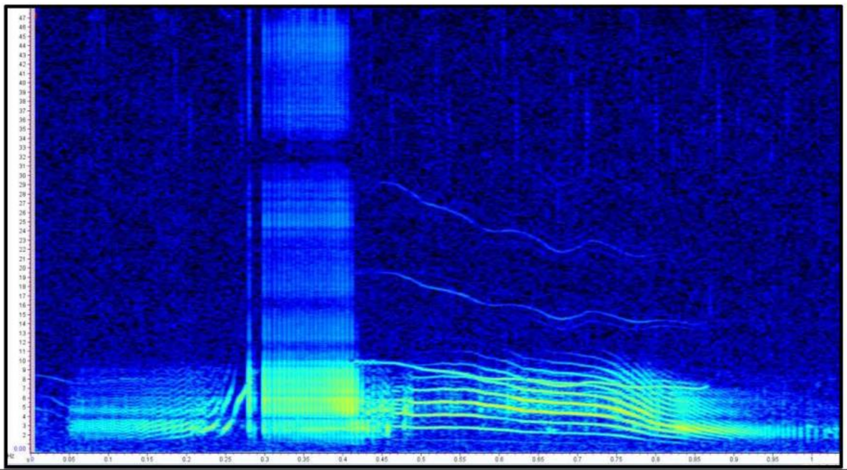
Killer whales (Orcinus orca) are found in all oceans of the world. In Antarctic waters, five ecotypes have been described, each displaying distinct differences in morphological features, foraging behaviours, habitat and diet preferences, and genetic structure. Acoustic recordings of Type C killer whales were collected between December 2012 and January 2013 in McMurdo Sound, Ross Sea, Antarctica. Spectrograms of acoustic data were examined for characteristic patterns of Type C vocalizations, calls were collectively grouped according to their spectral parameters and a call type catalogue was produced.

Compiled by Rebecca Wellard.

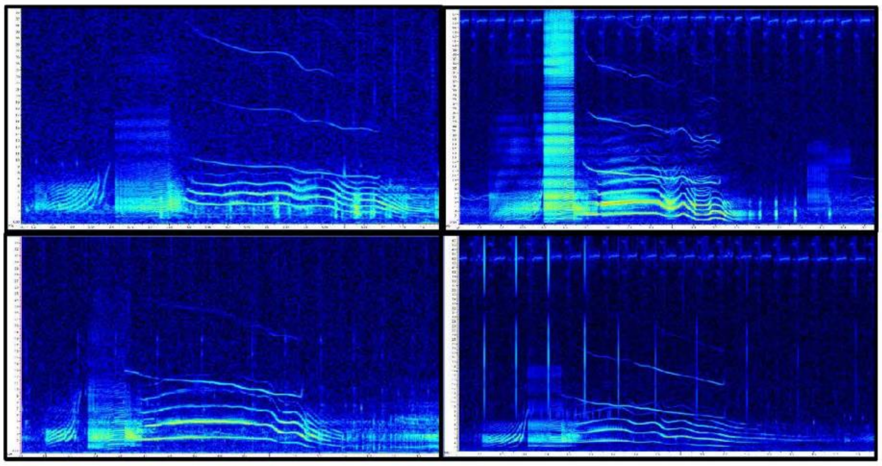
CALL TYPE McM1

This is a multi-component and biphonic call consisting of 4 components. Part 1 is a burst-pulse sound with the pulse repetition rate (PRR) increasing towards the end. The PRR can be read off the spectrogram as the sideband spacing (SBS). Part 2 is a series of single pulses. Parts 3 and 4 are a biphonation. Part 3 is a burst-pulse sound with an SBS of roughly 1kHz. The PRR decreases towards the end and some calls end as a series of distinct pulses. Part 4 is a biphonic whistle with harmonics that decrease in frequency over time. Weak sidebands are sometimes visible indicating amplitude-modulation (AM).

n = 101



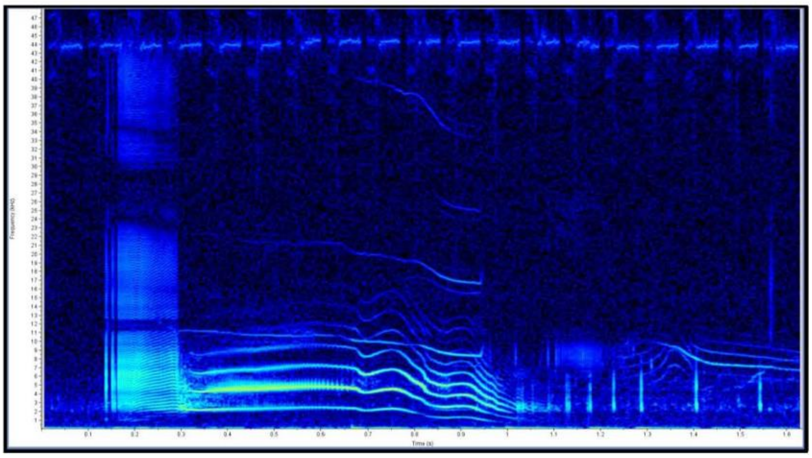
Call Type	Component	Statistic	Dur [s]	Fmin [Hz]	Fmax [Hz]	Fdelta [Hz]	BW 90% [Hz]	Fpeak [Hz]	Fcentre [Hz]	Q1F [Hz]	Q3F [Hz]	MinEnt [bits]	MaxEnt [bits]	AvgEnt [bits]	Dur90% [s]	Fstart [Hz]	Fend [Hz]	Ext	Infl	FM [1/s]	Steps
1	1	Mean	0.21	1007	12988	11981	3612	2791	3021	2588	3790	3.4	6.8	5.0	0.16						
n=101		*SD*	0.09	478	5032	4997	1790	623	858	396	1301	0.5	0.4	0.5	0.06						
	2	Mean	0.18	830	31350	30521	9743	4073	4402	2951	6354	5.1	7.2	6.2	0.14						
		SD	0.03	367	14593	14686	10008	4041	2185	1190	4682	0.7	0.9	0.8	0.05						
	3	Mean	0.85	884	14401	13517	4502	4155	4071	3012	4852	3.6	6.5	4.3	0.54						
		SD	0.23	321	5315	5407	1840	1140	904	794	880	0.9	0.5	0.4	0.12						
	4	Mean	0.60	7284	12809	5525	3054	8536	8798	8161	9642	2.8	6.0	3.7	0.44	12492	8893	3	3	5.3	0
		SD	0.12	1289	1084	1181	1228	1893	1597	1572	1556	0.7	0.5	0.5	0.10	1826	1746	3	3	5.3	0
	Entire	Mean	1.25	752	30358	29606	5805	4153	4048	2979	4802	3.3	6.9	4.8	0.76						
		SD	0.30	396	13139	13327	3194	1143	952	779	979	0.7	0.8	0.3	0.17						



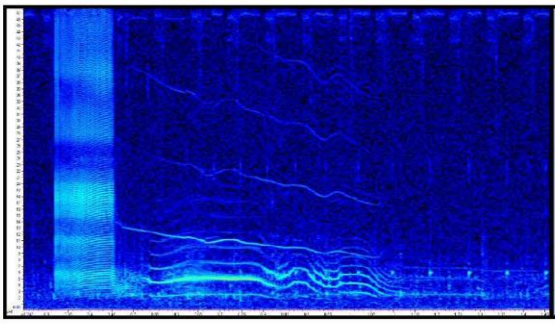
CALL TYPE McM1A

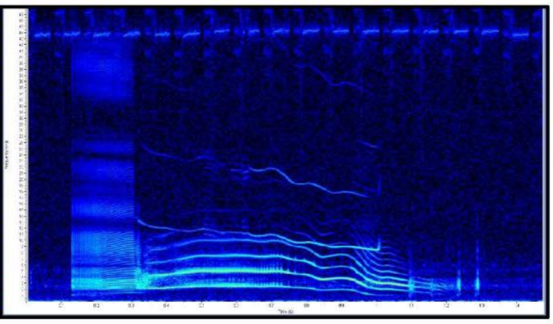
This is a 3-component and biphonic call. Due to the first component in Call Type McM1 missing, this call is deemed a variation and hence called Call Type McM1A. Part 1 is a series of single pulses. Part 2 is a burst-pulse sound with a SBS of roughly 1kHz. The PRR decreases towards the end. Some calls end as series of distinct pulses. Part 3 is a biphonic whistle with harmonics and weak sidebands. It decreases in frequency over time.

n = 40



Call Type	Component	Statistic	Dur [s]	Fmin [Hz]	Fmax [Hz]	Fdelta [Hz]	BW 90% [Hz]	Fpeak [Hz]	Fcentre [Hz]	Q1F [Hz]	Q3F [Hz]	MinEnt [bits]	MaxEnt [bits]	AvgEnt [bits]	Dur90% [s]	Fstart [Hz]	Fend [Hz]	Ext	Infl	FM [1/s]	Steps
1a	1	Mean	0.22	1634	43989	42355	20361	3188	6352	3609	8824	5.1	8.5	7.2	0.19						
n=40		*SD*	0.04	304	9059	9170	11167	978	4395	1735	4816	1.2	0.6	0.7	0.04						
	2	Mean	0.78	1061	14350	13289	6469	4881	4881	3621	5414	4.1	6.8	4.6	0.60						
		SD	0.14	477	1768	2002	1756	1719	1317	569	1474	0.8	0.4	0.4	0.12						
	3	Mean	0.68	7950	13116	5166	2953	9211	9398	8818	10184	2.8	6.0	3.7	0.54	13116	9390	4	4	5.3	0
		SD	0.12	799	1013	934	630	1271	1045	973	898	0.8	0.4	0.3	0.17	1013	1110	3	2	3.5	0
	Entire	Mean	0.94	907	43937	43030	14133	4881	4922	3650	6768	3.7	7.2	5.3	0.73						
		SD	0.12	615	8997	9387	9608	1719	1318	711	3702	0.8	0.9	0.6	0.10						

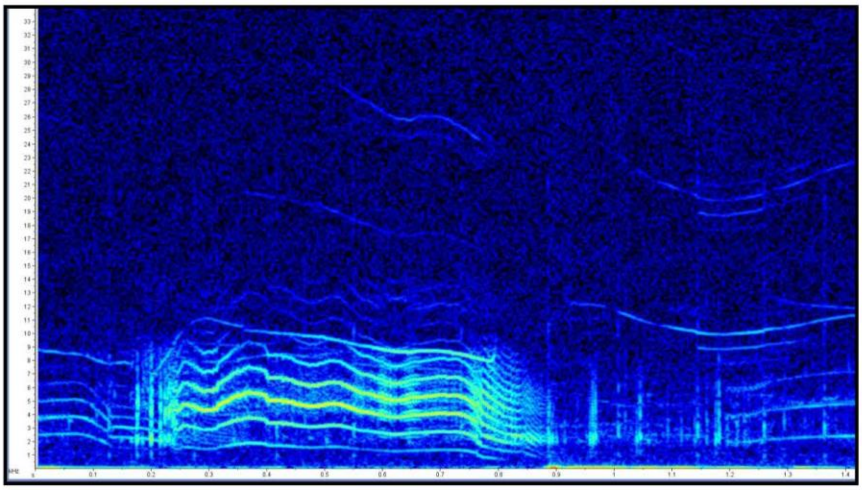




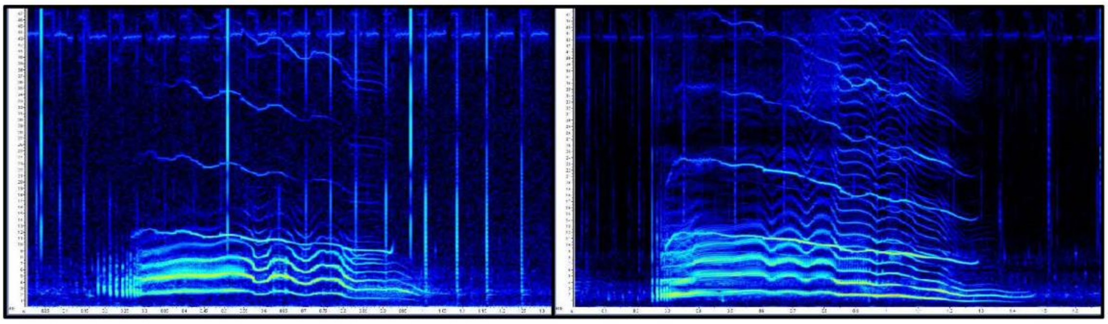
CALL TYPE McM2

This is a 3-component biphonic call. Part 1 is a series of distinct pulses. Part 2 is a burst-pulse sound with an approximate 1kHz SBS. Part 3 is the biphonic whistle with harmonics that first increases in frequency and then decreases in frequency over time.

n = 111



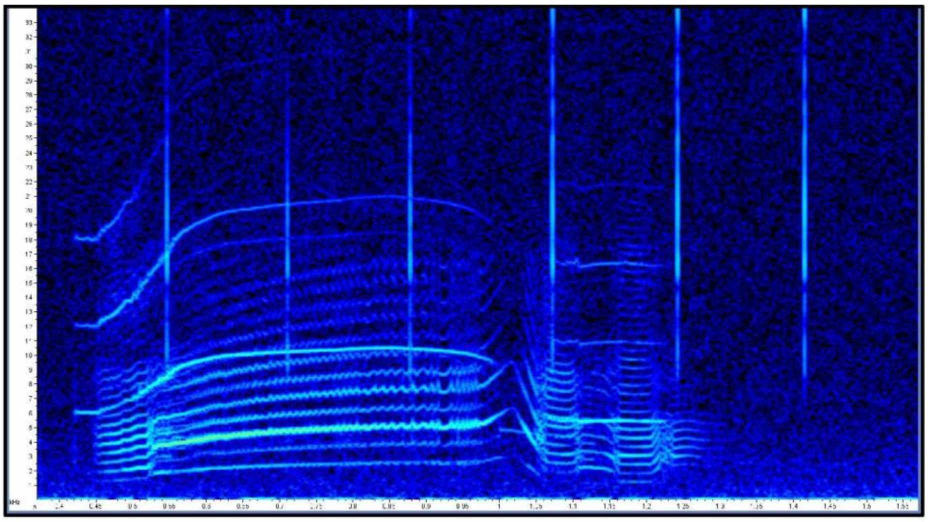
Call Type	Component	Statistic	Dur [s]	Fmin [Hz]	Fmax [Hz]	Fdelta [Hz]	BW 90% [Hz]	Fpeak [Hz]	Fcentre [Hz]	Q1F [Hz]	Q3F [Hz]	MinEnt [bits]	MaxEnt [bits]	AvgEnt [bits]	Dur90% [s]	Fstart [Hz]	Fend [Hz]	Ext	Infl	FM [1/s]	Steps
2	1	Mean	0.13	1162	14684	13522	3788	3089	3110	2510	3895	4.0	6.7	5.4	0.10						
n=111		*SD*	0.09	472	8727	8833	1826	1098	865	636	1005	0.8	0.9	0.5	0.06						
	2	Mean	0.82	915	16564	15648	5836	3750	3787	3199	4695	3.5	6.7	4.3	0.58						
		SD	0.17	330	8864	8921	2048	1197	1049	953	931	0.8	0.7	0.4	0.12						
	3	Mean	0.70	7778	12064	4285	2688	9504	9581	8817	10273	2.5	5.3	3.3	0.51	10227	9207	3	4	5.6	0
		SD	0.14	1226	1545	1195	830	1693	1406	1357	1357	0.6	0.5	0.6	0.13	2579	1591	2	3	4.2	0
	Entire	Mean	0.88	986	16115	14924	5878	3766	3769	3183	4685	3.2	6.0	4.2	0.61						
		SD	0.18	420	8783	8178	2006	1211	1047	954	926	0.7	0.6	0.5	0.13						



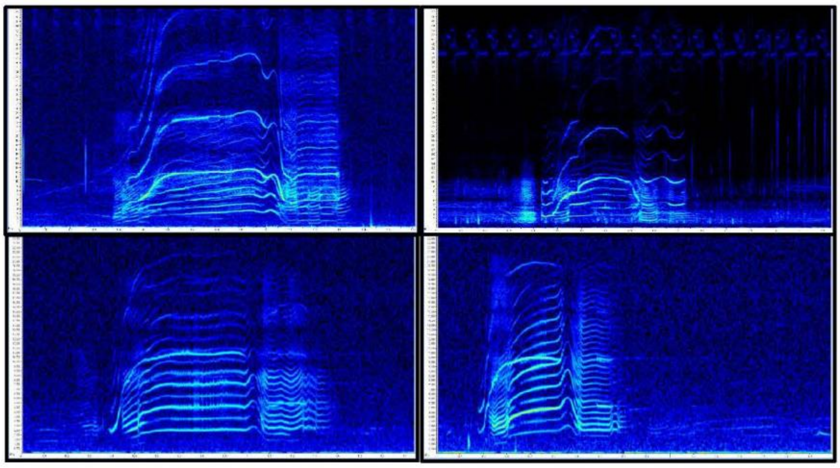
CALL TYPE McM3

This is a 2-component biphonic call. Part 1 is a burst-pulse sound starting at a low SBS (i.e., low PRR), increasing SBS to approximately 1 kHz, and then decreasing SBS towards the end of the component. Part 2 is a biphonic whistle with harmonics that starts as an upsweep, then remains flat before dropping to a constant-wave at a lower frequency.

n = 130



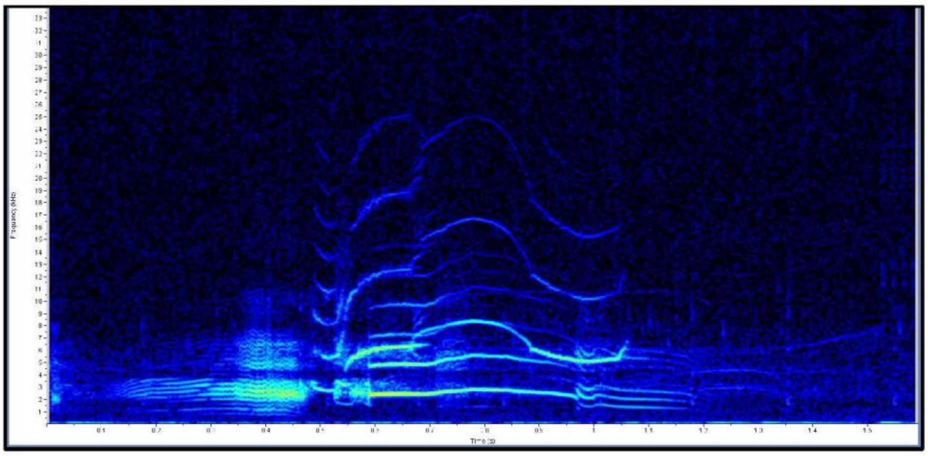
Call Type	Component	Statistic	Dur [s]	Fmin [Hz]	Fmax [Hz]	Fdelta [Hz]	BW 90% [Hz]	Fpeak [Hz]	Fcentre [Hz]	Q1F [Hz]	Q3F [Hz]	MinEnt [bits]	MaxEnt [bits]	AvgEnt [bits]	Dur90% [s]	Fstart [Hz]	Fend [Hz]	Ext	Infl	FM [1/s]	Steps
3	1	**Mean**	0.84	981	17114	16133	7341	3996	4369	3300	6534	3.9	7.2	4.9	0.64						
n=130		***SD***	0.19	376	7939	7963	4150	1857	1913	962	2677	0.9	0.8	0.6	0.14						
	2	**Mean**	0.61	3628	10666	7037	4686	5661	6120	5248	7511	3.1	5.9	4.1	0.50	4020	7989	2	3	4.8	1
		SD	0.18	1634	1524	1852	2016	2247	2393	1963	2421	0.6	0.7	0.4	0.18	1569	2883	1	1	2.2	1
	Entire	**Mean**	0.86	987	17328	16341	7425	3984	4373	3308	6533	3.8	7.2	5.0	0.65						
		SD	0.18	388	7674	7723	4044	1867	1911	973	2657	0.9	0.7	0.5	0.14						



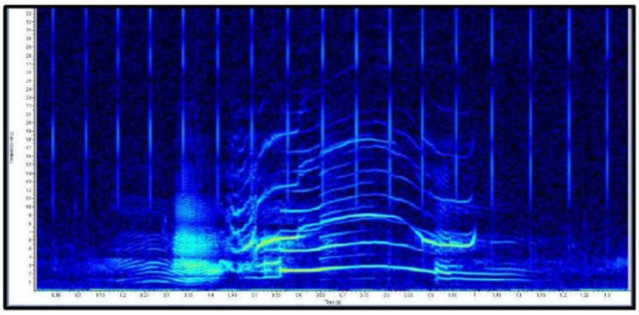
CALL TYPE McM3A

This is a 2-component biphonic call. This call is deemed a variation of Call McM3 due to the first pulse component starting well before the biphonic whistle commences. Part 1 is a burst-pulse sound starting at a low SBS (low PRR), increasing SBS to approximately 1 kHz, then decreasing SBS towards the end of the component. Part 2 is a biphonic whistle with harmonics that consists of an upsweeping contour and then decreases in frequency over time.

n = 30



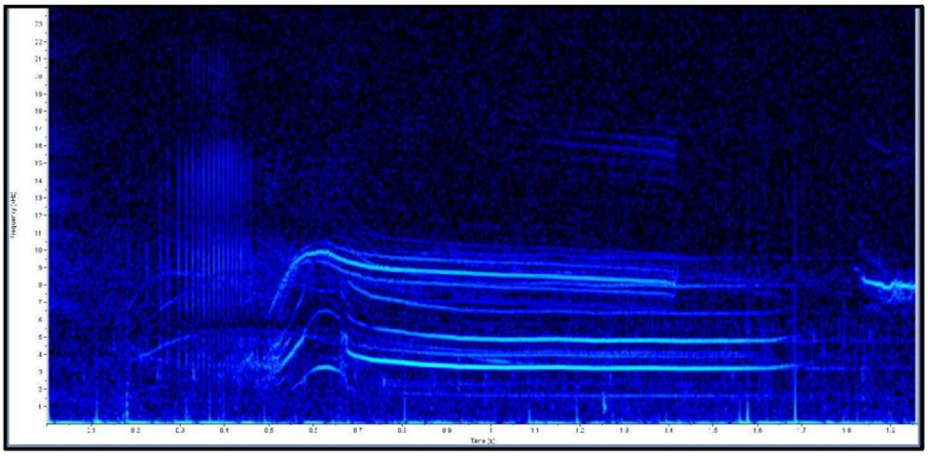
Call Type	Component	Statistic	Dur [s]	Fmin [Hz]	Fmax [Hz]	Fdelta [Hz]	BW 90% [Hz]	Fpeak [Hz]	Fcentre [Hz]	Q1F [Hz]	Q3F [Hz]	MinEnt [bits]	MaxEnt [bits]	AvgEnt [bits]	Dur90% [s]	Fstart [Hz]	Fend [Hz]	Ext	Infl	FM [1/s]	Steps
3a	1	Mean	0.98	681	17377	16696	4297	2398	2961	2375	4586	2.9	7.0	4.4	0.45						
n=30		*SD*	0.10	182	5073	5180	2200	104	1052	125	1933	0.7	0.8	0.3	0.14						
	2	Mean	0.45	3178	9832	6654	3742	4250	4898	4102	5656	2.7	6.0	3.6	0.28	3030	7461	2	3	6.8	2
		SD	0.11	1094	1028	1906	2284	1719	1374	1330	1276	0.7	0.3	0.6	0.17	1571	3939	1	1	2.5	1
	Entire	Mean	0.98	612	17316	16704	4297	2398	2961	2375	4586	2.9	7.0	4.4	0.45						
		SD	0.10	245	5073	5260	2200	104	1052	125	1933	0.7	0.8	0.3	0.14						



