Faculty of Science and Engineering

School of Earth and Planetary Science

Variability in Baleen Whale Acoustical Ecology: Implications for Optimal Monitoring Using Passive Acoustics

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This thesis is presented for the Degree of

Doctor of Philosophy in Applied Physics

of

Curtin University

July 2020

Declaration of authorship

I, Angela Recalde-Salas, 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.

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 numbers EC_2013_27 and AEC_2013_28.

Date: 19 of July 2020

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“Walk in kindness toward the Earth and every living being. Without kindness and compassion for all of Mother Nature’s creatures, there can be no true joy; no internal peace, no happiness. Happiness flows from caring for all sentient beings as if they were your own family, because in essence they are. We are all connected to each other and to the Earth.”

Sylvia Dolson

“*The oceans are the planet's last great living wilderness, man's only remaining frontier on Earth, and perhaps his last chance to prove himself a rational species.”*

John L. Culliney

Abstract

The potential impacts of man-made underwater noise in the oceans has been of growing concern in recent decades. To monitor marine fauna populations that produce sound and assessing potential impacts, passive acoustic monitoring (PAM) has become popular because of its relatively low cost. Although PAM has great potential for monitoring of baleen whale populations, the acoustical baseline to develop an optimal monitoring plan is yet in development. To optimise PAM for baleen whales and improve the accuracy on ecological parameters estimates (e.g. population trends), its biases and limitations need to be understood.

This study aimed to improve our current knowledge of biases and limitations of PAM for pygmy blue whales (*Balaenoptera musculus brevicauda*) and humpback whales (*Megaptera novaeangliae*) that migrate through Geographe Bay, Western Australia. Underwater sound recording using a single stationary recorder and land-based theodolite tracking were undertaken concurrently during the whale migratory season in 2010-2011 and 2013-2014. These data were used to: (1) describe the acoustic repertoire of each species, where information had not been reported previously (2) compare commonly used methods for measuring relative indices of abundance; including acoustic energy, counts of vocalising groups of whales (based on the known acoustic repertoire), and counts of groups of whales observed visually, (3) evaluate biological, environmental, and anthropogenic influences on numbers of vocalising groups detected in recordings (‘vocalisation rates’), (4) compare estimated detection probabilities for each species under different environmental and anthropogenic conditions using acoustic and visual observations and (5) make recommendations for the development of optimal monitoring protocols for pygmy blue and humpback whales in Western Australia using PAM. Sounds in the vocal repertoire included 17 non-song sounds produced by humpback whales and five by blue whales. Vocalisation rates varied widely between species, with humpback whales detected more frequently than pygmy blue whales. Vocalisation rates also varied among years and over each migratory season, and between the type of sound (song or non-song); but not with environmental conditions and vessel presence. Sound energy measured in the form of signal-to-noise ratio was highly correlated with number of vocalising groups for humpback whales but only when temporal factors and presence of vessels was accounted for. Correlation between sound energy and number of groups visually counted was low for both species. Overall, humpback whales had a higher acoustic detection probability and were vocal for longer periods of time than blue whales. In contrast to pygmy blue whales, humpback whales had cohort-specific detection biases with groups of mother-calf pairs or multiple adults having a lower probability of detection. As a result of detection biases and variability in vocalisation rates over time and between species and sound types identified in this study, it is clear that PAM protocols cannot be generalised over the two species. A concurrent acoustic and visual observation pilot study is recommended where possible before undertaken a purely PAM-based program, if knowledge of a species' acoustic behaviour and ecology within certain habitats is unknown. In this way, recording schedules can be optimised and species-specific adjustments can be made to maximise the likelihood of detecting less vocal species or quieter cohorts. Ultimately, optimizing monitoring to achieve these goals will improve the accuracy of knowledge gained. Thus, species that require long-term monitoring, such as baleen whales, could perhaps have an initial higher-cost pilot study with the aim of a longer-term more cost-effective approach (PAM); thus making improving the basis for conservation and management of baleen whales more widely accessible.

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This thesis is dedicated to my family and friends who supported and encouraged me every step of the way; to all the dreamers who fight for making a difference in this crazy world; and to mother earth

Acknowledgments

Since finishing my undergraduate studies, one of my goals was to pursue a PhD program. I knew little about the hard and lonely journey that a PhD is, and even more when you are in a country that is not your own, with a language that is not your own, with no friends and little money. Since starting this journey, ups and downs, sickness and fears have crossed my path, but all these experiences helped me to grow as a professional and more important as a human being. The knowledge you acquire during a PhD program goes beyond the academic scope; you learn so much from supervisors, friends, fellow students, mentors, academics, administration and everyone around you. I want to acknowledge and thank them all.