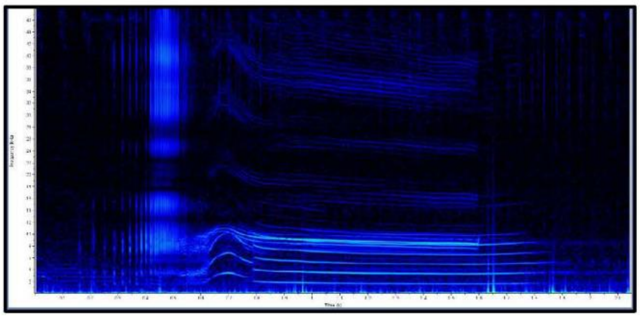
CALL TYPE MCM4

This is a 3-component biphonic call. Part 1 consists of a series of distinct pulses. Part 2 is burst-pulse sound with an SBS of up to 2kHz. Part 3 is a biphonic whistle with harmonics and weak sidebands (amplitude-modulated) and consists of an upsweeping contour followed by a constant wave.

n = 59



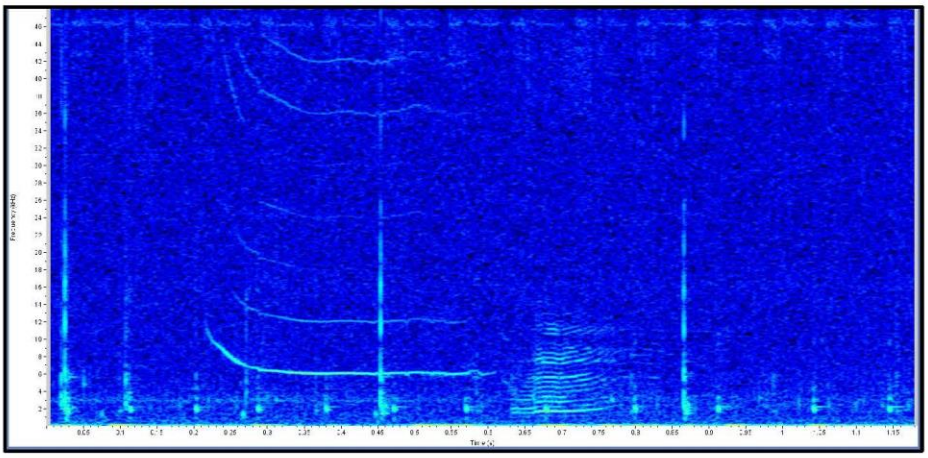
Call Type	Component	Statistic	Dur [s]	Fmin [Hz]	Fmax [Hz]	Fdelta [Hz]	BW 90% [Hz]	Fpeak [Hz]	Fcentre [Hz]	Q1F [Hz]	Q3F [Hz]	MinEnt [bits]	MaxEnt [bits]	AvgEnt [bits]	Dur90% [s]	Fstart [Hz]	Fend [Hz]	Ext	Infl	FM [1/s]	Steps
4	1	**Mean**	0.37	1254	26573	25319	17746	3156	4980	3168	8797	5.2	7.8	6.8	0.31						
n=59		***SD***	0.12	584	15639	15218	12721	1722	3463	1728	8965	0.7	1.0	0.6	0.11						
	2	**Mean**	1.30	1348	22927	21579	4809	4836	3945	3246	4965	4.3	7.3	4.4	0.82						
		SD	0.12	335	16081	15979	2418	2529	1450	216	2186	0.9	0.9	0.7	0.07						
	3	**Mean**	1.10	5199	10607	5408	4098	6836	7250	6414	8250	3.9	5.3	4.5	0.83	5199	8192	1	2	2.1	0
		SD	0.10	1131	770	1226	1203	1893	1553	1985	673	0.9	0.8	0.6	0.18	1131	790	0.4	0.4	0.5	0
	Entire	**Mean**	1.66	1091	26521	25430	7426	4836	3965	3258	5020	4.8	7.4	5.0	1.08						
		SD	0.16	465	15555	15331	8278	2529	1474	239	2217	1.2	1.0	0.5	0.13						



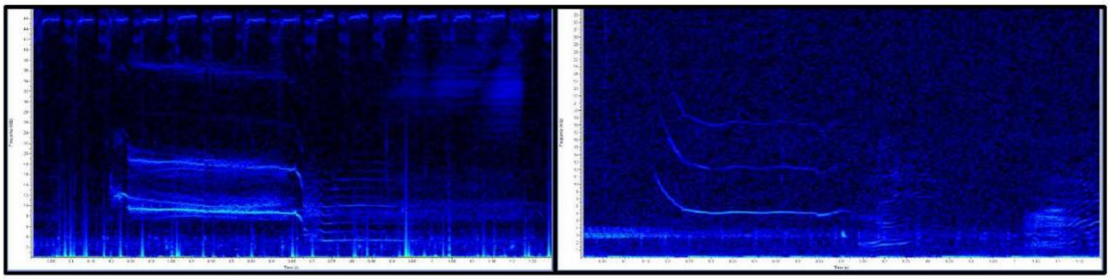
CALL TYPE McM5

This is a 2-component call. Part 1 is a whistle with harmonics starting as a downsweep and ending as a constant wave. Part 2 is burst-pulse sound with SBS (PRR) ranging from approximately 500Hz to 1kHz.

n = 84



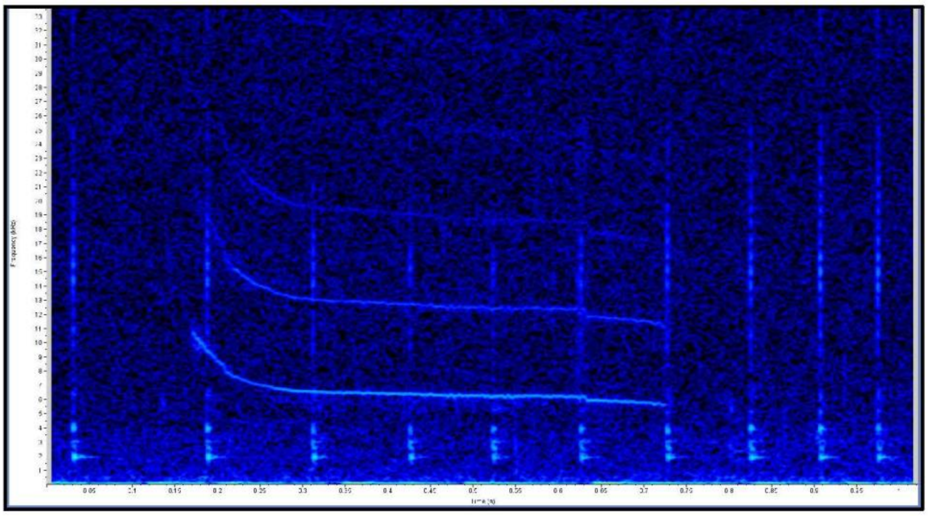
Call Type	Component	Statistic	Dur [s]	Fmin [Hz]	Fmax [Hz]	Fdelta [Hz]	BW 90% [Hz]	Fpeak [Hz]	Fcentre [Hz]	Q1F [Hz]	Q3F [Hz]	MinEnt [bits]	MaxEnt [bits]	AvgEnt [bits]	Dur90% [s]	Fstart [Hz]	Fend [Hz]	Ext	Infl	FM [1/s]	Steps
5	1	**Mean**	0.41	4963	10589	5626	2079	6215	6171	5890	6596	2.4	6.1	3.2	0.31	10589	5029	0.4	0.4	1.0	0
n=84		***SD***	0.09	644	2274	2149	1781	1261	1299	1143	1793	0.2	0.6	0.5	0.10	2274	674	1	1	2.2	0
	2	**Mean**	0.23	1360	11226	9865	5824	2824	3127	2358	4831	4.5	6.8	5.8	0.18						
		SD	0.13	903	3626	3476	2065	1709	1317	851	1742	0.6	0.4	0.5	0.11						
	Entire	**Mean**	0.66	1365	12255	10890	6416	6356	5950	4693	7006	4.3	6.9	4.6	0.47						
		SD	0.14	897	3299	3169	3040	2974	1083	1648	2612	1.3	0.4	0.5	0.13						



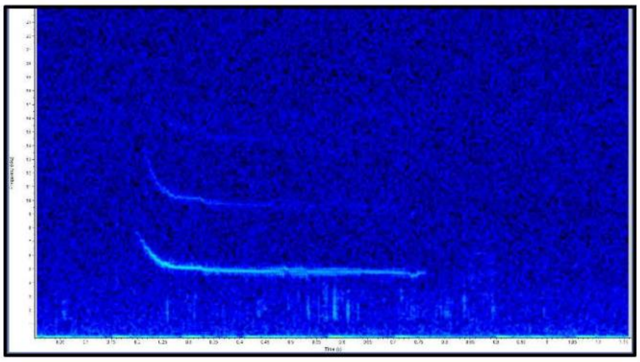
CALL TYPE McM5A

This is a single-component call. This call is deemed a variation of primary call McM5 due to the second component missing. This call consists of a whistle with harmonics starting as a downsweep and ending as a constant wave.

n = 43



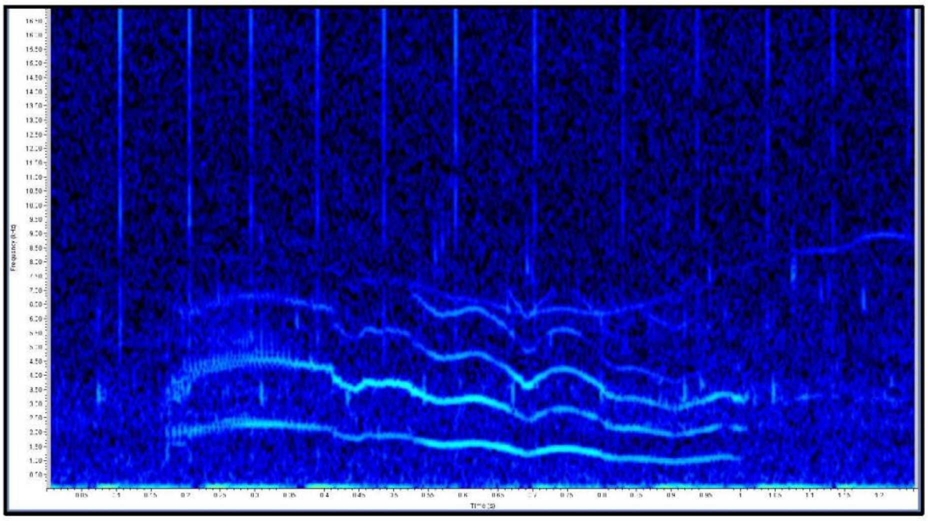
Call Type	Component	Statistic	Dur [s]	Fmin [Hz]	Fmax [Hz]	Fdelta [Hz]	BW 90% [Hz]	Fpeak [Hz]	Fcentre [Hz]	Q1F [Hz]	Q3F [Hz]	MinEnt [bits]	MaxEnt [bits]	AvgEnt [bits]	Dur90% [s]	Fstart [Hz]	Fend [Hz]	Ext	Infl	FM [1/s]	Steps
5a	1	**Mean**	0.50	5322	9482	4160	2729	6115	6281	5917	6646	2.3	4.6	3.1	0.41	9482	5397	0.1	0.1	0.2	0.3
n=43		***SD***	0.10	1419	1898	1199	1202	1455	1471	1446	1546	0.9	0.9	0.9	0.09	1898	1629	0.3	0.3	0.6	1



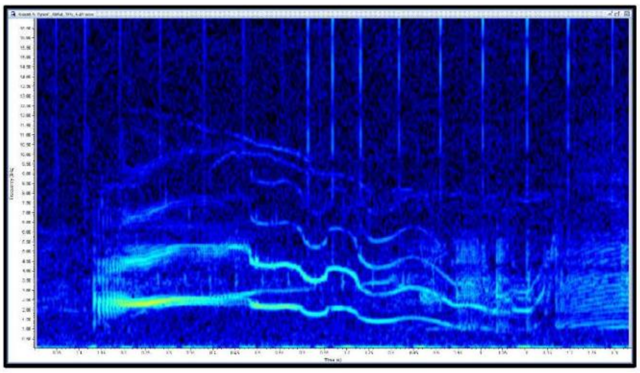
CALL TYPE McM6

This is a 2-component call. Part 1 consists of a series of distinct pulses. As the PRR increases, the spectrogram displays these as an upsweeping contour. Part 2 is burst-pulse sound with a SBS of 1kHz to 2kHz, decreasing towards the end.

n = 13



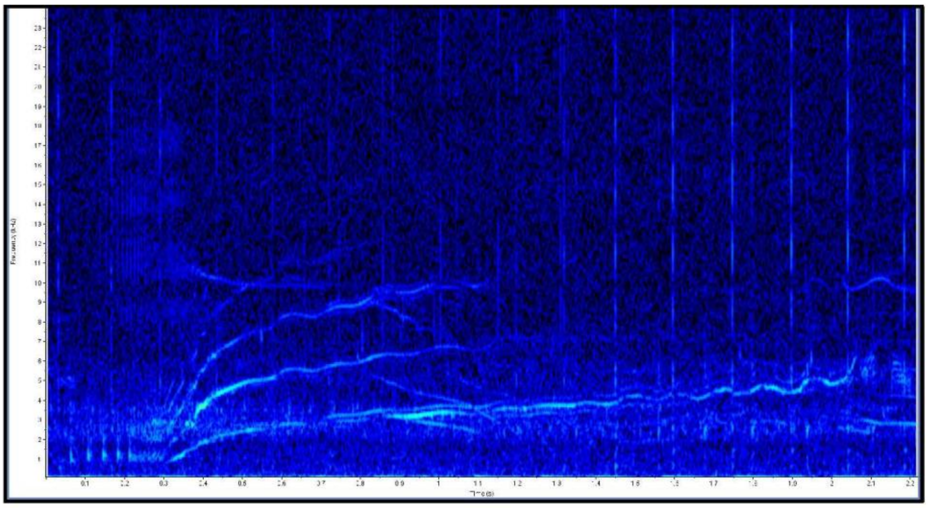
Call Type	Component	Statistic	Dur [s]	Fmin [Hz]	Fmax [Hz]	Fdelta [Hz]	BW 90% [Hz]	Fpeak [Hz]	Fcentre [Hz]	Q1F [Hz]	Q3F [Hz]	MinEnt [bits]	MaxEnt [bits]	AvgEnt [bits]	Dur90% [s]	Fstart [Hz]	Fend [Hz]	Ext	Infl	FM [1/s]	Steps
6	1	**Mean**	0.10	915	8405	7491	3328	2313	2453	2250	3578	4.0	6.2	5.2	0.10						
n=13		***SD***	0.03	361	998	1323	1219	72	135	81	1001	0.7	0.2	0.6	0.00						
	2	**Mean**	0.69	956	8877	7921	2922	2688	2578	2016	3094	3.4	6.3	4.3	0.47						
		SD	0.18	395	916	814	665	636	406	447	615	0.5	0.2	0.3	0.15						
	Entire	**Mean**	0.80	746	8974	8228	2969	2688	2578	2031	3156	3.8	6.3	4.4	0.50						
		SD	0.18	67	748	716	728	636	406	420	638	0.7	0.2	0.4	0.20						



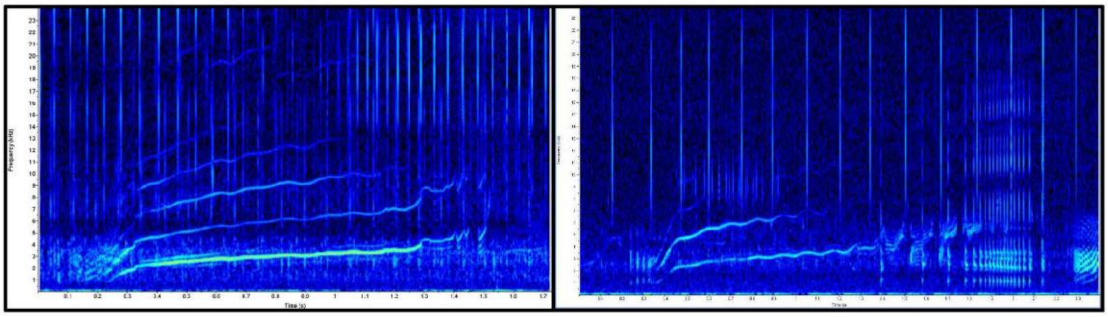
CALL TYPE McM7

This is a singular whistle with a high number of extrema and inflection points and therefore high frequency-modulation. Harmonics are present and some calls start out with distinct pulses and others have steps towards the end of the call. There are signs of AM evidenced by occasional weak sidebands.

n = 88



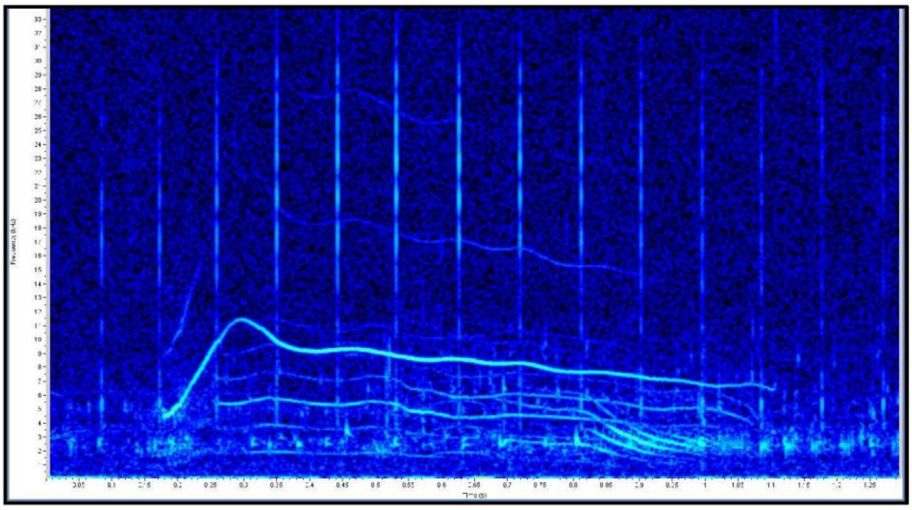
Call Type	Component	Statistic	Dur [s]	Fmin [Hz]	Fmax [Hz]	Fdelta [Hz]	BW 90% [Hz]	Fpeak [Hz]	Fcentre [Hz]	Q1F [Hz]	Q3F [Hz]	MinEnt [bits]	MaxEnt [bits]	AvgEnt [bits]	Dur90% [s]	Fstart [Hz]	Fend [Hz]	Ext	Infl	FM [1/s]	Steps
7	1	**Mean**	1.38	1309	4714	3406	1990	3188	3094	2734	3542	2.0	4.6	2.9	1.15	1309	4650	7	7	5.4	4
n=88		***SD***	0.54	765	1324	1235	876	991	803	658	932	0.5	0.5	0.6	0.49	765	1331	9	10	6.5	4



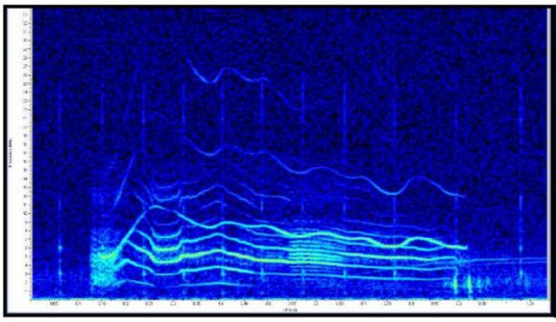
CALL TYPE McM8

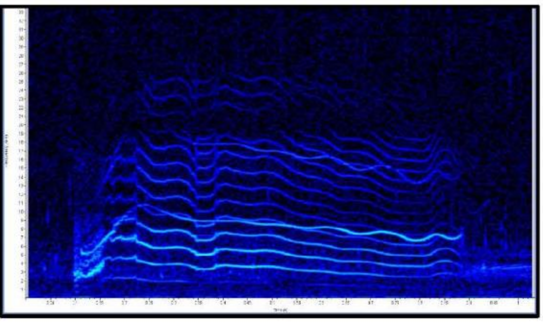
This is a 2-component biphonic call. Part 1 is a burst-pulse sound with an SBS of approximately 1 kHz. Part 2 is a biphonic whistle that is highly frequency-modulated with harmonics that consists of an upsweeping contour followed by a slow downsweep.

n = 36



Call Type	Component	Statistic	Dur [s]	Fmin [Hz]	Fmax [Hz]	Fdelta [Hz]	BW 90% [Hz]	Fpeak [Hz]	Fcentre [Hz]	Q1F [Hz]	Q3F [Hz]	MinEnt [bits]	MaxEnt [bits]	AvgEnt [bits]	Dur90% [s]	Fstart [Hz]	Fend [Hz]	Ext	Infl	FM [1/s]	Steps
8	1	Mean	0.81	1511	15779	14268	6181	4540	5826	3917	7232	3.6	6.2	4.6	0.66						
n=36		*SD*	0.08	733	5399	5479	984	1340	930	578	1138	0.4	0.7	0.4	0.05						
	2	Mean	0.83	4386	11219	6833	4078	5136	6690	5538	7527	2.8	5.7	3.8	0.64	5016	7204	12	13	15.9	0
		SD	0.09	223	915	1027	725	529	1231	674	1092	0.3	0.5	0.3	0.05	719	983	2	2	2.9	0
	Entire	Mean	0.84	1408	15930	14522	6194	4821	5792	3897	7199	3.5	6.5	4.6	0.69						
		SD	0.08	722	5255	5412	972	1030	824	556	1126	0.4	0.5	0.4	0.07						

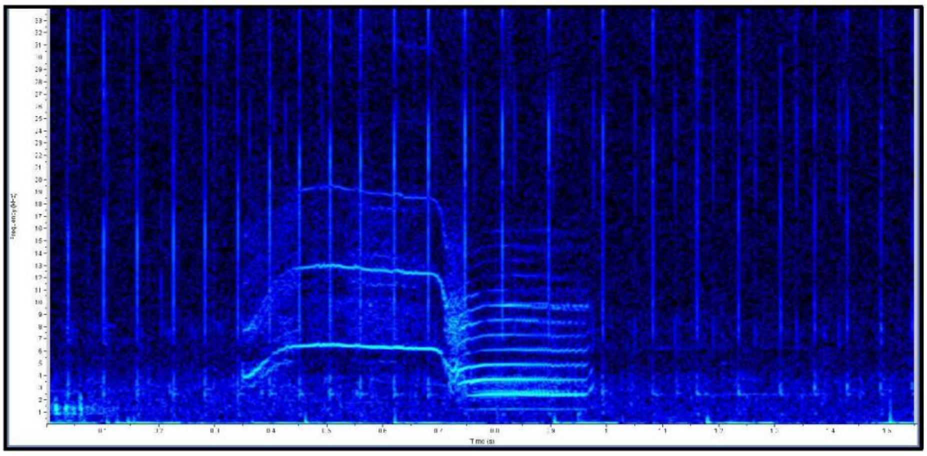




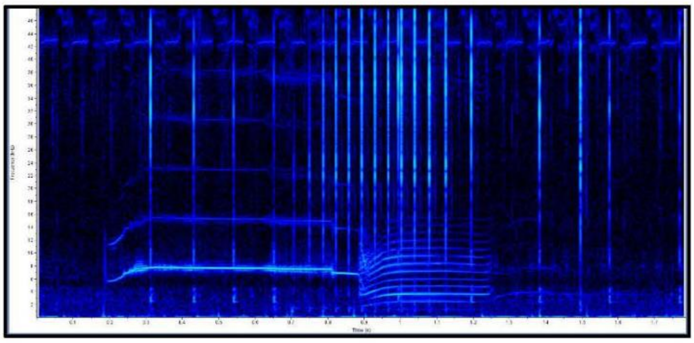
CALL TYPE McM9

This is a 2-component call. Part 1 is a whistle with harmonics and occasional weak sidebands indicative of amplitude-modulation. Part 2 is a burst-pulse sound with a constant SBS of approximately 1 kHz.

n = 19



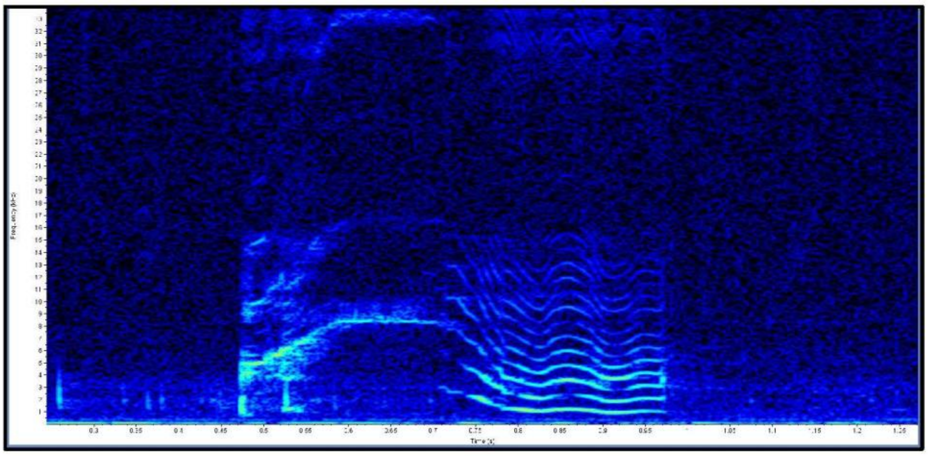
Call Type	Component	Statistic	Dur [s]	Fmin [Hz]	Fmax [Hz]	Fdelta [Hz]	BW 90% [Hz]	Fpeak [Hz]	Fcentre [Hz]	Q1F [Hz]	Q3F [Hz]	MinEnt [bits]	MaxEnt [bits]	AvgEnt [bits]	Dur90% [s]	Fstart [Hz]	Fend [Hz]	Ext	Infl	FM [1/s]	Steps
9	1	Mean	0.63	4368	7098	2730	1113	6773	6797	6656	6902	2.6	5.1	2.6	0.50	4461	5501	3	4	5.6	2
n=19		*SD*	0.21	620	654	333	864	814	721	730	709	0.7	0.4	0.2	0.14	635	339	1	2	2.0	1
	2	Mean	0.36	915	18218	17303	6773	3457	3562	2941	5016	3.3	7.4	4.7	0.28						
		SD	0.06	445	835	522	3970	234	115	449	2178	0.3	0.5	0.3	0.05						
	Entire	Mean	0.99	873	18364	17490	6129	5379	5508	4195	6832	3.4	7.4	3.9	0.78						
		SD	0.25	322	852	570	2729	2404	2028	2094	772	0.7	0.4	0.5	0.21						



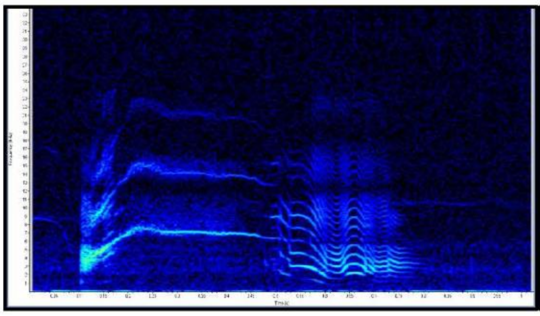
CALL TYPE McM10

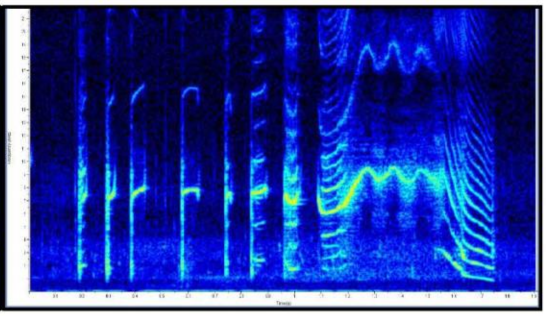
This is a 3-component call. Part 1 is a burst-pulse sound. Part 2 is a whistle with harmonics. Part 3 is a burst-pulse sound with a SBS of approximately 1 kHz. Some calls in this category were observed as rhythmic repeated call sequences of the primary call McM10.

n = 95



Call Type	Component	Statistic	Dur [s]	Fmin [Hz]	Fmax [Hz]	Fdelta [Hz]	BW 90% [Hz]	Fpeak [Hz]	Fcentre [Hz]	Q1F [Hz]	Q3F [Hz]	MinEnt [bits]	MaxEnt [bits]	AvgEnt [bits]	Dur90% [s]	Fstart [Hz]	Fend [Hz]	Ext	Infl	FM [1/s]	Steps
10	1	Mean	0.07	1905	19587	17681	4084	4932	4805	4321	5401	3.3	7.0	4.9	0.05						
n=95		*SD*	0.02	1081	5445	5655	2212	911	828	842	883	0.6	0.9	0.7	0.05						
	2	Mean	0.25	4402	7544	3142	2258	5526	5724	5281	6304	2.7	5.4	3.5	0.16	4578	5770	2	2	10.1	0
		SD	0.08	685	1230	993	867	924	879	741	1022	0.5	0.7	0.7	0.06	705	1247	2	2	6.7	0
	3	Mean	0.28	955	24704	23749	9025	3027	3586	2406	5303	3.7	7.5	5.4	0.21						
		SD	0.07	522	12452	12721	10074	1787	1557	570	3047	1.2	0.9	0.9	0.05						
	Entire	Mean	0.54	843	25262	24420	8663	4465	4705	3585	6570	3.4	7.6	5.0	0.41						
		SD	0.11	523	12178	12504	9681	1631	1412	1137	2408	1.1	0.9	0.8	0.11						

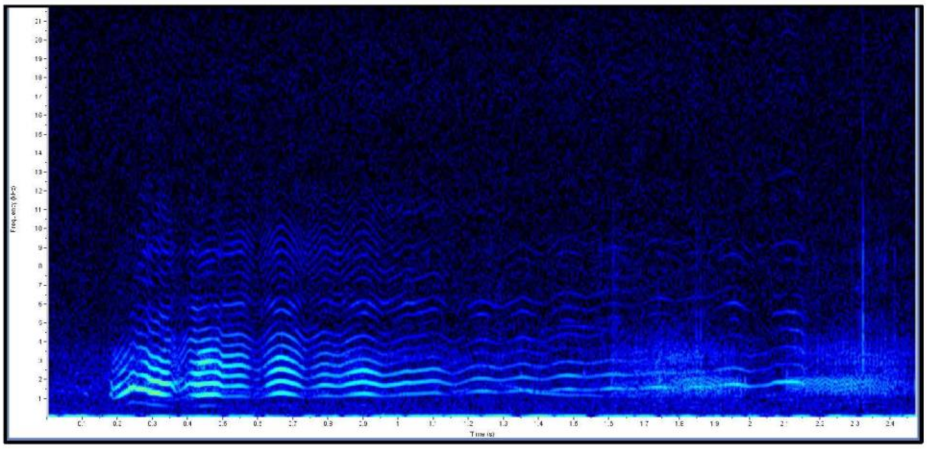




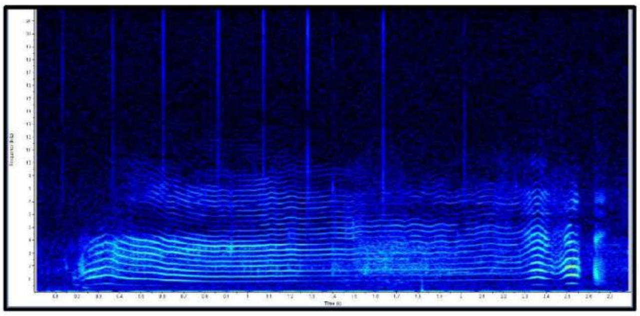
CALL TYPE McM11

This is a single-component call consisting of a burst-pulse sound with a SBS of approximately 500Hz.

n = 36



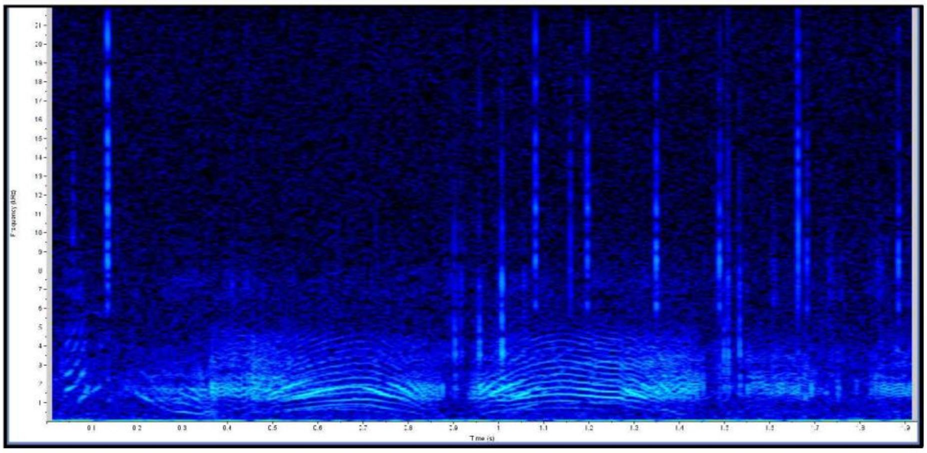
Call Type	Component	Statistic	Dur [s]	Fmin [Hz]	Fmax [Hz]	Fdelta [Hz]	BW 90% [Hz]	Fpeak [Hz]	Fcentre [Hz]	Q1F [Hz]	Q3F [Hz]	MinEnt [bits]	MaxEnt [bits]	AvgEnt [bits]	Dur90% [s]	Fstart [Hz]	Fend [Hz]	Ext	Infl	FM [1/s]	Steps
11	1	Mean	1.65	413	13998	13585	2894	1690	1892	1548	2678	4.1	7.7	5.4	1.23						
n=36		*SD*	0.38	119	3415	3374	2124	263	188	153	514	1.4	1.0	0.8	0.39						



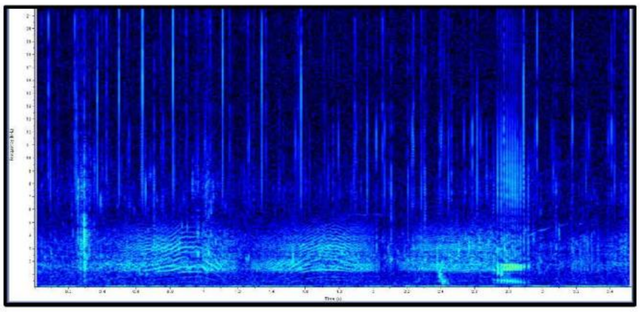
CALL TYPE McM12

This is a single-component call consisting of a burst-pulse sound starting with an increasing SBS and then decreasing SBS. Calls are often repeated and appear as a 'reflection' of each other.

n = 65



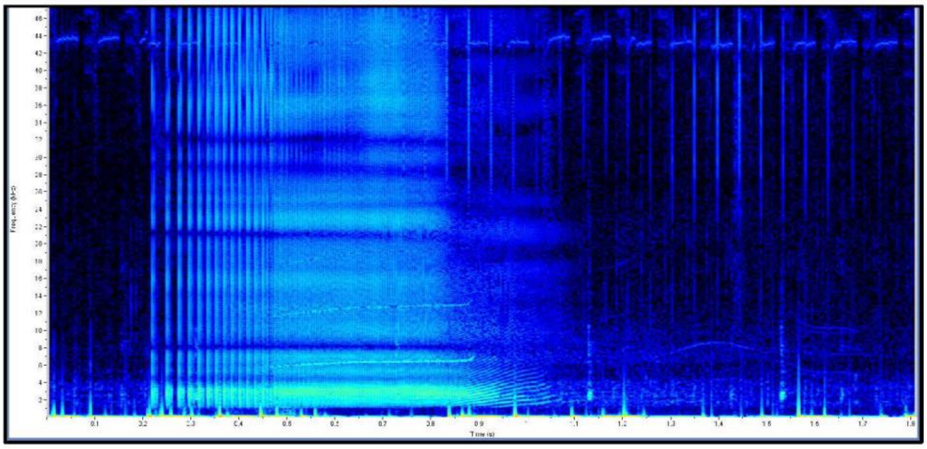
Call Type	Component	Statistic	Dur [s]	Fmin [Hz]	Fmax [Hz]	Fdelta [Hz]	BW 90% [Hz]	Fpeak [Hz]	Fcentre [Hz]	Q1F [Hz]	Q3F [Hz]	MinEnt [bits]	MaxEnt [bits]	AvgEnt [bits]	Dur90% [s]	Fstart [Hz]	Fend [Hz]	Ext	Infl	FM [1/s]	Steps
12	1	Mean	0.75	271	5824	5553	2531	1504	1910	1451	2629	4.8	7.2	6.1	0.58						
n=65		*SD*	0.19	99	404	380	357	568	319	97	503	0.6	0.1	0.3	0.15						



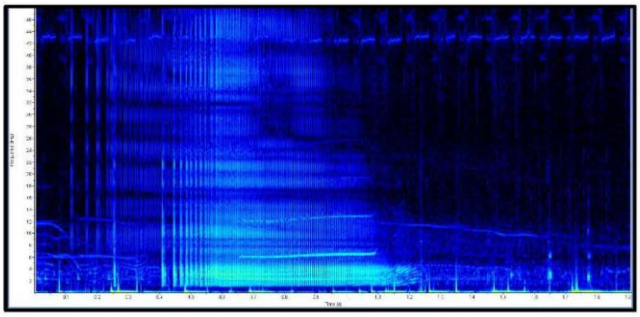
CALL TYPE McM13

This is a 2-component biphonic call. Part 1 starts as distinct pulses at increasing PRR, continuing as a burst-pulse sound. Part 2 is a biphonic whistle with harmonics and very little frequency-modulation.

n = 3



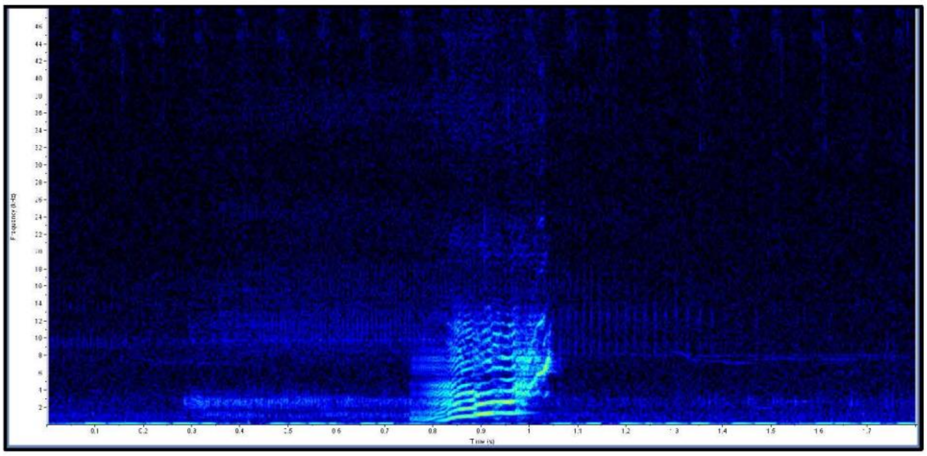
Call Type	Component	Statistic	Dur [s]	Fmin [Hz]	Fmax [Hz]	Fdelta [Hz]	BW 90% [Hz]	Fpeak [Hz]	Fcentre [Hz]	Q1F [Hz]	Q3F [Hz]	MinEnt [bits]	MaxEnt [bits]	AvgEnt [bits]	Dur90% [s]	Fstart [Hz]	Fend [Hz]	Ext	Infl	FM [1/s]	Steps
13	1	Mean	0.81	1251	47492	46241	28094	4656	4734	3125	8797	5.9	8.4	7.1	0.60						
n=3		***SD***	0.08	409	544	951	10723	2828	2477	866	4902	0.5	0.9	0.4	0.00						
	2	Mean	0.44	5521	7494	1973	1578	6859	6594	6141	6984	3.6	5.0	4.4	0.40	6269	6745	0	0	0	0
		SD	0.01	118	362	250	379	882	420	47	665	0.4	0.1	0.4	0.00	1415	945	0	0	0	0



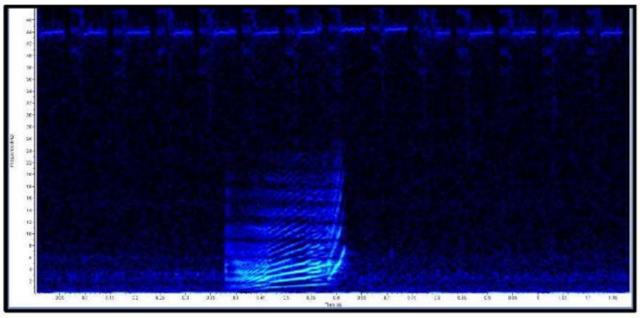
CALL TYPE McM14

This is a single-component burst-pulse sound with increasing SBS (PRR).

n = 16



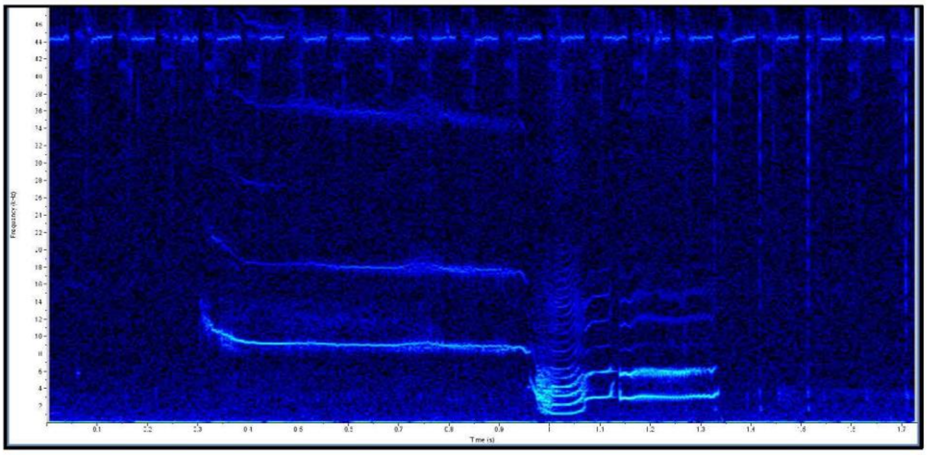
Call Type	Component	Statistic	Dur [s]	Fmin [Hz]	Fmax [Hz]	Fdelta [Hz]	BW 90% [Hz]	Fpeak [Hz]	Fcentre [Hz]	Q1F [Hz]	Q3F [Hz]	MinEnt [bits]	MaxEnt [bits]	AvgEnt [bits]	Dur90% [s]	Fstart [Hz]	Fend [Hz]	Ext	Infl	FM [1/s]	Steps
14	1	Mean	0.30	278	28188	27910	3636	2745	2842	2001	3516	3.3	7.2	5.0	0.20						
n=16		*SD*	0.10	130	7315	7369	1834	955	496	584	326	0.1	0.2	0.4	0.08						



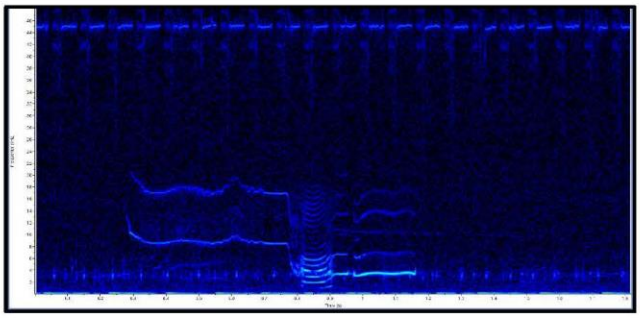
CALL TYPE McM15

This is a 3-component call. Part 1 is a whistle with harmonics. Part 2 a burst-pulse sound with a SBS of 500Hz. Part 3 is another burst-pulse sound with a SBS of 2kHz.