First of all, the official thanks. This study was part of the South West Whale Ecology Study (SouWEST, https://souwest.org/). SouWEST was supported by grants from Australian Geographic; the International Fund of Animal Welfare (IFAW); The Department of Fisheries from Western Australia; and Holsworth Wildlife Research Endowment (Equity Trustees Charitable Foundation and the Ecological Society of Australia). I would also like to thank the Department of Spatial Sciences at Curtin University for lending their theodolites to us. To our SouWEST Partners, Chris Burton from Western Whale Research, Ron Glencross from Dunsborough Coast and Land Care (DCALC) and Iain Wise, thank you for your support and help during fieldwork. In addition, thank you to Eric Kniest from the University of Newcastle for helping us set up Cyclops and VADAR for theodolite tracking and for all his advice for land-based data analysis. Also to Sea Rescue for their unconditional support deploying and retrieving the recorders in Geographe Bay.

Secondly, I would like to thank my four supervisors, Dr. Chandra Salgado Kent, Dr. Christine Erbe, Dr. Hugh Possingham and Dr. Robert McCauley.

Chandra was my principal supervisor, but more than that a mentor and a friend. Thank you for all your support and for been so patient; for teaching me to see the good in every situation always and for showing me how to be diplomatic in complex circumstances. I also want to thank you for teaching me that accepting your limits is not weakness but strength. I will always treasure those fieldwork adventures where surrounded by nature you show me how to handle difficult situations and conquer my fears (snakes included!). But most of all, thank you for showing me how to be compassionate and give volunteers a great life experience. Having had my fair share of not so positive volunteer and work experiences, working with a researcher that values everyone's capabilities was an inspiration. I especially wanted to thank you for supporting my ideas, even when they sounded a little bit unconventional, and for guiding me to achieve them through very constructive discussions. You help me to be more critical not only of others ideas but of my own. Thank you for everything you teach me during the last seven years of working together and for your friendship. I hope our friendship continues and that we keep working together for many years more. *Por cierto, las arepas son colombianas!*

Christine, although we did not have the opportunity to spend much time together or to share fieldwork, I learnt so much from you, not just about physics but also about how to be a strong and compassionate leader. Thank you for having the patience to explain to me the same basic concepts over and over again, and for answering my really silly questions. I know many times we ended up “lost in translation” because of my poor communication skills or my bad grammar, but I am glad we always managed to sort the obstacles and find solutions. I really admire your optimism, your strength and your enthusiasm for new ideas, even the crazy ones. Thank you for your support and understanding at all times.

Hugh, I cannot thank you enough for all your mentorship and advice, for opening the doors of your lab, for giving me the opportunity to learn and grow as part of CEED and, for always giving me some time in your crazy schedule. Thank you for always encouraging me to do my best and to search for answers beyond regular questions. You lead by example and show me that we can make a difference in the world if we ask the right questions, collaborate with people from different fields and backgrounds, and look beyond our own expertise. Thank you for all your support.

Rob, thank you for giving access to your Port Hedland dataset and your support.

As well as having four amazing supervisors, I was very fortunate to have great colleagues at the Centre for Marine Science and Technology (CMST) and during my visits to the University of Queensland. The wonderful staff from CMST, Iain Parnum, Alec Duncan, Malcolm Perry, Dave Minchin, Miles Parsons and Alexandre Gavrilov. Thank you for all your support, for your encouraging words during this journey, for Matlab coding help and advice, for your guidance through physics concepts, for teaching me and helping me set up fieldwork gear, and for all the laughs. It has been a privilege to be part of CMST. To my fellow CMST students, Bec Wellard, Arti Verma, Marta Galindo, Jamie McWilliam, Shyam Madhusudhana, Matt Koessler and Sue Mason, thank you for all the support, the laughs, the beers and the personal growth during these five years. It was a pleasure to share this journey with you all.