n = 89



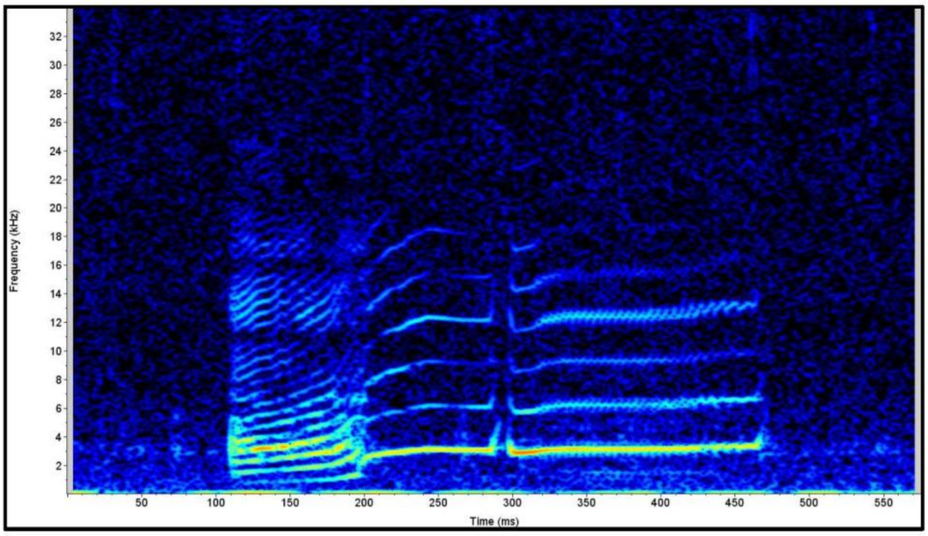
Call Type	Component	Statistic	Dur [s]	Fmin [Hz]	Fmax [Hz]	Fdelta [Hz]	BW 90% [Hz]	Fpeak [Hz]	Fcentre [Hz]	Q1F [Hz]	Q3F [Hz]	MinEnt [bits]	MaxEnt [bits]	AvgEnt [bits]	Dur90% [s]	Fstart [Hz]	Fend [Hz]	Ext	Infl	FM [1/s]	Steps
15	1	**Mean**	0.53	4542	11385	6843	4492	6507	7762	6800	8305	3.1	6.3	4.6	0.45	10905	5022	5	5	9.2	0
n=89		***SD***	0.15	1668	2636	2212	2110	2342	1625	1751	1767	0.5	0.5	0.8	0.15	3335	2258	5	5	9.5	1
	2	**Mean**	0.15	1065	15129	14064	3896	3394	3463	2881	4144	3.3	6.8	4.9	0.11						
		SD	0.04	550	6644	6822	1226	782	641	547	610	0.6	0.7	0.4	0.04						
	3	**Mean**	0.33	1835	14652	12817	2639	3408	3560	3298	4095	2.7	7.2	4.2	0.25						
		SD	0.10	729	7203	7272	1571	722	683	566	830	0.4	0.7	0.6	0.09						
	Entire	**Mean**	0.99	960	16666	15706	6480	3215	3596	3080	4754	3.2	7.4	5.0	0.74						
		SD	0.20	484	7170	7276	2998	619	503	494	1306	1.0	0.6	0.5	0.22						



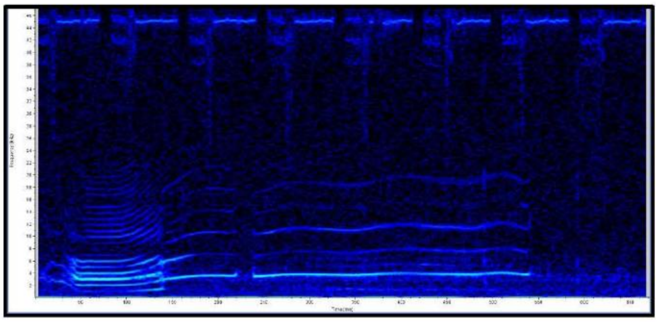
CALL TYPE McM15A

This is a 2-component call and a variation of call type McM15 as the first component of McM15 is missing here. Part 1 is a burst-pulse sound with a SBS of 500Hz. Part 2 is another burst-pulse with a SBS of 2kHz.

n = 54



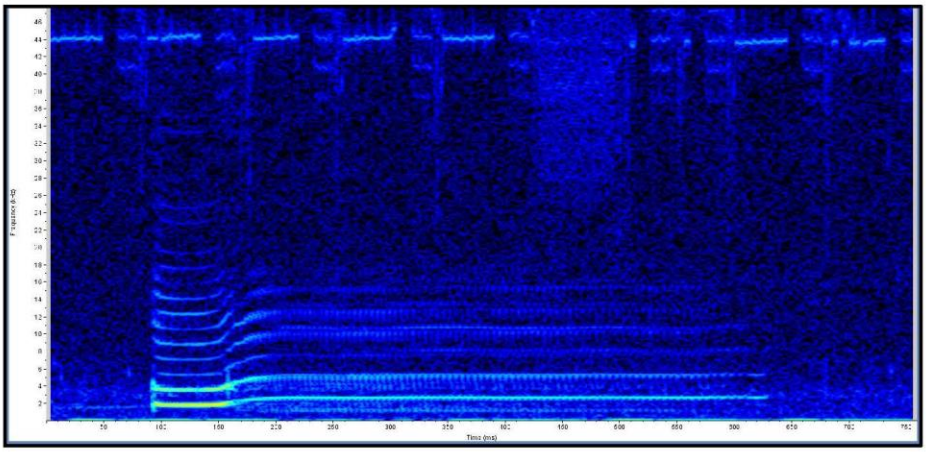
Call Type	Component	Statistic	Dur [s]	Fmin [Hz]	Fmax [Hz]	Fdelta [Hz]	BW 90% [Hz]	Fpeak [Hz]	Fcentre [Hz]	Q1F [Hz]	Q3F [Hz]	MinEnt [bits]	MaxEnt [bits]	AvgEnt [bits]	Dur90% [s]	Fstart [Hz]	Fend [Hz]	Ext	Infl	FM [1/s]	Steps
15a	1	Mean	0.16	622	21200	20578	4275	3384	3422	2934	3862	2.6	6.5	4.1	0.12						
n=54		*SD*	0.06	211	6329	6357	2131	308	301	451	476	0.5	0.8	0.5	0.04						
	2	Mean	0.35	1879	21000	19121	4144	3234	3183	3000	3956	1.8	6.9	3.1	0.27						
		SD	0.08	532	4795	4644	4465	865	551	444	968	0.5	0.5	0.8	0.07						
	Entire	Mean	0.51	599	22273	21674	4486	3422	3347	2873	3914	2.8	6.9	3.5	0.42						
		SD	0.09	229	5076	5109	2813	304	359	326	606	1.7	0.5	0.7	0.08						



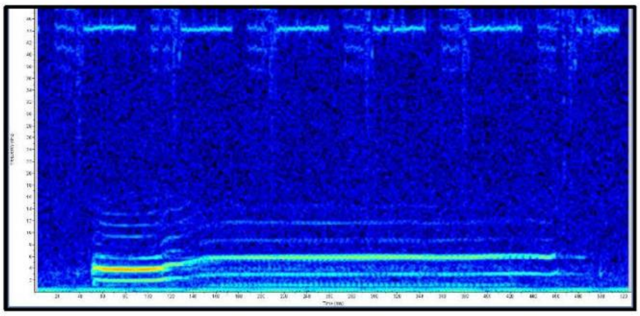
CALL TYPE McM16

This is a burst-pulse sound starting with a SBS of 1kHz increasing to 2kHz.

n = 7



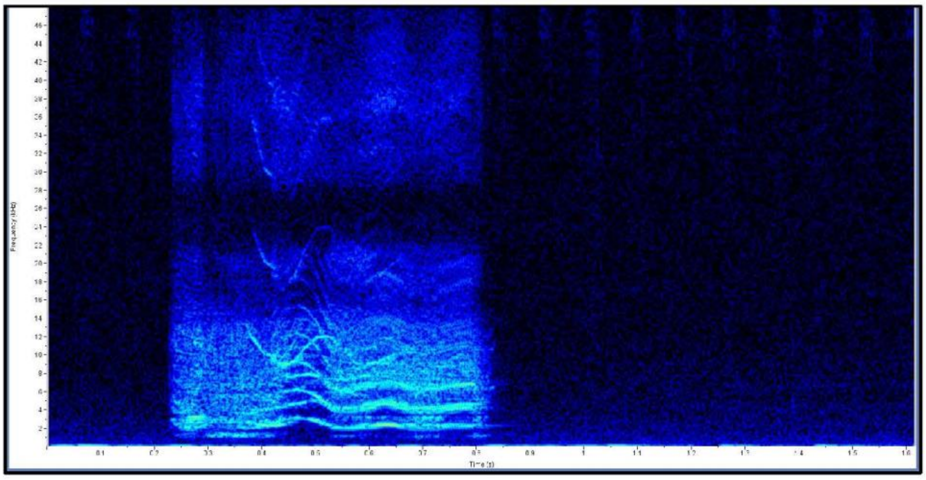
Call Type	Component	Statistic	Dur [s]	Fmin [Hz]	Fmax [Hz]	Fdelta [Hz]	BW 90% [Hz]	Fpeak [Hz]	Fcentre [Hz]	Q1F [Hz]	Q3F [Hz]	MinEnt [bits]	MaxEnt [bits]	AvgEnt [bits]	Dur90% [s]	Fstart [Hz]	Fend [Hz]	Ext	Infl	FM [1/s]	Steps
16	1	Mean	0.42	1193	15750	14557	2652	3134	2826	2451	3502	2.9	6.2	3.7	0.27						
n=7		***SD***	0.07	394	6030	5899	600	1291	855	890	841	1.6	0.4	0.9	0.10						



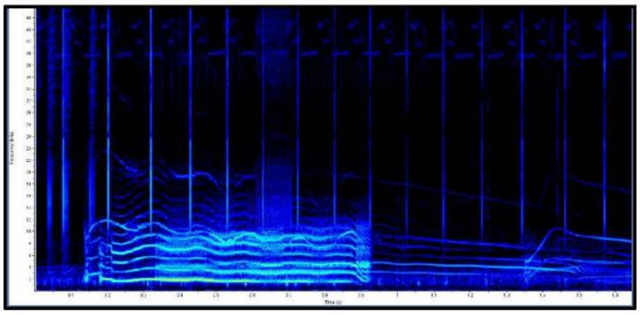
CALL TYPE McM17

This is a 2-component biphonic call consisting of a burst-pulse sound with an SBS of 1-2 kHz and a biphonic whistle with harmonics and high frequency-modulation.

n = 3



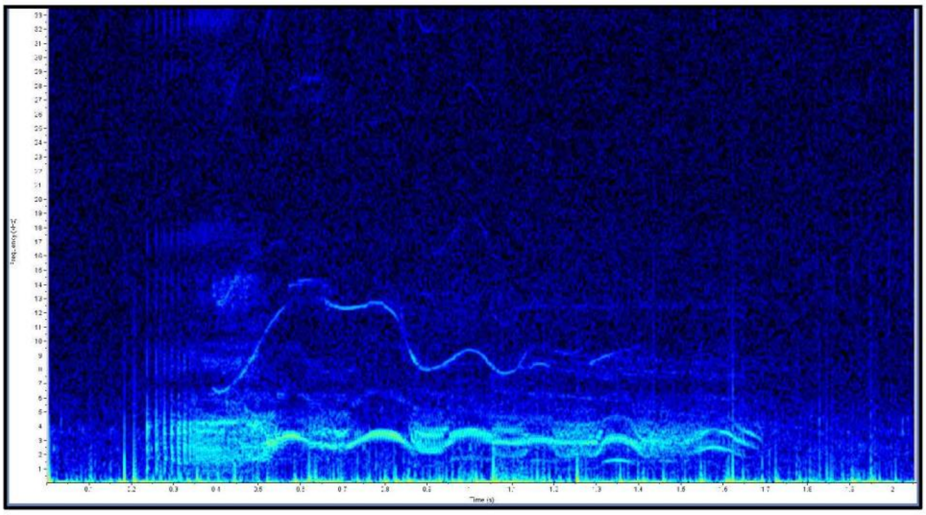
Call Type	Component	Statistic	Dur [s]	Fmin [Hz]	Fmax [Hz]	Fdelta [Hz]	BW 90% [Hz]	Fpeak [Hz]	Fcentre [Hz]	Q1F [Hz]	Q3F [Hz]	MinEnt [bits]	MaxEnt [bits]	AvgEnt [bits]	Dur90% [s]	Fstart [Hz]	Fend [Hz]	Ext	Infl	FM [1/s]	Steps
17	1	**Mean**	0.65	857	25578	24721	6078	2109	2844	2156	4359	3.6	6.2	4.3	0.50						
n=3		***SD***	0.12	166	1091	1251	3342	366	1382	430	2268	0.8	0.1	0.8	0.10						
	2	**Mean**	0.59	5540	13063	7523	3313	6016	6656	6125	7547	2.7	5.8	4.1	0.43	7977	8831	7	8	14.0	0
		SD	0.18	3289	1090	3069	985	3382	3851	3484	4357	0.2	0.5	0.5	0.06	6141	2165	3	3	1.1	0
	Entire	**Mean**	0.66	880	25615	24735	6078	2109	2844	2156	4359	3.5	6.2	4.3	0.50						
		SD	0.13	186	1078	1255	3342	366	1382	430	2268	0.8	0.1	0.8	0.10						



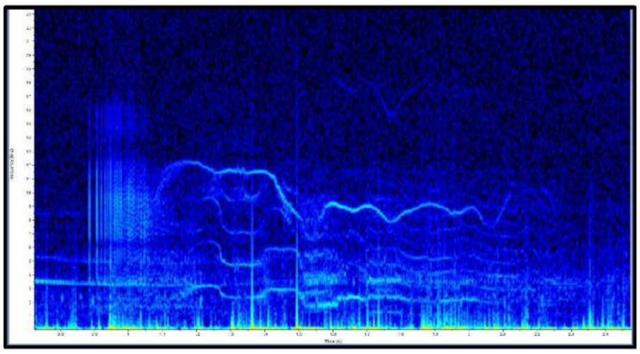
CALL TYPE McM18

This is a 3-component biphonic call. Part 1 consists of distinct pulses. Part 2 is a burst-pulse sound with variable SBS. Part 3 is a biphonic whistle with harmonics and high frequency-modulation.

n = 3



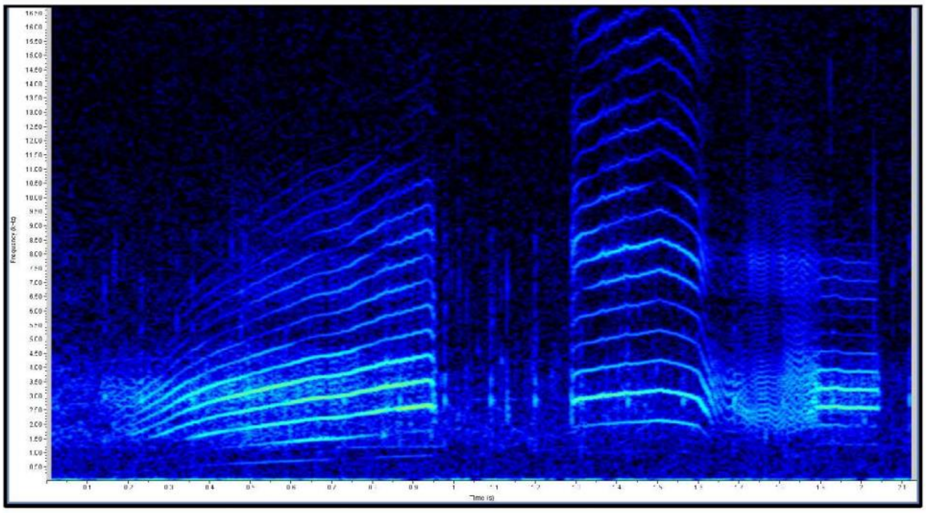
Call Type	Component	Statistic	Dur [s]	Fmin [Hz]	Fmax [Hz]	Fdelta [Hz]	BW 90% [Hz]	Fpeak [Hz]	Fcentre [Hz]	Q1F [Hz]	Q3F [Hz]	MinEnt [bits]	MaxEnt [bits]	AvgEnt [bits]	Dur90% [s]	Fstart [Hz]	Fend [Hz]	Ext	Infl	FM [1/s]	Steps
18	**1**	**Mean**	0.26	1821	29203	27382	9125	14359	16047	13969	18313	3.6	7.5	6.4	0.20						
n=3		***SD***	0.10	790	16317	15705	6100	19677	19374	19252	20831	0.5	1.5	1.7	0.10						
	2	**Mean**	1.22	1305	11467	10161	6875	4469	5125	2969	6313	3.8	5.9	4.6	1.00						
		SD	0.04	222	2361	2162	4441	2907	3357	871	3217	1.2	0.9	1.1	0.10						
	3	**Mean**	1.09	6163	12938	6775	5500	8516	9078	8313	10844	3.2	5.7	4.0	0.87	7050	9404	12	12	11.1	0
		SD	0.21	1275	523	1530	1597	683	404	423	1172	0.8	0.8	0.7	0.21	2351	801	3	4	3.6	0
	Entire	**Mean**	1.48	1305	29175	27870	16531	14234	14703	12531	17484	4.0	6.9	5.3	1.00						
		SD	0.06	247	16269	16091	18337	19789	19703	17321	20664	1.7	1.4	1.6	0.26						



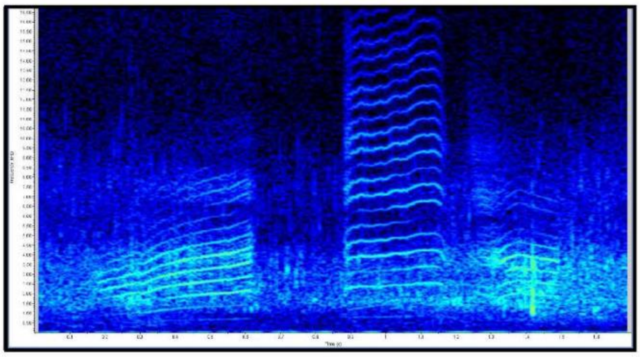
CALL TYPE McM19

This is a 4-component monophonic call. All components are burst-pulse sounds. There is a gap in between the first and second components.

n = 2



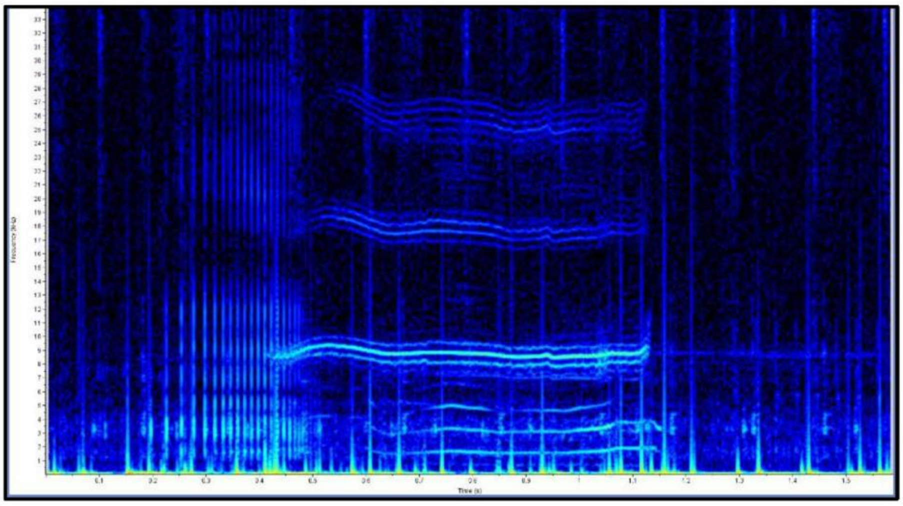
Call Type	Component	Statistic	Dur [s]	Fmin [Hz]	Fmax [Hz]	Fdelta [Hz]	BW 90% [Hz]	Fpeak [Hz]	Fcentre [Hz]	Q1F [Hz]	Q3F [Hz]	MinEnt [bits]	MaxEnt [bits]	AvgEnt [bits]	Dur90% [s]	Fstart [Hz]	Fend [Hz]	Ext	Infl	FM [1/s]	Steps
19	**1**	**Mean**	0.64	531	14492	13960	2390	3058	2885	2369	3467	3.1	6.2	4.2	0.45						
n=2		***SD***	0.21	26	2047	2021	213	670	61	305	213	0.9	0.1	0.7	0.07						
	2	**Mean**	0.36	715	22050	21336	7171	3402	3424	2649	3919	3.6	6.9	4.6	0.30						
		SD	0.06	130	0	130	1492	731	579	396	1096	1.7	0.4	1.2	0.00						
	3	**Mean**	0.17	1044	12293	11249	4113	3187	2972	2153	3596	4.7	6.3	5.7	0.15						
		SD	0.10	26	648	674	1431	853	244	365	274	0.5	0.0	0.3	0.07						
	4	**Mean**	0.19	898	9307	8409	1873	1916	2606	2196	3424	3.5	6.3	4.2	0.10						
		SD	0.01	78	52	26	1370	944	30	548	274	1.2	0.3	1.2	0.00						
	Entire	**Mean**	1.62	513	22017	21504	2842	1916	2885	2304	3488	3.5	6.8	4.8	1.35						
		SD	0.37	52	46	98	914	944	61	396	305	1.2	0.8	0.6	0.21						



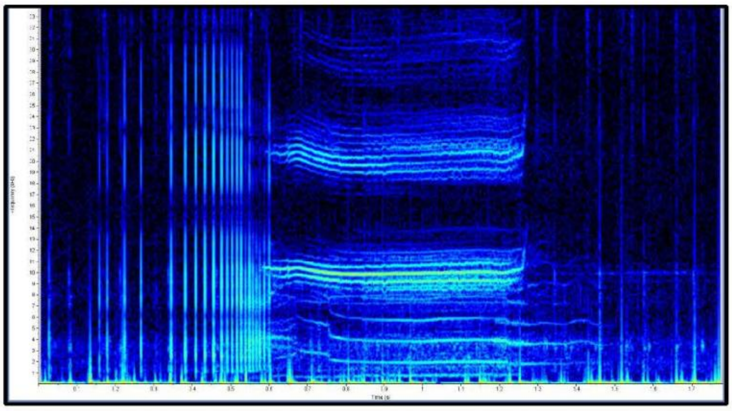
CALL TYPE McM20

This is a 3-component biphonic call. Part 1 is a series of distinct pulses increasing in PRR. Part 2 is a burst-pulse sound with a SBS of 2 kHz. Part 3 is a biphonic whistle with harmonics and amplitude-modulation.

n = 4



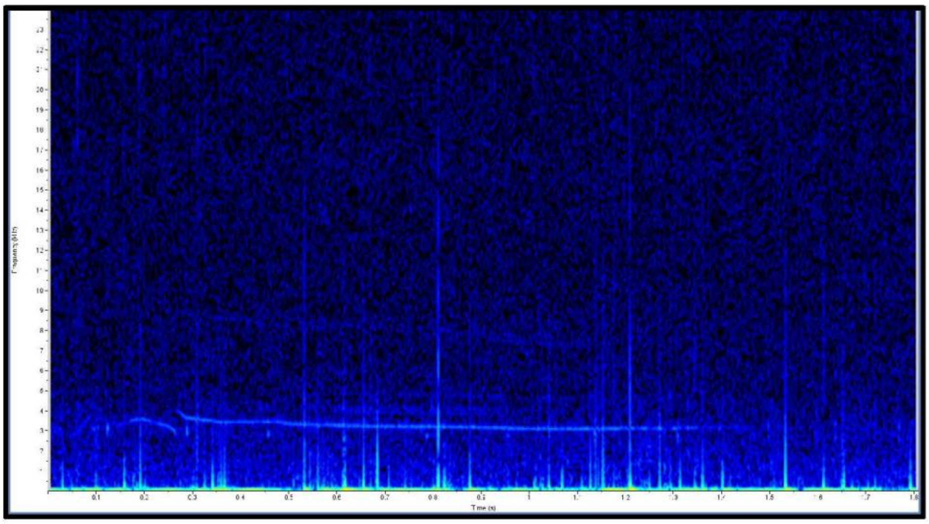
Call Type	Component	Statistic	Dur [s]	Fmin [Hz]	Fmax [Hz]	Fdelta [Hz]	BW 90% [Hz]	Fpeak [Hz]	Fcentre [Hz]	Q1F [Hz]	Q3F [Hz]	MinEnt [bits]	MaxEnt [bits]	AvgEnt [bits]	Dur90% [s]	Fstart [Hz]	Fend [Hz]	Ext	Infl	FM [1/s]	Steps
20	1	**Mean**	0.33	1668	36294	34626	19723	3820	5496	4184	9410	4.5	7.8	6.5	0.28						
n=4		***SD***	0.10	992	7897	8299	12658	4389	3067	2463	3355	1.0	1.0	0.9	0.05						
	2	**Mean**	0.93	1406	9125	7720	6668	4711	4629	3023	6152	2.9	5.4	4.2	0.63						
		SD	0.18	349	2138	1890	1174	3014	2996	1786	3062	1.0	0.5	0.8	0.15						
	3	**Mean**	0.78	7907	11747	3840	1523	8883	9141	8883	9633	2.1	4.9	2.5	0.58	9792	8635	3	4	4.5	0
		SD	0.14	1725	2072	2181	1472	835	532	811	673	0.7	1.2	0.9	0.10	3922	753	1	1	1.8	1
	Entire	**Mean**	1.24	830	36215	35385	11742	5496	7277	4242	9176	3.3	6.4	4.9	0.85						
		SD	0.23	492	7880	8171	4006	4161	2703	3239	1010	1.4	1.1	0.9	0.06						



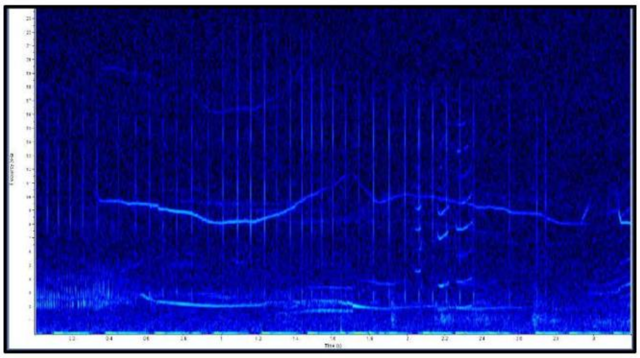
CALL TYPE McM21

This is a singular whistle with a long duration, low number of extrema and inflection points and hence low frequency-modulation rate.

n = 42



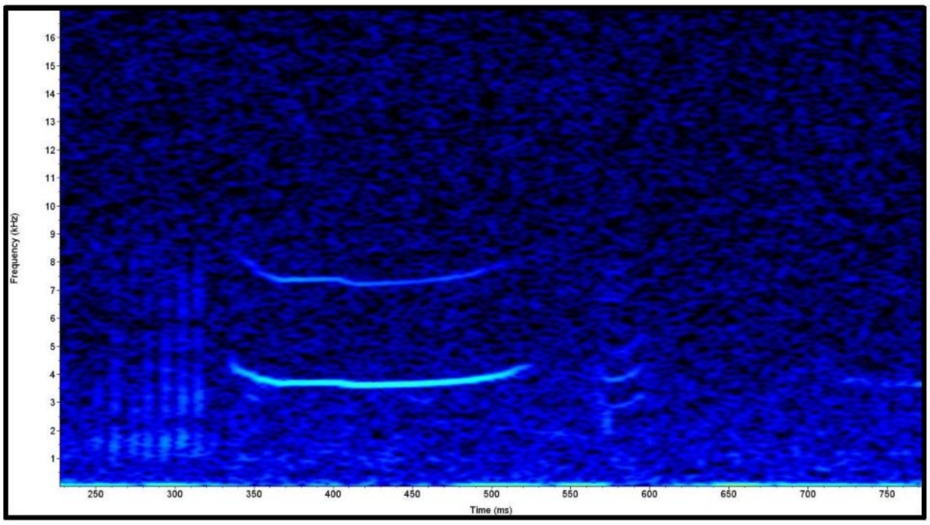
Call Type	Component	Statistic	Dur [s]	Fmin [Hz]	Fmax [Hz]	Fdelta [Hz]	BW 90% [Hz]	Fpeak [Hz]	Fcentre [Hz]	Q1F [Hz]	Q3F [Hz]	MinEnt [bits]	MaxEnt [bits]	AvgEnt [bits]	Dur90% [s]	Fstart [Hz]	Fend [Hz]	Ext	Infl	FM [1/s]	Steps
21	1	**Mean**	1.24	3863	6054	2190	1602	4534	4640	4372	5060	2.8	4.7	3.4	0.96	5166	4480	2	2	1.3	0
n=42		***SD***	0.60	2518	3587	1150	1065	2855	2909	2696	3207	0.8	0.9	1.1	0.49	3292	2681	3	3	1.9	0



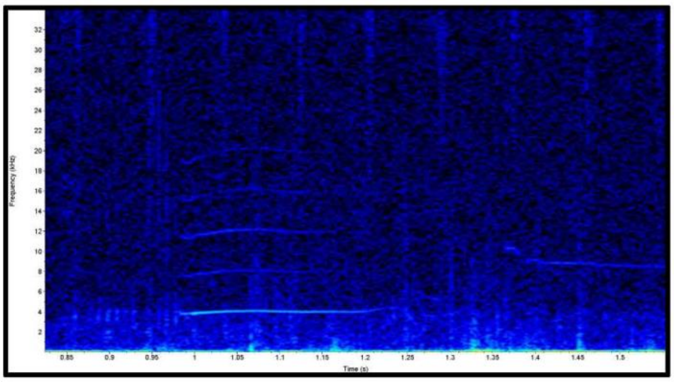
CALL TYPE McM22

This is a singular whistle with a short duration, low number of extrema and inflection points and hence low frequency-modulation rate.

n = 52



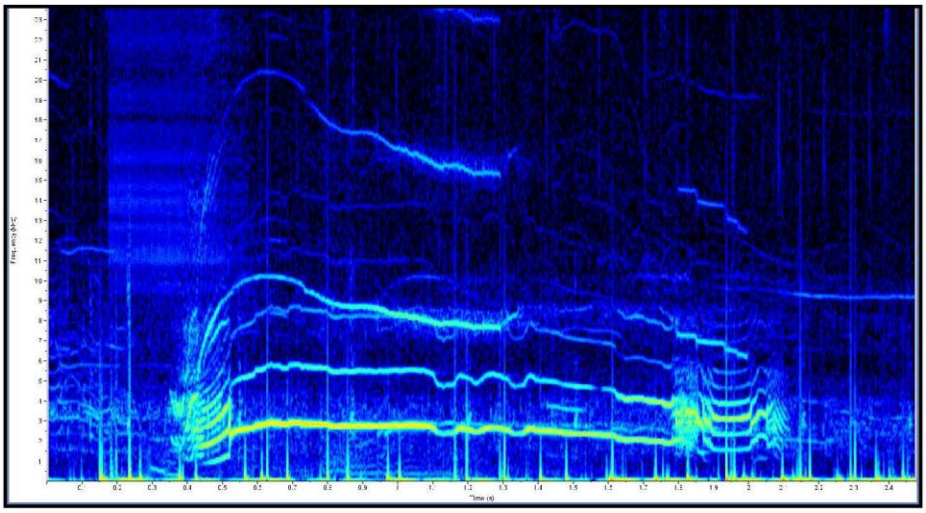
Call Type	Component	Statistic	Dur [s]	Fmin [Hz]	Fmax [Hz]	Fdelta [Hz]	BW 90% [Hz]	Fpeak [Hz]	Fcentre [Hz]	Q1F [Hz]	Q3F [Hz]	MinEnt [bits]	MaxEnt [bits]	AvgEnt [bits]	Dur90% [s]	Fstart [Hz]	Fend [Hz]	Ext	Infl	FM [1/s]	Steps
22	1	**Mean**	0.19	5456	7773	2317	1120	5830	5960	5829	6206	2.3	4.8	3.0	0.14	7459	6972	1	1	7.3	0
n=52		***SD***	0.08	3241	4166	1436	1056	3211	3261	3206	3398	0.6	1.0	0.8	0.08	4232	4044	1	0	7.5	0



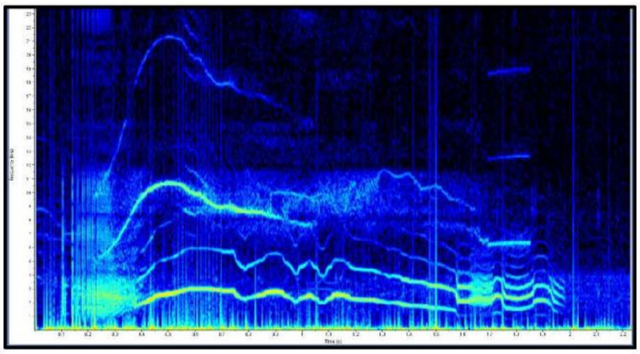
CALL TYPE McM23

This is a 4-component biphonic call. Part 1 is a burst-pulse sound, which sometimes starts as distinct pulses. Part 2 is a whistle with high frequency-modulation. Part 3 is another burst-pulse sound. Part 4 is a biphonic whistle with harmonics that commences as an upsweep and then decreases in frequency.

n = 6



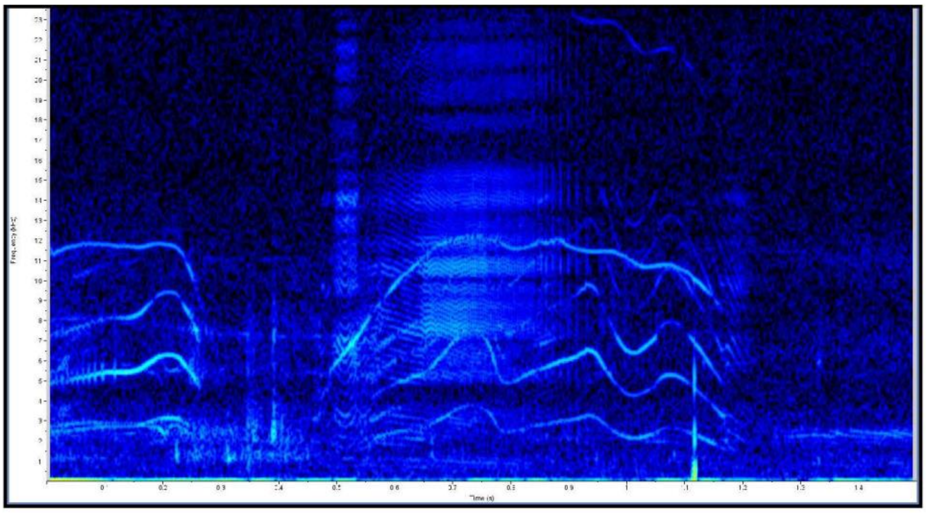
Call Type	Component	Statistic	Dur [s]	Fmin [Hz]	Fmax [Hz]	Fdelta [Hz]	BW 90% [Hz]	Fpeak [Hz]	Fcentre [Hz]	Q1F [Hz]	Q3F [Hz]	MinEnt [bits]	MaxEnt [bits]	AvgEnt [bits]	Dur90% [s]	Fstart [Hz]	Fend [Hz]	Ext	Infl	FM [1/s]	Steps
23	**1**	**Mean**	0.28	904	32617	31714	3906	2570	2805	2258	3336	3.7	6.9	5.1	0.20						
n=6		***SD***	0.10	411	16560	16402	1722	418	283	323	359	0.8	1.1	0.9	0.09						
	2	**Mean**	0.97	1284	3190	1906	953	2547	2687	2438	2898	1.6	3.8	2.1	0.75	2032	1339	8	9	10.9	0
		SD	0.41	233	447	535	343	378	348	275	361	0.6	0.7	0.6	0.34	464	311	4	4	5.0	0
	3	**Mean**	0.56	1175	11143	9967	3016	2648	2859	2508	3305	2.7	5.8	4.0	0.43						
		SD	0.32	349	5582	5484	1794	418	284	368	523	0.9	0.8	0.9	0.31						
	4	**Mean**	1.08	2978	10481	7502	3875	4219	4977	4188	6070	2.4	5.0	3.3	0.80	3067	8088	4	5	5.2	0
		SD	0.34	1407	1175	1859	2408	2303	2490	2262	3205	0.9	1.2	0.9	0.28	1469	1178	3	3	4.2	0
	Entire	**Mean**	1.81	890	32566	31675	4172	2625	2789	2516	3141	2.8	6.3	3.7	1.25						
		SD	0.64	412	15192	15066	2640	267	227	121	222	0.8	1.0	1.0	0.57						



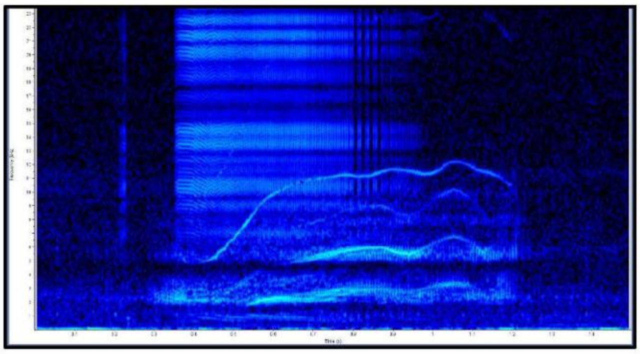
CALL TYPE McM24

This is a 2-component biphonic call. Part 1 is a burst-pulse sound with an SBS of 1-3 kHz. Part 2 is a biphonic whistle that starts as an upsweep but ends as a downsweep. Note that in the first image displayed here the burst-pulse sound from 0.5 to 0.9 s in the background is a call from a different animal.

n = 6



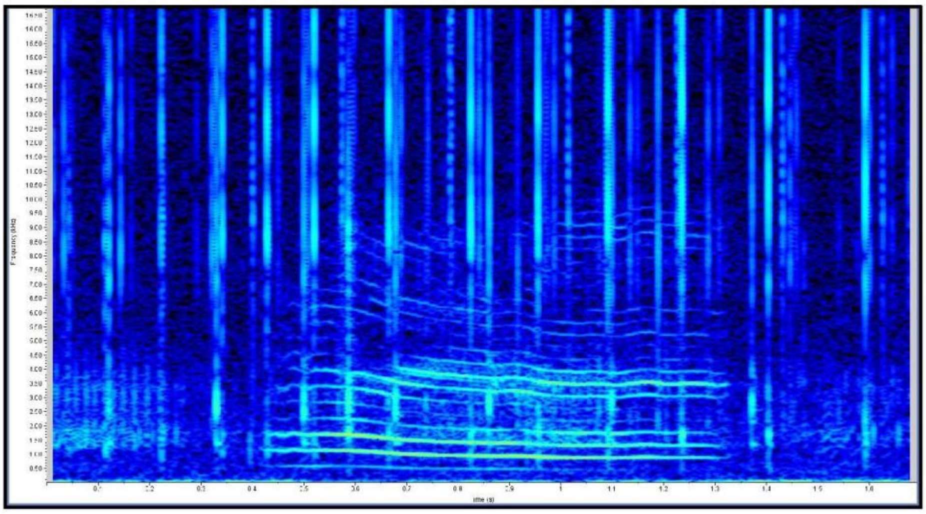
Call Type	Component	Statistic	Dur [s]	Fmin [Hz]	Fmax [Hz]	Fdelta [Hz]	BW 90% [Hz]	Fpeak [Hz]	Fcentre [Hz]	Q1F [Hz]	Q3F [Hz]	MinEnt [bits]	MaxEnt [bits]	AvgEnt [bits]	Dur90% [s]	Fstart [Hz]	Fend [Hz]	Ext	Infl	FM [1/s]	Steps
24	1	**Mean**	0.79	1528	11513	9985	7398	4578	5898	3859	7398	3.4	6.3	5.1	0.62						
n=6		***SD***	0.16	321	2403	2485	2130	2278	2659	1946	2466	0.5	0.3	0.5	0.13						
	2	**Mean**	0.79	4562	12581	8019	5930	6680	7047	6477	9062	2.9	5.9	4.8	0.62	4610	10515	7	8	9.6	0
		SD	0.15	1184	497	1030	1007	2018	1811	1711	1717	0.4	0.6	0.4	0.04	1253	2130	2	2	2.2	0
	Entire	**Mean**	0.82	1543	13276	11733	8406	4516	6008	3953	7641	3.6	6.4	5.3	0.65						
		SD	0.16	330	1613	1664	2127	2198	2580	2020	2345	0.9	0.3	0.5	0.10						



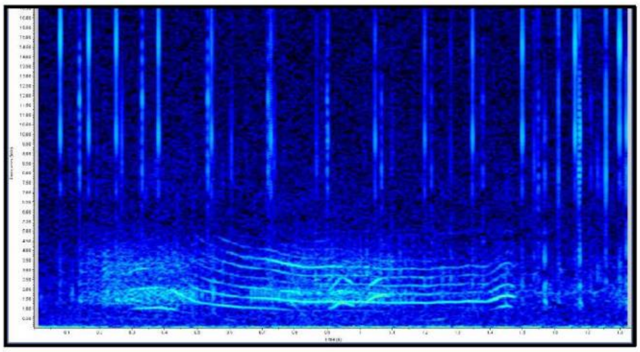
CALL TYPE McM25

This is a single component burst-pulse sound with SBS ranging from 500Hz to 1kHz.

n = 15



Call Type	Component	Statistic	Dur [s]	Fmin [Hz]	Fmax [Hz]	Fdelta [Hz]	BW 90% [Hz]	Fpeak [Hz]	Fcentre [Hz]	Q1F [Hz]	Q3F [Hz]	MinEnt [bits]	MaxEnt [bits]	AvgEnt [bits]	Dur90% [s]	Fstart [Hz]	Fend [Hz]	Ext	Infl	FM [1/s]	Steps
25	1	**Mean**	1.04	350	9552	9202	4422	1177	1450	1077	2383	2.9	6.6	4.5	0.77						
n=15		***SD***	0.33	149	2575	2713	3024	436	174	224	717	0.4	0.6	0.5	0.31						



Appendix 4: Antarctic Type B1 and B2 Killer Whale Call Catalogue from the Antarctic Peninsula

This Appendix includes the Call Type Catalogue as referred to in Chapter 4 of this thesis.

Antarctic Type B1 and B2 Killer Whale Call Catalogue from the Antarctic Peninsula

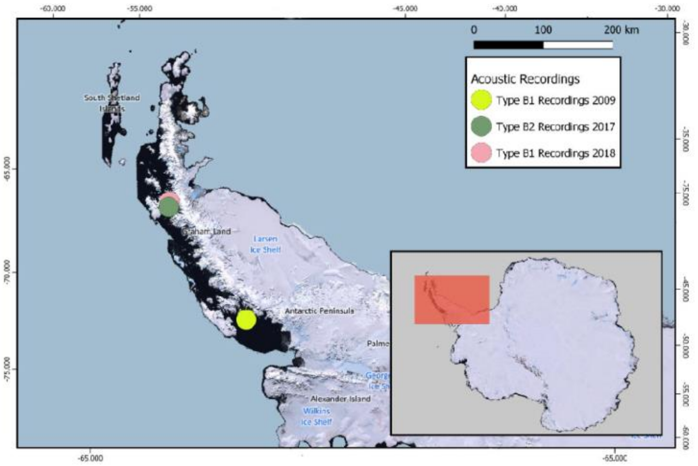
Killer whales (Orcinus orca) are found in all oceans of the world. In Antarctic waters, five ecotypes have been described, each displaying distinct differences in morphological features, foraging behaviours, diet preferences, and genetic structure. Acoustic recordings of Type B1 and B2 killer whales were collected between 2009 and 2018 on the Antarctic Peninsula. Spectrograms of acoustic data were examined for characteristic patterns of Type B1 and B2 vocalizations, calls were collectively grouped according to their spectral parameters using a k-means cluster analysis and a call type catalogue was produced.

Compiled by Rebecca Wellard.

Rebecca Wellard Antarctica Type B Call Catalogue 2018

Ecotype B1 killer whales were recorded in two different locations. The first hydrophone recordings of Type B1 killer whales were made in January 2009 when a group of 10 killer whales were encountered in Rothera on the Antarctic Peninsula. Animals were exhibited feeding and socialising during and after preying upon an Antarctic Minke whale.