To the staff and students of the Centre for Biodiversity and Conservation Science (CBCS) and the Centre of Excellence for Environmental Decisions (CEED) at the University of Queensland, thank you for all your support, encouragement, and very productive chats. I really appreciate how you made me feel welcome every time I visited, thank you for helping me to see a different point of view to my PhD questions. From day to day conversations, coffee breaks and seminars, I was able to look at my research problems with a different perspective. In particular, I would like to thank Dr Jeff Hanson and Dr Matthew Holden, for their support and advice on statistical analysis and R coding. To my amazing office mates, Hernán Caceres, María Martinez, Andrew Rogers, Bonnie Mapping, Angela Guerrero, Jimmy Choi and Joseph Bennet for all the chats, coffee breaks, support and encouragement. You guys are awesome.

This thesis had not been possible without the help of my amazing fieldwork volunteers: Catherine Attard, Marie Attard, Jo-Marie Acebes, Susan Chalmers, Emma Gates, Sharon Livermore, Damien Morales, Lydia Neta, Sara Niksic, Estenio Paiva, Deborah Pinto Fernandes, Lucy Rudd, Shae Small and Huiying Wu. Thank you all for your dedication and patience, for always giving your best and for all your support.

Now, for the personal thanks. First, I would like to thank my family, in particular, my mom Julia Rocio Salas, my auntie Patricia Salas and my granddad Alfredo Salas. You taught me to be perseverant, confident, respectful, and to always fight for my dreams. What you taught me helped me to overcome difficult times and never give up. You are the reason I try to do my best every day; I just want you to be proud of me. Thank you for believing in me, for all your support and encouragement. *Gracias por estar conmigo sin importar la distancia!*

To the Ciardis, my Australian family, Anita, John, John Antonio, Joseph, Tracy and Chris. I cannot thank you enough for all your love, for hosting me as part of your family during all these years and for always believing in me. You have always been my light in darkness and there for me no matter what. This thesis would not have happened without your help. To my Perth families; the Sosa Zelaya and Quigleys. Jose, Patricia, Clara Luz, Karen, Patrick and Tahlia, I cannot thank you enough for all the laughs, for adopting me every Christmas and making me feel at home; for your help and your words of encouragement; and for opening your houses for me to stay in during this last year.

To my Colombian friends, who have been there through time differences and disappearing for long periods of time during fieldwork and thesis writing, thank you for standing by my side all these years. Catalina Sanchez, our chats about life, helped me to put things in perspective and to see the light at the end of the tunnel. I don´t know what I would have done without our midnight chats. Xyomara Carretero, Xyo, we guided each other through this crazy journey, I was so lucky to have one of my closest friends also doing a PhD in the same country. Thank you for being there when I needed you the most, for bringing me back to reality every time I freak out and for reminding me of the reason behind all this when I wanted to quit. To Cata Cotes, Felipe Velez, Betty Vallejo, Paola Mendez, Tianna Mejia, Caro Corrales, although we did not talk frequently enough, your random messages and chats gave me strength and remind me the fun part of life. You all are awesome!

My Australian friends. My Brissie friends: Anita Murray, Elisa Girola, Diego Correa, Maria Martinez, Sofia Lopez, Felipe Suarez, Diana Barajas and Catalina Adarme, thanks for hosting me during my random visits to Brisbane, for the talks and laughs, you all made the PhD journey easier and fun. To my Perth friends, my whale and PhD sister Sarah Marley, I can´t believe it was seven years ago that we ran our first field season together. It was a pleasure to share this journey with you, to learn about Scottish sarcasm and British TV shows, thanks for the random/weird facts about science, life and everything in between. Thank you for being there through good and bad times and for believing and convincing me that I can make it through when I was feeling hopeless. To Phil Bouchet, thank you for all your support, for being there when I needed a chat, a hug or just to sit in silence. Thank you for all the encouragement, stats chats and R coding advice. Thank you for the movie discussions, for always helping me to see everything from a different perspective and for helping to pronounce Ferrero Rocher perfectly. *Ce fut un plaisir de partager ce temps avec vous*! Sarah, Phil, hope our paths cross again soon. To Monse Landeros, who would have thought that a chat over skype about life in Australia and opportunities at CMST would end up in a close friendship? Thank you for all the laughs, coffee breaks, movies and crazy adventures. It was great to have the support and camaraderie of a fellow Latin-American. To Libby Ooi, my hiking mate. Thank you for all the chats, the fun and the exercise. I don´t think I will have survived the thesis writing without our weekly walks. To Bethan Parnum, it has been a pleasure to share so many moments with your family and to see those boys grow up. To my dancing friends from the Dance Workshop, Joji Ravina, Elise Giamo, Jesse Smith, Justin McNamara and Para Isidro. Dancing always kept me sane. Thank you for all the fun, for not laughing at my complete lack of coordination and for constantly reminding me that when I finish my thesis, I will have more time to dance.