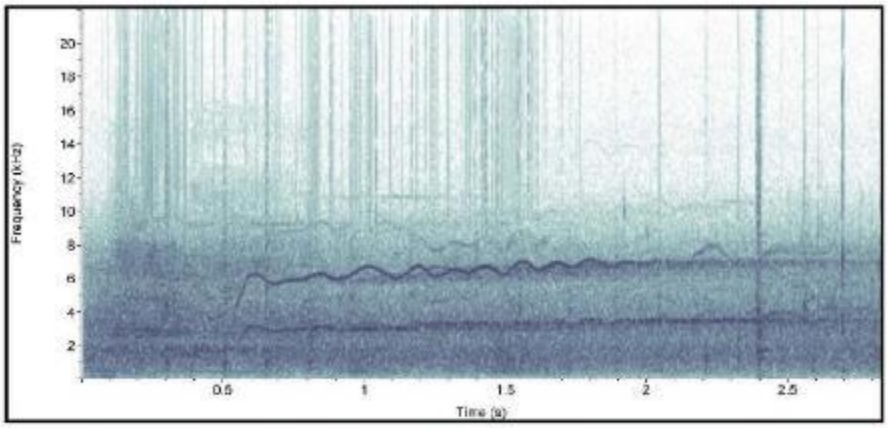
The second series of acoustic recordings were collected via opportunistic tagging in March 2018 when a group of approximately 8 Type B1 killer whales were encountered in Paradise Bay. A Customized Animal Tracking Solutions (CATS) tag was affixed to the dorsal surface of an individual female killer with suction cups, with acoustic recordings extracted from data obtained with this digital acoustic recording tag.

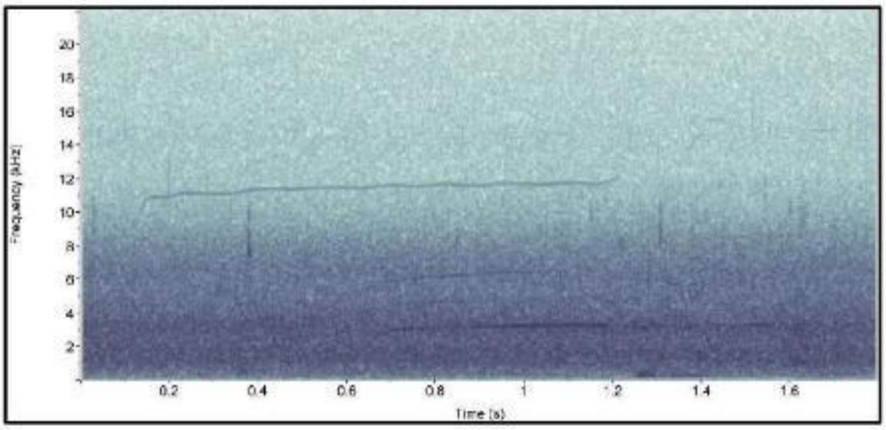


GROUP B1 01

Group TypeB1_01. These whistles exhibited the highest number of extrema and inflection points along with the longest duration. Most whistles had harmonics. This group comprised of 81 whistles.

Call Group	*n*		Duration [s]	Fmin [Hz]	Fmax [Hz]	Fdelta [Hz]	Fstart [Hz]	Fend [Hz]	Ext	Infl	FM [1/s]
TYPEB1_01	81	Mean	1.0	3895	7268	3373	4341	6196	6	7	7
		SD	0.4	2179	2410	1627	2544	2366	4	5	4
		Range: minimum	0.4	678	2766	1070	678	1357	0	0	0
		Range: maximum	2.2	10157	13059	8073	10751	13059	23	24	17

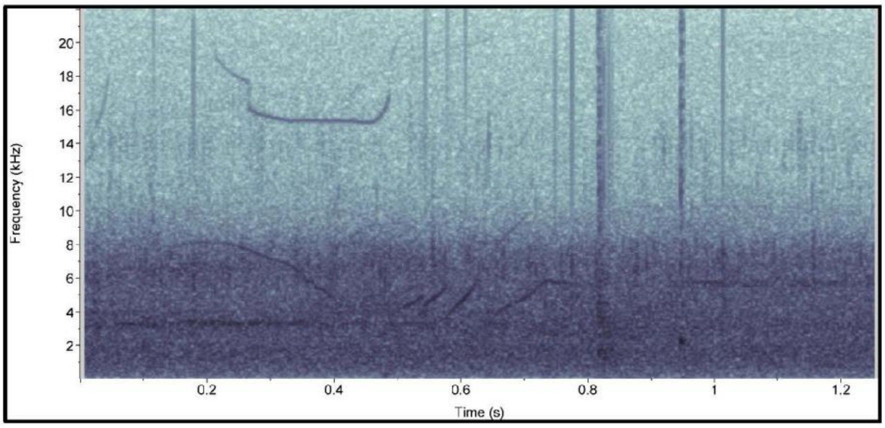


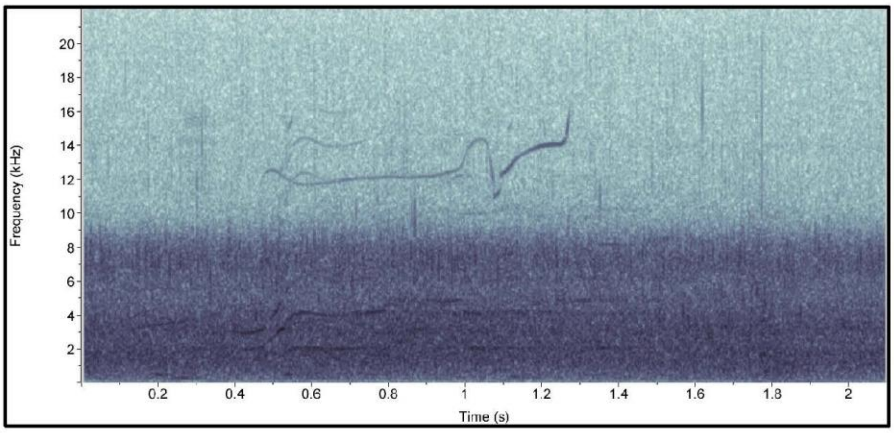


GROUP B1_02

Group TypeB1_02. This group comprised of 71 whistles. These whistles were high in frequency with a high frequency modulation rate. They also showed the highest frequency range (Fdelta) amongst all whistle groups.

Call Group	*n*		Duration [s]	Fmin [Hz]	Fmax [Hz]	Fdelta [Hz]	Fstart [Hz]	Fend [Hz]	Ext	Infl	FM [1/s]
TYPEB1_02	71	**Mean**	0.4	10914	16704	5790	11892	16481	2	3	8
		SD	0.3	2020	2062	1618	2408	2145	2	2	7
		Range: minimum	0.1	5093	12445	3782	5093	10243	0	0	0
		Range: maximum	1.6	18174	22050	10333	20263	21921	9	10	33

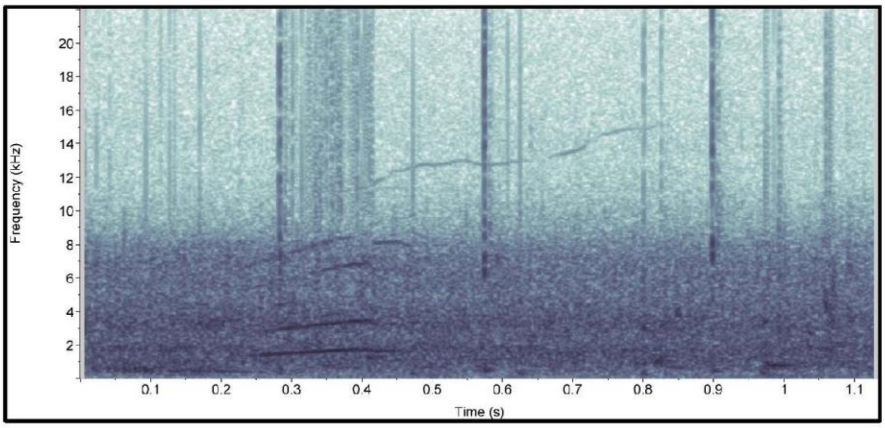


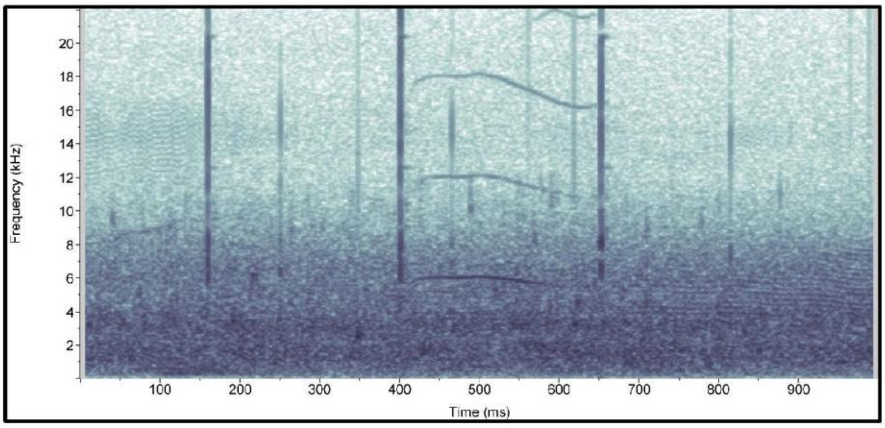


GROUP B1_03

Group TypeB1_03. These whistles had the lowest frequencies and a low number of local extrema and inflection points. They were also short in duration. There were a total of 336 whistles in this group.

Call Group	*n*		Duration [s]	Fmin [Hz]	Fmax [Hz]	Fdelta [Hz]	Fstart [Hz]	Fend [Hz]	Ext	Infl	FM [1/s]
TYPEB1_03	336	Mean	0.3	2589	4226	1637	2882	3740	1	2	7
		SD	0.2	1171	1350	900	1344	1338	1	2	10
		Range: minimum	0.0	51	428	250	186	155	0	0	0
		Range: maximum	1.0	5399	8073	5654	6450	6262	8	9	55

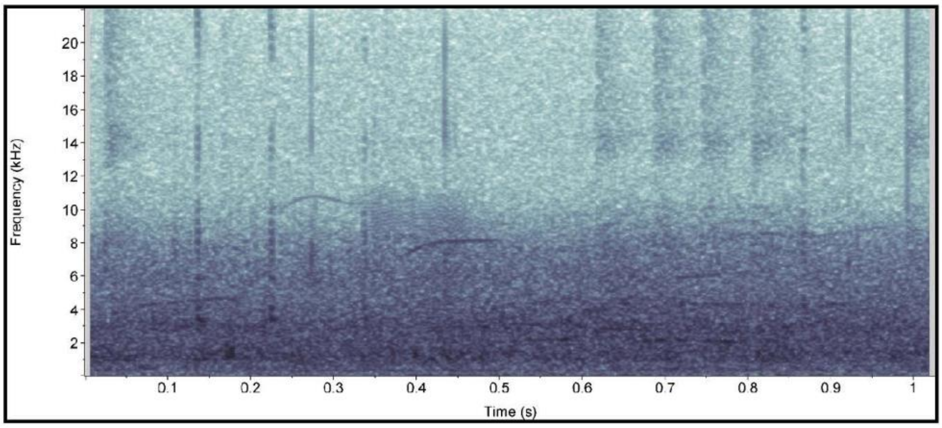


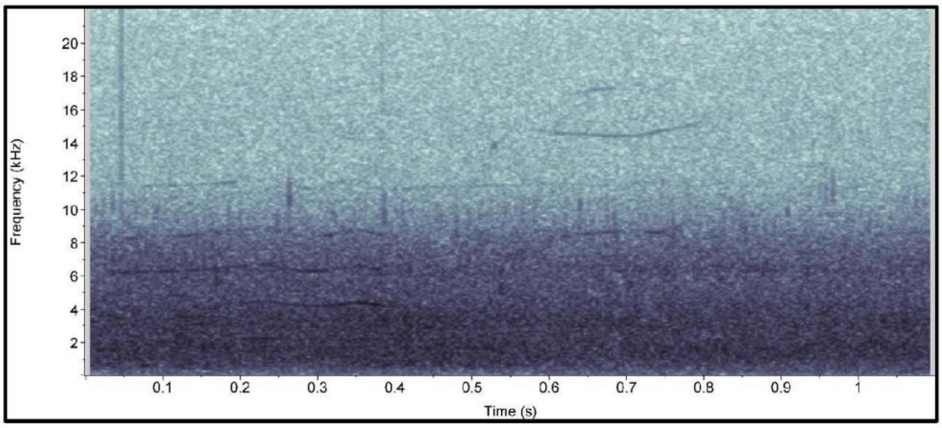


GROUP B1_04

Group TypeB1_04. This group of whistles had the highest frequency, highest frequency modulation rate and were the shortest in duration. They also had the lowest frequency range. There were a total of 207 whistles categorized in this group.

Call Group	*n*		Duration [s]	Fmin [Hz]	Fmax [Hz]	Fdelta [Hz]	Fstart [Hz]	Fend [Hz]	Ext	Infl	FM [1/s]
TYPEB1_04	**207**	**Mean**	0.3	12218	14097	1879	12842	13643	1	2	9
		SD	0.2	1816	1904	764	1904	2185	2	2	12
		Range: minimum	0.0	8053	10886	572	8981	1520	0	0	0
		Range: maximum	0.9	20526	22050	3604	21467	21206	9	10	67

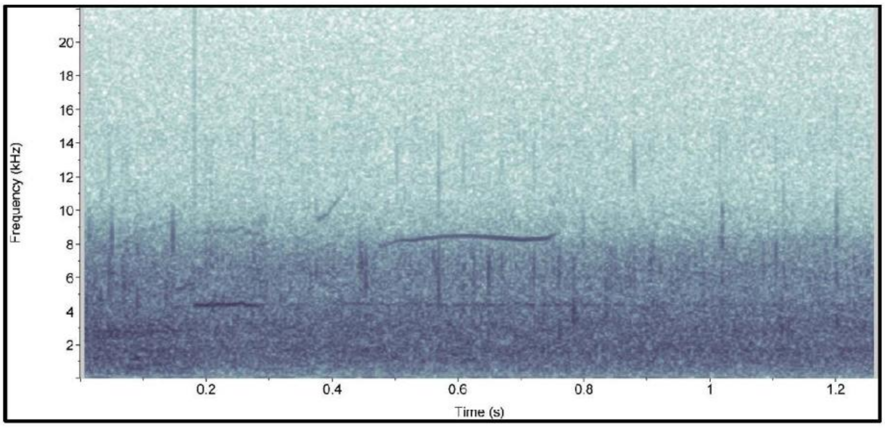


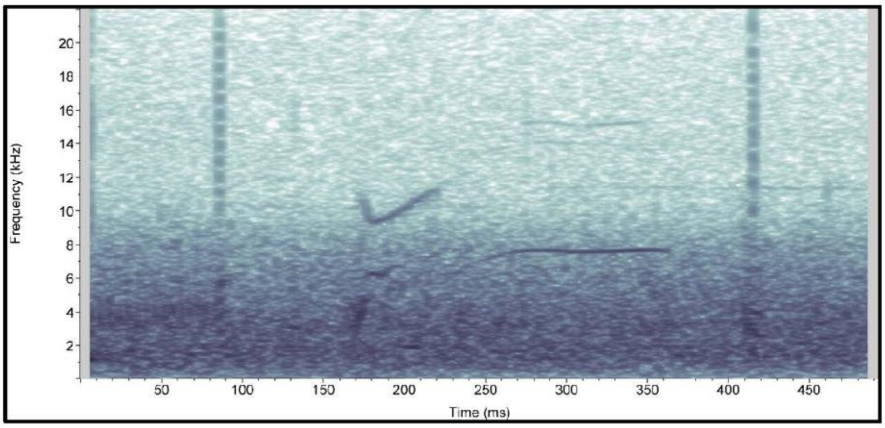


GROUP B1_05

Group TypeB1_05. This group of whistles were short in duration and had the lowest number of extrema and inflections, although also had a high frequency modulation rate, which is representative of the short duration time of each call. There were a total of 367 whistles categorized in this group.

Call Group	*n*		Duration [s]	Fmin [Hz]	Fmax [Hz]	Fdelta [Hz]	Fstart [Hz]	Fend [Hz]	Ext	Infl	FM [1/s]
TYPEB1_05	367	**Mean**	0.2	5703	8531	2828	6705	7396	1	2	10
		SD	0.2	1631	1389	1560	1954	1825	1	1	12
		Range: minimum	0.0	1246	5542	429	1246	1979	0	0	0
		Range: maximum	1.0	10003	14436	8830	13001	11978	6	7	61

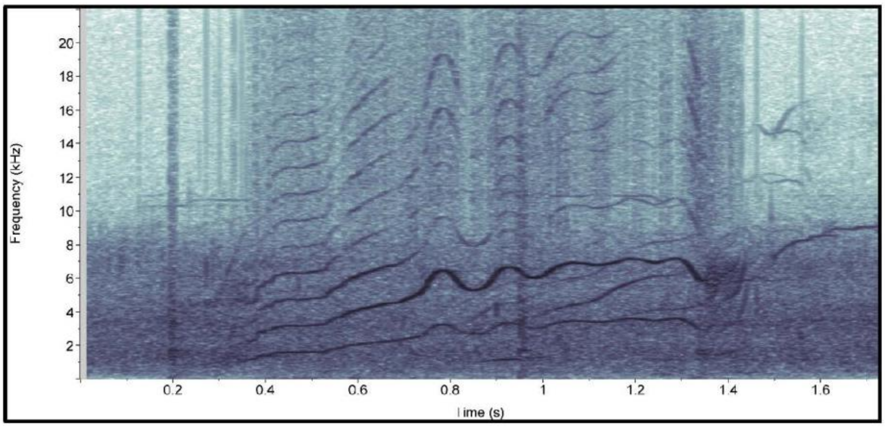


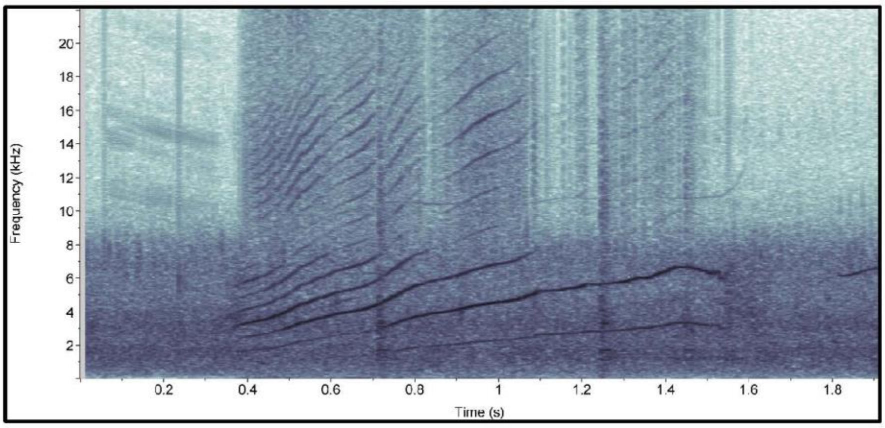


GROUP B1_06

Group TypeB1_06. These burst-pulse sounds had a long duration with the 1st quartile frequency averaging most energy at 2.3 kHz and the 3rd quartile frequency averaging most energy at 4.1 kHz. This group comprised of 124 burst-pulse sounds.

Call Group	*n*		Duration [s]	Fmin [Hz]	Fmax [Hz]	Q1Freq [Hz]	Q3Freq [Hz]	Avg Entropy [bits]	BW 90% [Hz]	Fcentre [Hz]	Fdelta [Hz]	Dur90% [s]	Min Entropy [bits]	Max Entropy [bits]	Fpeak [Hz]
TYPEB1_06	124	Mean	1.3	807	18457	2358	4077	5	5031	3135	17650	1.1	4	6	3204
		SD	0.4	683	5690	896	1184	1	1871	1026	5774	0.3	1	1	1475
		Range: minimum	0.6	37	1867	281	633	3	961	398	1593	0.8	2	5	188
		Range: maximum	2.6	3653	24000	5814	7106	8	19664	6675	23830	2.2	7	10	7090

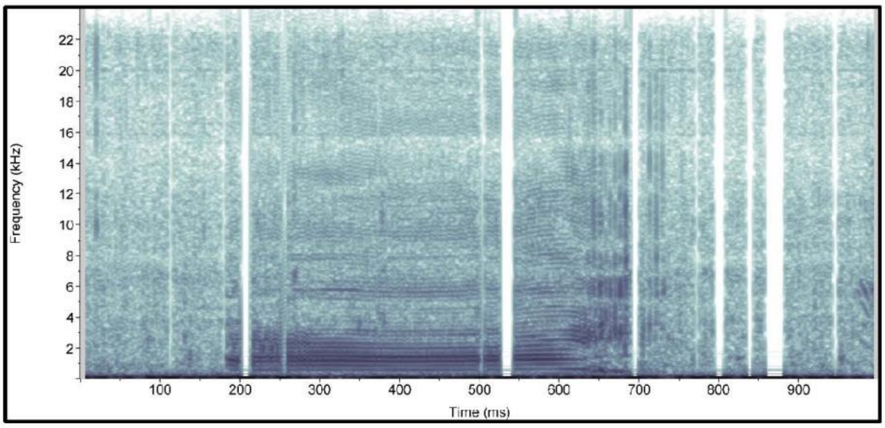


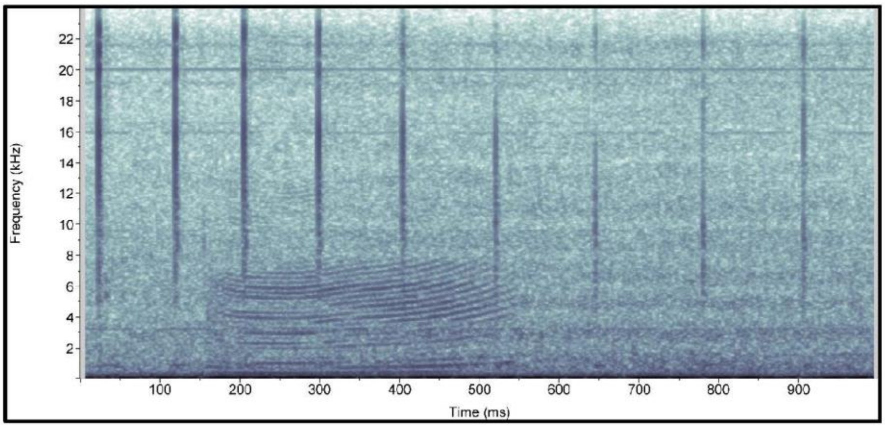


GROUP B1_07

Group TypeB1_07. These burst-pulse sounds were short in duration and had exhibited both the lowest frequencies and highest frequencies, resulting in the largest frequency range (Fdelta). These burst-pulse sounds had the lowest range of peak frequency at 0.94 kHz. This group comprised of 124 burst-pulse sounds.

Call Group	*n*		Duration [s]	Fmin [Hz]	Fmax [Hz]	Q1Freq [Hz]	Q3Freq [Hz]	Avg Entropy [bits]	BW 90% [Hz]	Fcentre [Hz]	Fdelta [Hz]	Dur90% [s]	Min Entropy [bits]	Max Entropy [bits]	Fpeak [Hz]
TYPEB1_07	124	Mean	0.6	446	14886	1125	2422	5	3613	1597	14440	0.4	3	6	1325
		SD	0.2	349	7279	698	1195	1	1976	899	7334	0.2	1	1	963
		Range: minimum	0.0	31	1375	94	94	1	47	94	1079	0.1	0	2	94
		Range: maximum	1.3	1577	24000	3015	4828	7	13078	4031	23897	0.8	6	10	4031

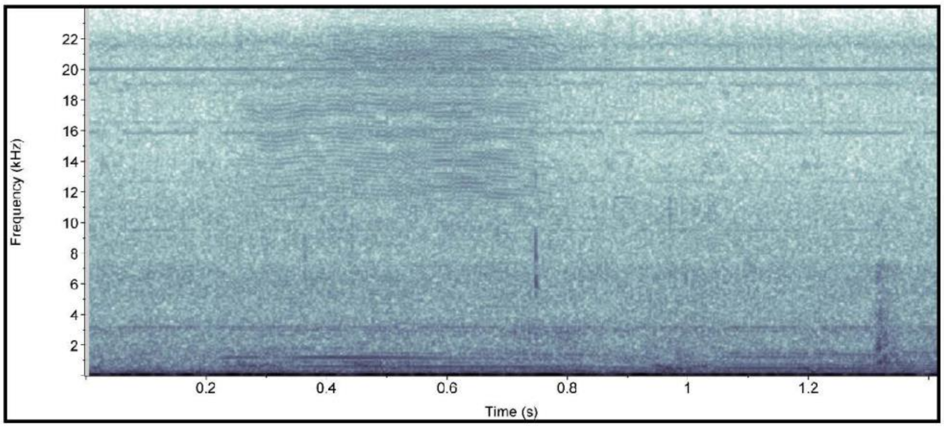


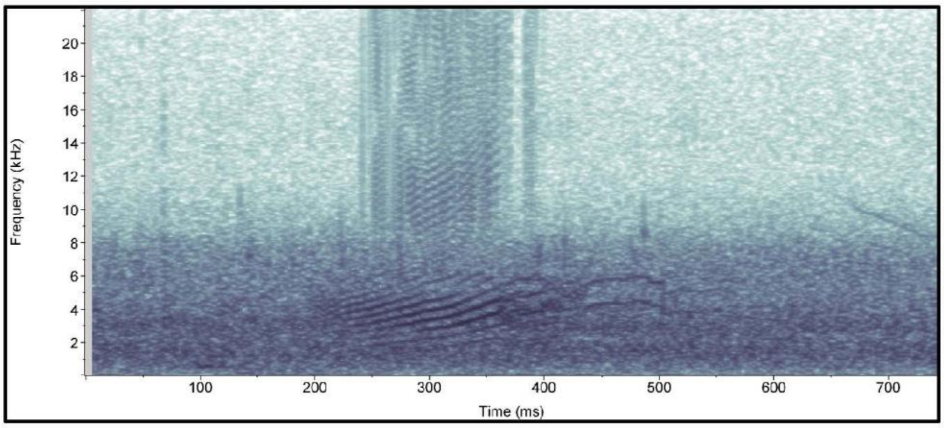


GROUP B1 08

Group TypeB1_08. These burst-pulse sounds were long in duration and highest in frequency. This category had the highest peak frequency measured at 20.6 kHz and also the highest 3rd quartile frequency at 20.2 kHz. This group comprised of 4 burst-pulse sounds.

Call Group	*n*		Duration [s]	Fmin [Hz]	Fmax [Hz]	Q1Freq [Hz]	Q3Freq [Hz]	Avg Entropy [bits]	BW 90% [Hz]	Fcentre [Hz]	Fdelta [Hz]	Dur90% [s]	Min Entropy [bits]	Max Entropy [bits]	Fpeak [Hz]
TYPEB1_08	4	Mean	0.9	6268	23507	8354	15543	8	12534	11306	17239	0.6	6	8	9629
		SD	0.9	3935	971	4581	4026	1	2769	4637	4376	0.5	2	1	7758
		Range: minimum	0.1	1263	22050	2718	11953	6	9776	5953	13681	0.1	4	8	2719
		Range: maximum	2.1	10248	24000	13664	20180	9	15563	17273	22736	1.2	8	10	20602

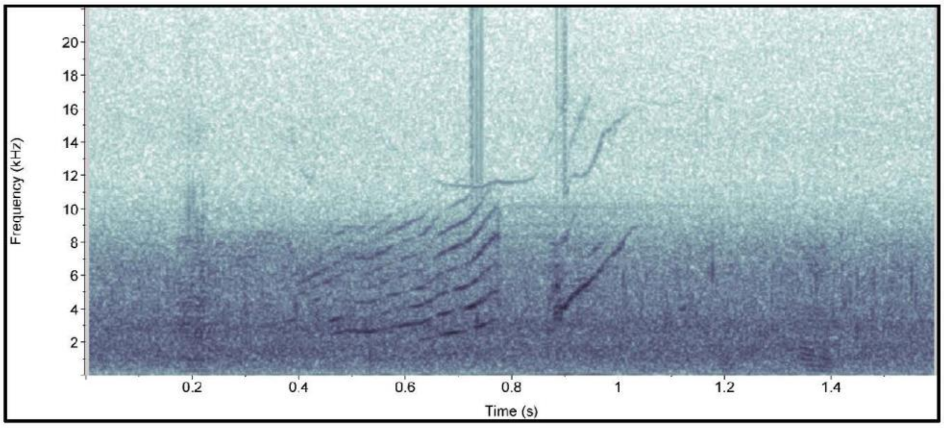


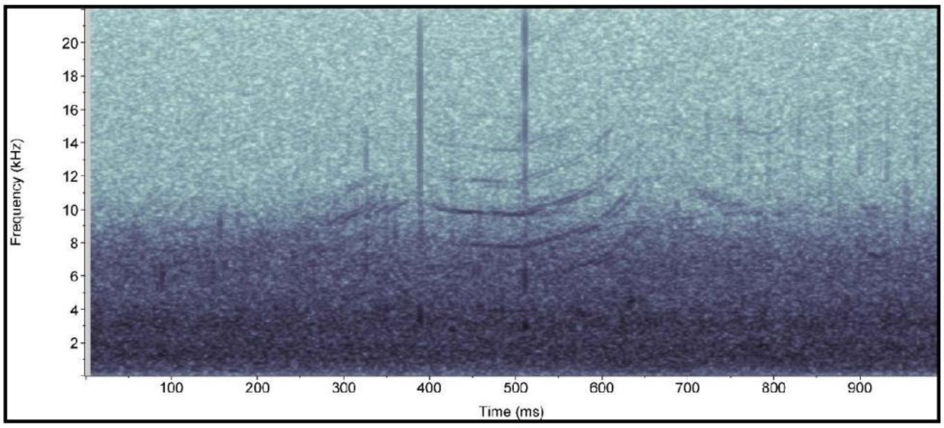


GROUP B1 09

Group TypeB1_09. These burst-pulse sounds were the shortest in duration, high in frequency, but surprisingly low in energy at the high frequencies, with the 3rd quartile frequency range highest at 8.9 kHz. There were a total of 290 burst-pulse sounds categorized in this group.

Call Group	*n*		Duration [s]	Fmin [Hz]	Fmax [Hz]	Q1Freq [Hz]	Q3Freq [Hz]	Avg Entropy [bits]	BW 90% [Hz]	Fcentre [Hz]	Fdelta [Hz]	Dur90% [s]	Min Entropy [bits]	Max Entropy [bits]	Fpeak [Hz]
TYPEB1_09	290	Mean	0.5	1388	18583	2900	4906	5	5074	3763	17195	0.4	4	7	3715
		SD	0.2	1245	5367	1089	1167	1	1635	1072	5817	0.2	1	1	1470
		Range: minimum	0.0	37	5856	603	2906	3	1034	1453	3574	0.1	1	4	328
		Range: maximum	1.0	8159	24000	8355	8953	9	14438	8441	23767	0.8	8	9	8441

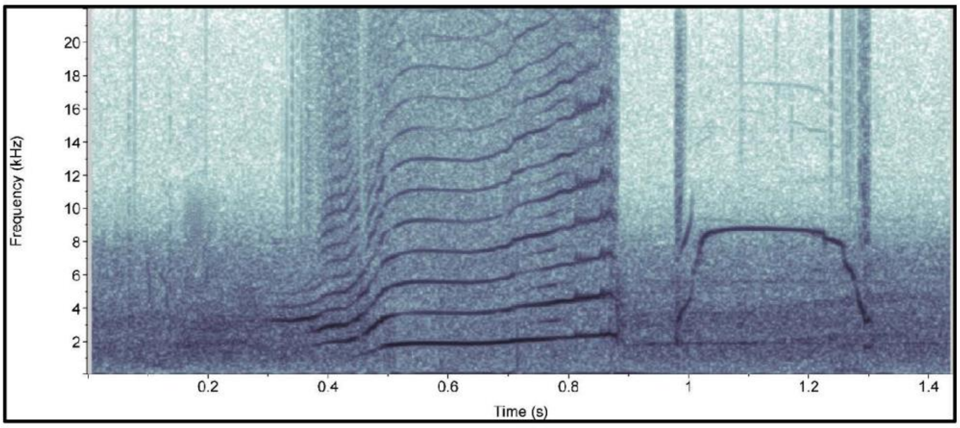


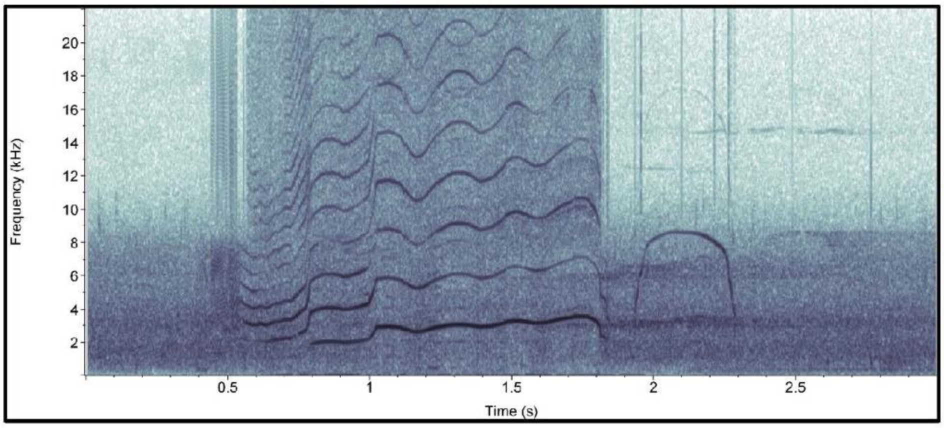


GROUP B1 10

Group TypeB1_10. This is a multi-component call consisting of 3 components. Part 1 is a burst-pulse sound with an approximate 500 Hz sideband spacing (SBS). Part 2 is a burst-pulse sound with a SBS of 1-2 kHz. Part 3 is a whistle, usually demonstrating a convex contour shape. This call was documented 61 times throughout the analysis, with little variation between each call. *All 3 components measured as an entire call are presented in this table for simplicity. Individual components were measured separately for comparative analysis.

Call Group	*n*		Duration [s]	Fmin [Hz]	Fmax [Hz]	Q1Freq [Hz]	Q3Freq [Hz]	Avg Entropy [bits]	BW 90% [Hz]	Fcentre [Hz]	Fdelta [Hz]	Dur90% [s]	Min Entropy [bits]	Max Entropy [bits]	Fpeak [Hz]
TYPEB1_10*	61	Mean	1.2	655	21619	2633	4391	6	5574	3475	20964	0.9	4	8	3542
		SD	0.3	512	1845	508	1028	0	1417	788	2072	0.2	1	0	1195
		Range: minimum	0.8	58	11732	1809	2110	5	3187	1917	10127	0.5	3	6	1787
		Range: maximum	2.0	2541	22050	3747	6740	7	9668	5814	22050	1.4	7	8	6503

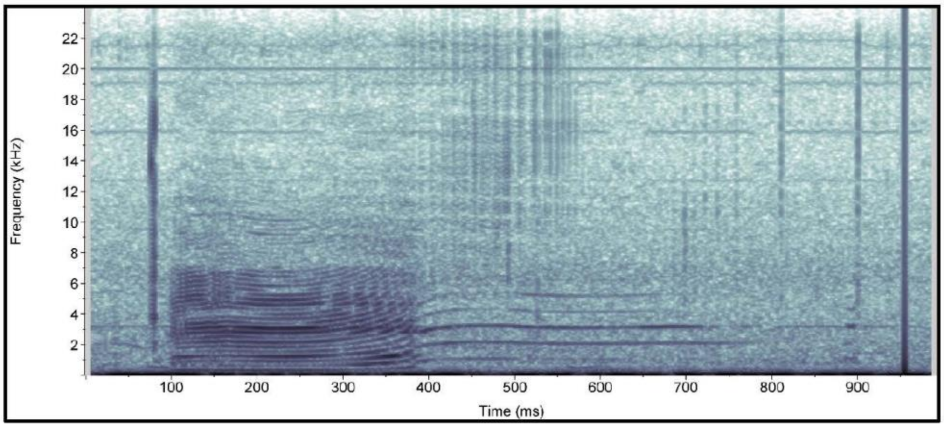


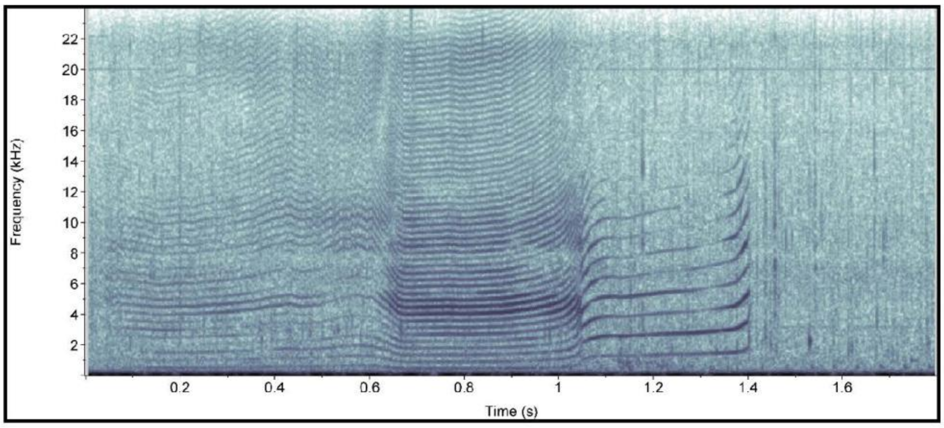


GROUP B1_11

Group TypeB1_11. This is a multi-component call consisting of two burst-pulse components. This call was repeated by Type B1 killer whales 28 times throughout recordings. This call is a burst-pulse sound that starts out with a side-band spacing (SBS) of approximately 0.1 kHz that increases over time to approximately 1 kHz SBS. *The two components measured as an entire call are presented in this table for simplicity. Individual components were measured separately for comparative analysis.

Call Group	*n*		Duration [s]	Fmin [Hz]	Fmax [Hz]	Q1Freq [Hz]	Q3Freq [Hz]	Avg Entropy [bits]	BW 90% [Hz]	Fcentre [Hz]	Fdelta [Hz]	Dur90% [s]	Min Entropy [bits]	Max Entropy [bits]	Fpeak [Hz]
TYPEB1_11*	28	Mean	1.1	354	22619	1764	4999	5	6481	3127	22265	0.7	4	7	2392
		SD	0.5	130	2265	1155	4082	1	4156	2032	2222	0.4	1	1	1859
		Range: minimum	0.4	128	15048	141	141	2	2063	141	14776	0.2	0	4	141
		Range: maximum	3.2	709	24000	3984	19547	7	20953	10641	23773	2.2	7	9	7969

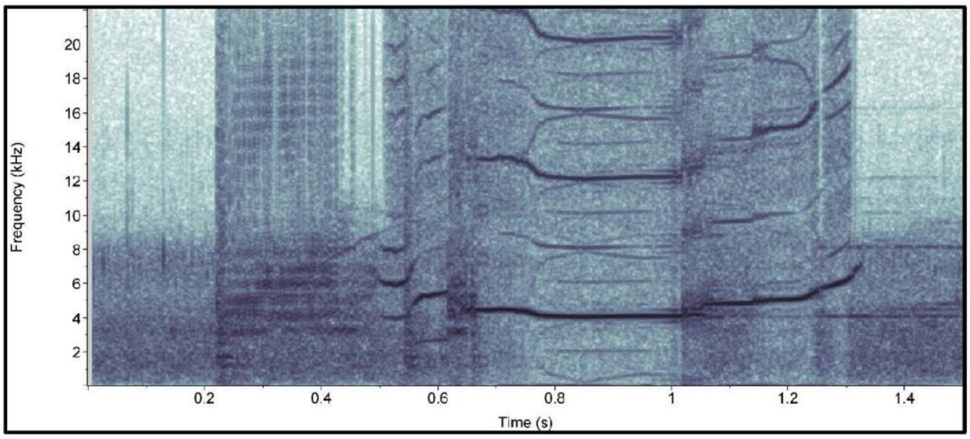




GROUP B1_12

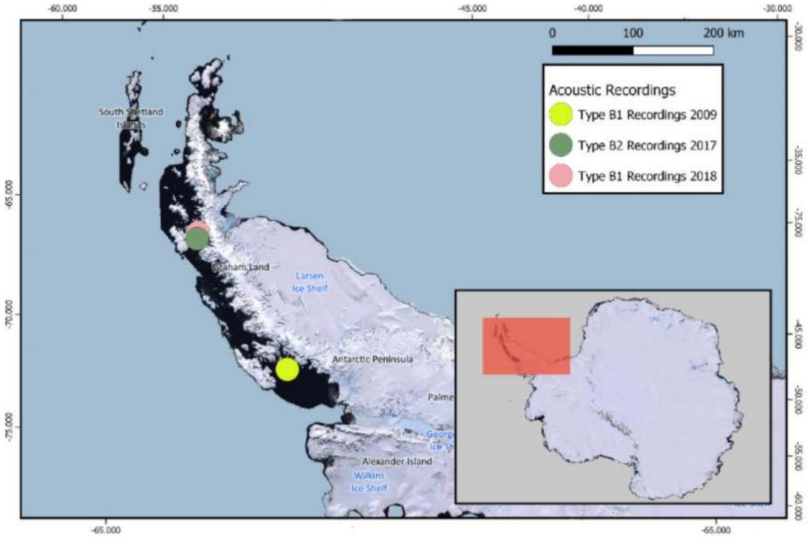
Group TypeB1_12. This is a two-component transition call which was observed once during recordings. Part 1 is a burst-pulse sound with an approximate 500 Hz sideband spacing (SBS). The call then transitions into part 2 which is a whistle that is pulsed in the middle. 0015_619 *The two components measured as an entire call are presented in this table for simplicity. Individual components were measured separately for comparative analysis.

Call Group	*n*		Duration [s]	Fmin [Hz]	Fmax [Hz]	Q1Freq [Hz]	Q3Freq [Hz]	Avg Entropy [bits]	BW 90% [Hz]	Fcentre [Hz]	Fdelta [Hz]	Dur90% [s]	Min Entropy [bits]	Max Entropy [bits]	Fpeak [Hz]
TYPEB1_12*	1	Measurements	1.1	2826	22050	4070	5233	5	8204	4436	19224	0.9	3	7	4070



TYPE B2 KILLER WHALE

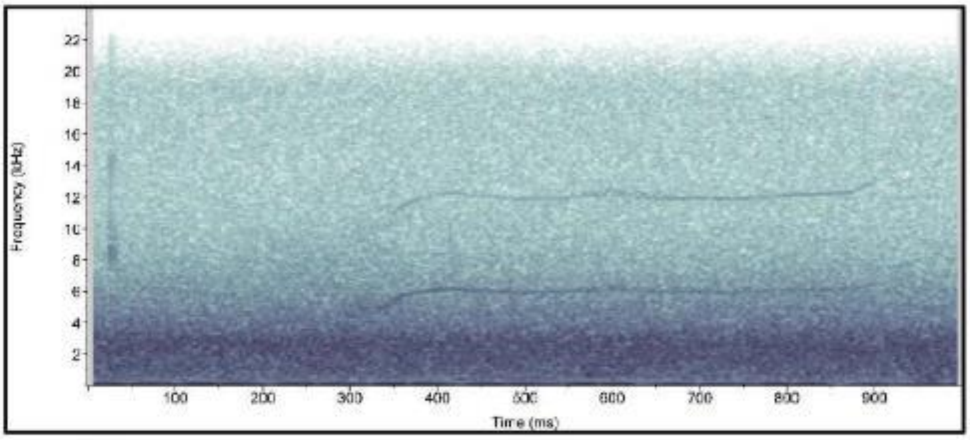
Hydrophone recordings of Type B2 killer whales were collected in 2017 when a group of approximately 20 killer whales were encountered in the Gerlache Strait. Behavioural state noted during this encounter included socializing, foraging and milling. A few individuals of this group were observed chasing a Gentoo penguin (*Pygoscelis papua*), although once this penguin was caught, they did not feed on it but instead peeled the skin off the head and neck. Animals then continued to socialise and mill throughout encounter.

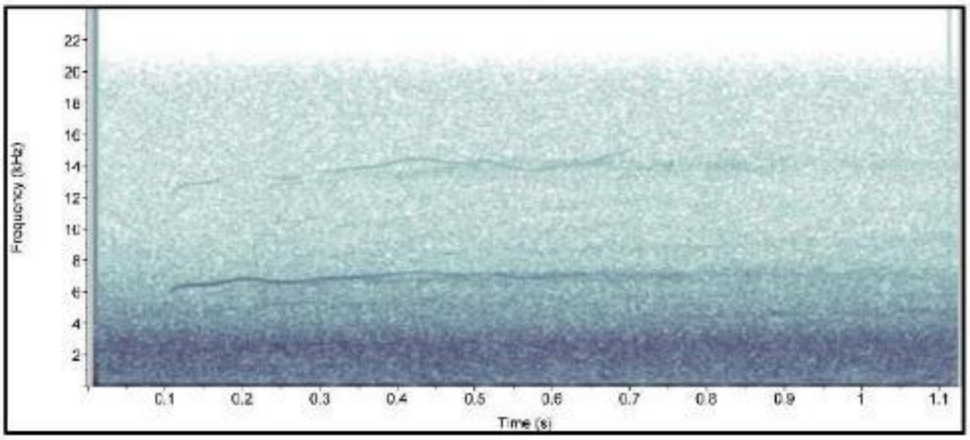


GROUP B2 01

Group TypeB2_01. These whistles were low in frequency and long in duration, with few extrema and inflection points. This group comprised of 111 whistles.

Call Group	*n*		Duration [s]	Fmin [Hz]	Fmax [Hz]	Fdelta [Hz]	Fstart [Hz]	Fend [Hz]	Ext	Infl	FM [1/s]
TYPEB2_01	111	Mean	0.4	5510	7984	2474	6648	6791	2	3	9
		SD	0.4	1211	1193	1125	1465	1482	3	3	9
		Range: minimum	0.1	2923	5795	453	703	3735	0	0	0
		Range: maximum	2.7	8690	11863	6316	9844	11098	13	14	33

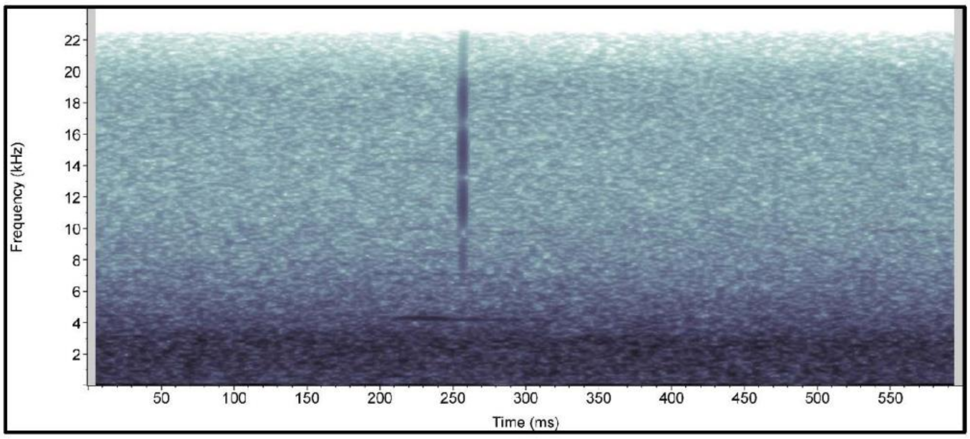


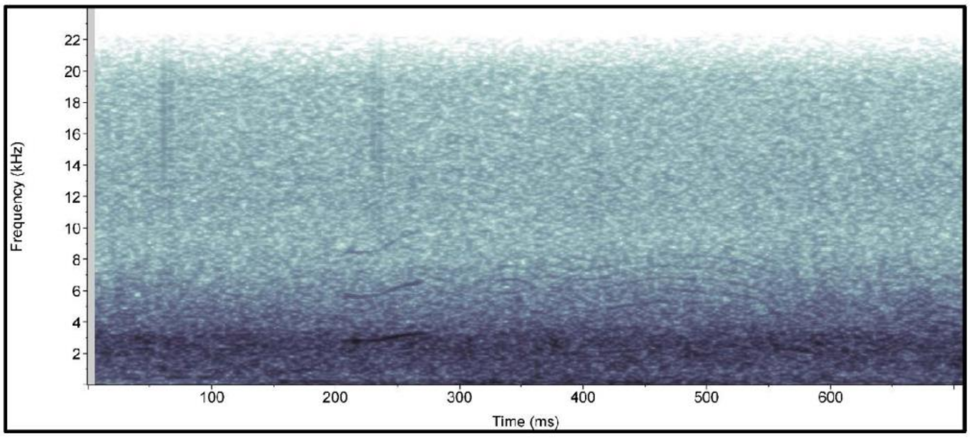


GROUP B2 02

Group TypeB1_02. This group comprised of 53 whistles. These whistles were the shortest in duration , had the lowest frequency and had the lowest number of local extrema and inflection points.

Call Group	*n*		Duration [s]	Fmin [Hz]	Fmax [Hz]	Fdelta [Hz]	Fstart [Hz]	Fend [Hz]	Ext	Infl	FM [1/s]
TYPEB2_02	53	**Mean**	0.4	2416	3942	1526	2998	2849	1	2	5
		SD	0.3	1508	1917	834	1654	1466	2	2	7
		Range: minimum	0.1	97	519	369	242	208	0	0	0
		Range: maximum	1.2	7280	8134	4778	5430	5024	8	9	34

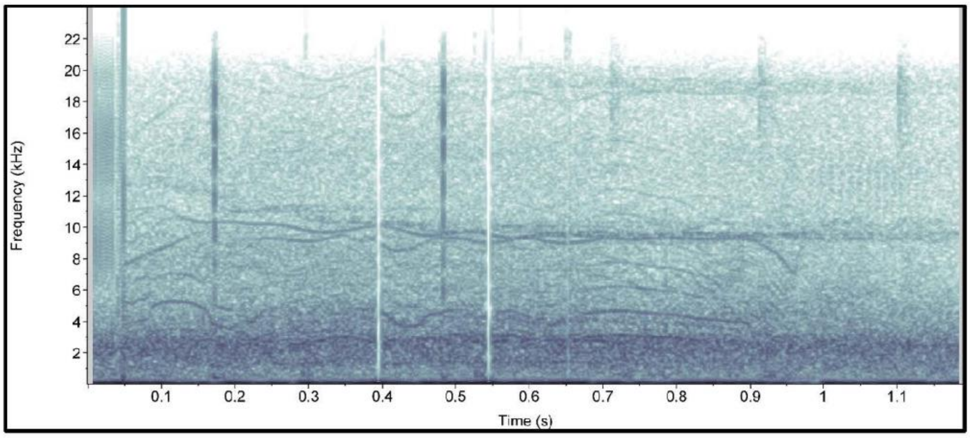


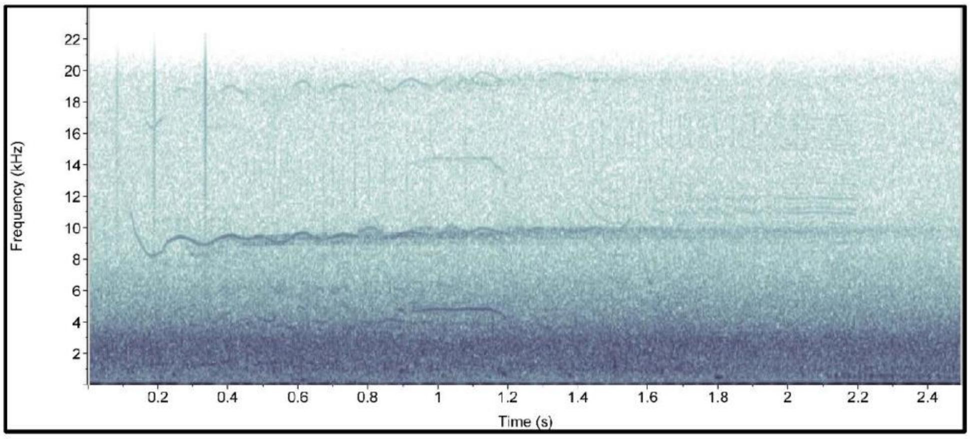


GROUP B2_03

Group TypeB2_03. These whistles had the longest duration (5.8 s), the highest frequency (20.1 kHz) and the highest number of local extrema and inflection points. A total of 51 whistles were categorised into this group.

Call Group	*n*		Duration [s]	Fmin [Hz]	Fmax [Hz]	Fdelta [Hz]	Fstart [Hz]	Fend [Hz]	Ext	Infl	FM [1/s]
TYPEB2_03	51	**Mean**	0.6	8083	12116	4034	11037	9379	3	3	7
		SD	0.8	2415	2041	2028	2053	2694	6	7	7
		Range: minimum	0.1	2856	10227	951	7914	3954	0	0	0
		Range: maximum	5.8	16806	20595	9655	19332	17684	39	40	27

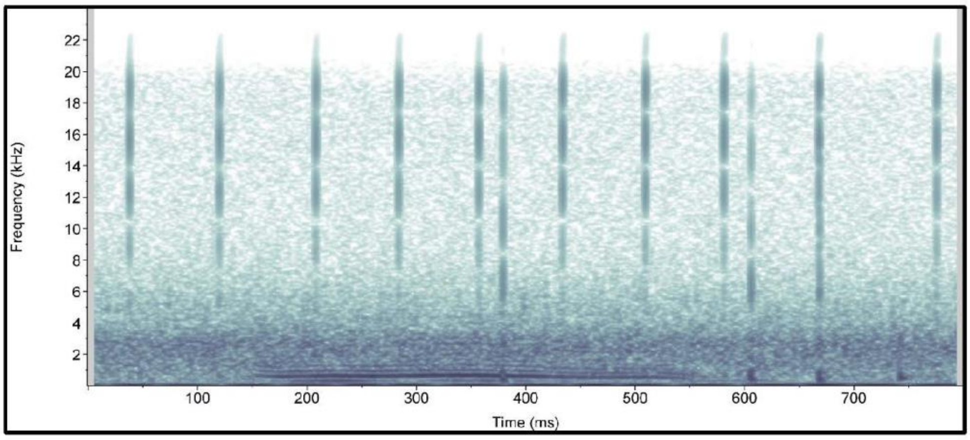


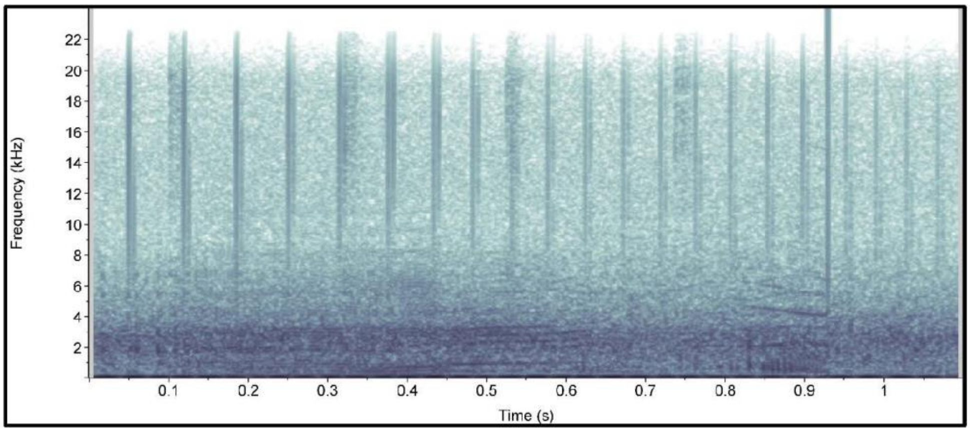


GROUP B2 04

Group TypeB2_04. These burst-pulse sounds were the lowest in frequency (0.24 kHz) with the 1st quartile frequency averaging most energy at 0.4 kHz and the 3rd quartile frequency averaging most energy at 1.2 kHz. This group comprised of 19 burst-pulse sounds.

Call Group	*n*		Duration [s]	Fmin [Hz]	Fmax [Hz]	Q1Freq [Hz]	Q3Freq [Hz]	Avg Entropy [bits]	BW 90% [Hz]	Fcentre [Hz]	Fdelta [Hz]	Dur90% [s]	Min Entropy [bits]	Max Entropy [bits]	Fpeak [Hz]
TYPEB2_04	19	Mean	0.3	114	5339	404	1276	5	1688	736	5225	0.2	4	6	431
		SD	0.2	76	5623	285	935	1	1080	609	5619	0.2	1	1	525
		Range: minimum	0.1	24	494	82	258	4	258	152	371	0.1	2	5	70
		Range: maximum	0.9	302	23231	1078	2719	7	3117	2297	23157	0.6	7	8	2461

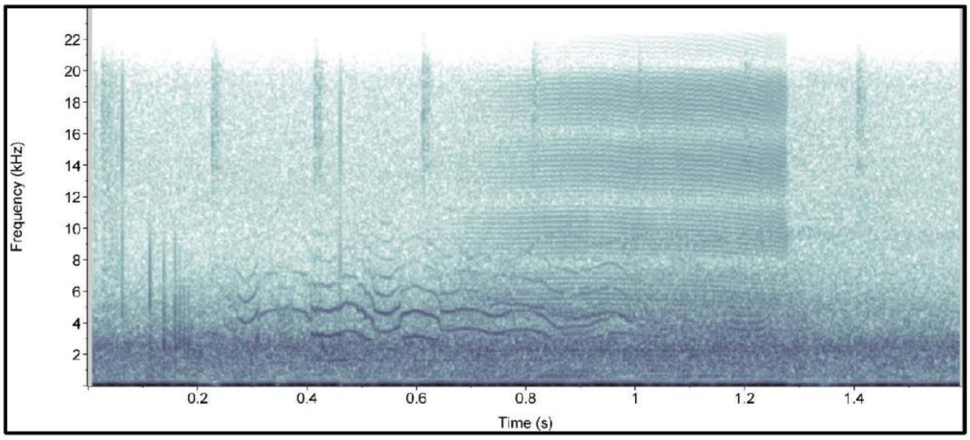


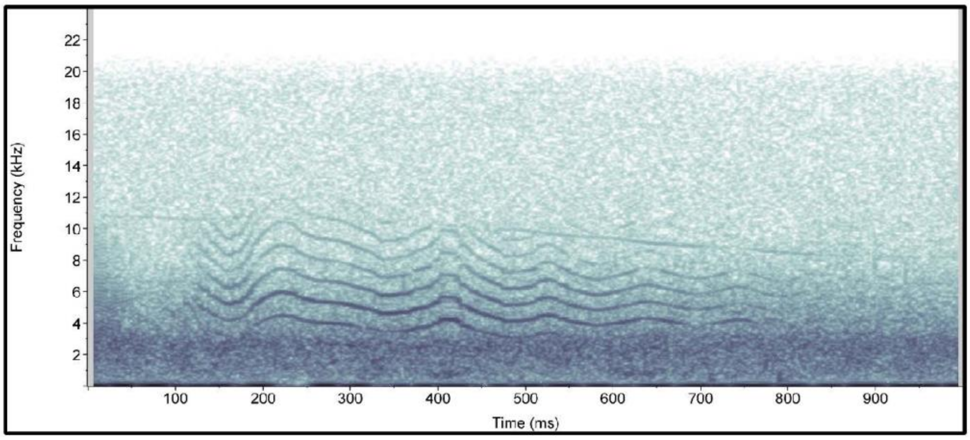


GROUP B2 05

Group TypeB2_05. These burst-pulse sounds were the longest in duration (1.2 s) and had the highest frequency (24 kHz). A total of 38 burst-pulse sounds were categorised into this group.

Call Group	*n*		Duration [s]	Fmin [Hz]	Fmax [Hz]	Q1Freq [Hz]	Q3Freq [Hz]	Avg Entropy [bits]	BW 90% [Hz]	Fcentre [Hz]	Fdelta [Hz]	Dur90% [s]	Min Entropy [bits]	Max Entropy [bits]	Fpeak [Hz]
TYPEB2_05	38	Mean	0.7	987	16461	2048	3072	5	2898	2556	15474	0.6	4	6	2561
		SD	0.3	896	5394	547	553	1	696	444	5791	0.2	1	1	650
		Range: minimum	0.2	136	6865	938	2438	4	1875	1969	6426	0.1	2	5	328
		Range: maximum	1.2	3031	24000	3282	4875	7	5297	3844	23547	1.0	7	8	4219

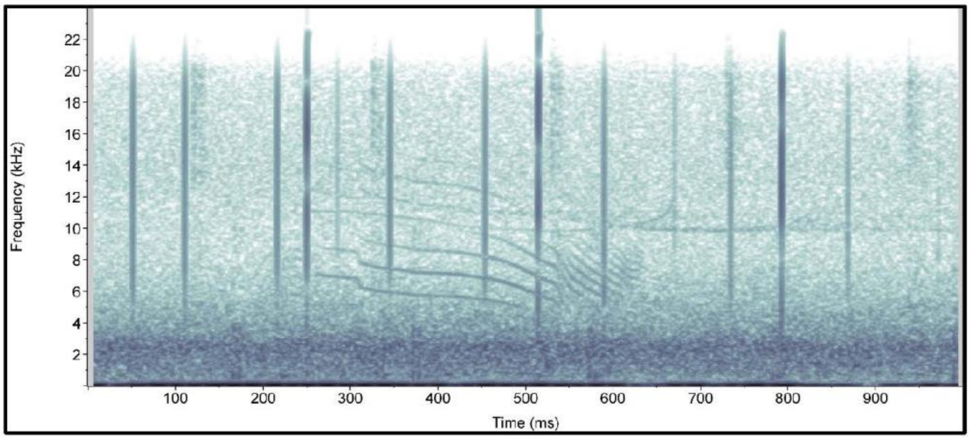


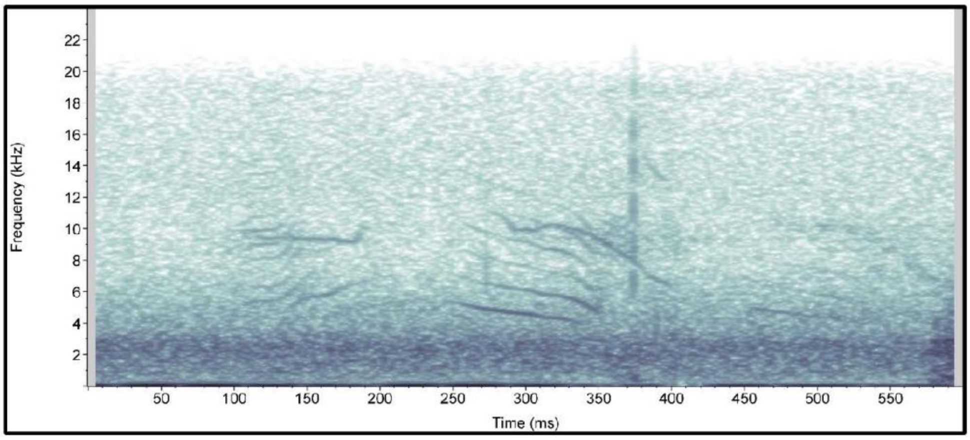


GROUP B2_06

Group TypeB2_06. These burst-pulse sounds were the shortest in duration (range of 0.1 – 0.4 s) and had the lowest frequency range (Fdelta). There were 5 burst-pulse sounds in this group.

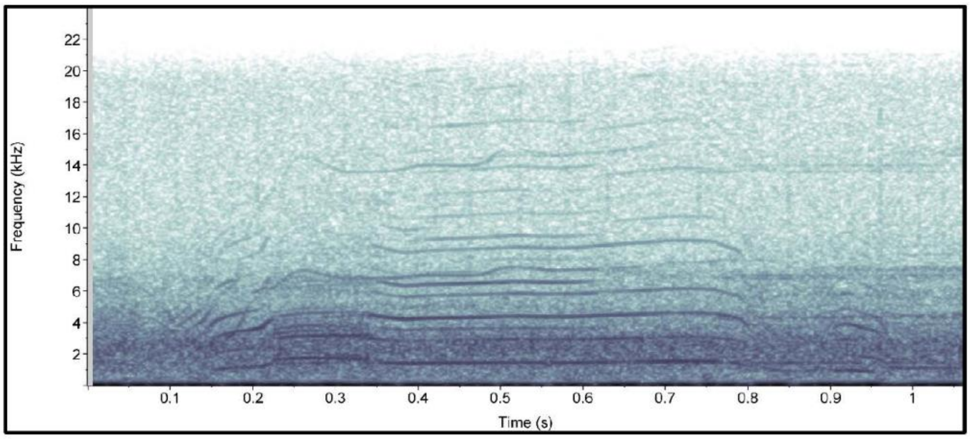
Call Group	*n*		Duration [s]	Fmin [Hz]	Fmax [Hz]	Q1Freq [Hz]	Q3Freq [Hz]	Avg Entropy [bits]	BW 90% [Hz]	Fcentre [Hz]	Fdelta [Hz]	Dur90% [s]	Min Entropy [bits]	Max Entropy [bits]	Fpeak [Hz]
TYPEB2_06	5	Mean	0.2	3858	15887	4416	7809	4	8456	5513	12028	0.2	3	6	4256
		SD	0.1	775	4011	820	4295	1	4304	1943	4638	0.1	1	1	1080
		Range: minimum	0.1	2964	11556	3141	4078	3	4594	3469	6503	0.1	2	5	3000
		Range: maximum	0.4	5052	20913	5438	14719	5	14344	8625	17949	0.4	4	8	5813

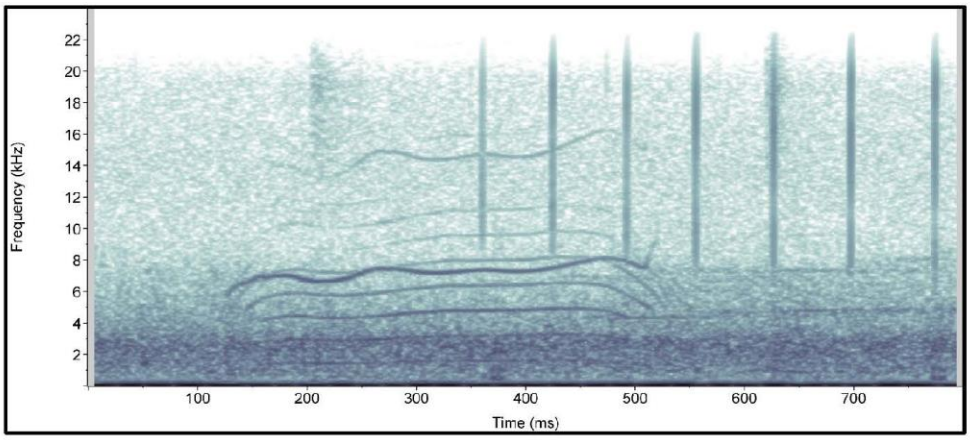




GROUP B2_07

Group TypeB2_07. This is a two-component biphonic call. Part 1 is a burst-pulse sound with an approximate 1 kHz sideband spacing (SBS). Part 2 is a biphonic whistle that usually commences and finishes with the burst-pulse, hence having the same approximate duration. This whistle exhibited contours with many local extrema and inflection points. There was a total of 12 calls categorised in this group.*The two components measured as an entire call are presented in this table for simplicity. Individual components were measured separately for comparative analysis.





GROUP B2 08

Group TypeB2_08. This is a two-component call that transitions from a whistle to a burst-pulse sound. Part 1 is a whistle with a small number of extrema and inflection points. Part 2 is a burst-pulse sound with sideband-spacing between 0.5 – 1 kHz. Calls had a duration of 0.4 to 1.8 s. There was a total of 3 calls categorised in this group. **The two components measured as an entire call are presented in this table for simplicity. Individual components were measured separately for comparative analysis.