One of the big challenges of this journey was getting sick during the last two years and not knowing the cause. I would like to thank Brendan McGann for all his advice about sick leave procedures and his general support, to my supervisors for their understanding, support and help, and to my friends that were there through ER runs, hospitalisations, medical appointments and exams; all I can say is thank you!. Your support was my rock and helped me overcome this time and get better! I cannot thank you enough for everything you did!

Finally, I would like to thank those silly whales that kept me awake all these years. Although studying you was sometimes very frustrating, I feel lucky to have had the chance to understand you a little bit better!

Publications arising from this thesis

Recalde-Salas A, Salgado Kent CP, Parsons MJG, Marley SA, McCauley RD (2014). Non-song vocalizations of pygmy blue whales in Geographe Bay, Western Australia. *The Journal of the Acoustical Society of America*, 135(5): EL213-218. (Chapter 2).

Recalde-Salas A, Erbe C, Salgado Kent CP, McCauley RD, Parsons MJG (2020). Non-song vocalizations of humpback whales in Western Australia. *Frontiers in Marine Science, 7: 141.* https://www.frontiersin.org/article/10.3389/fmars.2020.00141 (Chapter 2).

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. This project required a large team to collect the data and was part of the broad Southwestern Whale Study program (http://souwest.com) lead by Associate Professor Chandra Salgado Kent and Mr. Chris Burton. During the period of my thesis, I was a co-investigator of the program. In this role, I co-coordinated all aspects of the field work and land-based theodolite team data collection between 2010 and 2014, assisted in three of the four acoustic deployments, and undertook the last of the deployments. I designed the analytical methodology and constructed statistical models based on discussions with co-authors, supervisors and suggestions from mathematicians and statisticians with experience in the field, and carried out all data analyses. Contributors to fieldwork, logistics and statistical analysis are acknowledged in relevant chapters.

As principal supervisor, Associate Professor Chandra Salgado Kent provided advice and guidance on statistical analyses. As co-supervisor, Associate Professor Christine Erbe assisted with acoustic analysis (physics component) and provided code to calculate signal to noise ratios and extraction of physical characteristics of sounds. Co-supervisor Professor Hugh Possingham advised on mathematical and conservation approaches. Dr. Miles Parsons and Associate Professor Rob McCauley made available the long-term Port Hedland acoustic dataset.

I wrote all chapters, with feedback from Associate Professor Chandra Salgado Kent and Associate Professor Christine Erbe. Feedback for chapter 2 was also provided by Dr. Miles Parsons.

Angela Recalde Salas
Student

Dr. Chandra Salgado Kent
(Primary Supervisor)

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Chapter 1.

General Introduction

Baleen whale populations were decimated in the last century by whaling, and many have yet to recover (Thomas et al. 2015; Tulloch et al. 2018). Although populations have experienced different levels of recovery, they are now facing other threats as a result of changing environmental conditions and increasing human activities. For instance, the fitness of baleen whales may be impacted by changes in prey densities and distribution associated with climate change (Tulloch et al. 2018). Also, with a growing human population, whales are increasingly exposed to anthropogenic noise pollution worldwide (Thomas et al. 2015). The low frequencies of anthropogenic noise from hydrocarbon and mineral exploration and production, shipping, and other industrial development overlap with vocalisations produced by baleen whales to communicate (Clark et al. 2009; Hildebrand 2009; Rice et al. 2014; Williams et al. 2014). Thus, baleen whales may have less and less ability to communicate information vital to key life functions such as foraging and reproduction. Regardless of the currency or source of threats, to effectively protect and manage baleen whale populations there is a need to accurately identify and measure changes in ecological parameters such as animal abundance and distribution. By monitoring changes in measured parameters in critical habitats and associating those with potential impacts, management guidelines and government regulations can be implemented to mitigate impacts. Moreover, monitoring ecological parameters is crucial to evaluate long-term changes and the recovery of threatened populations.

Currently, a number of methods for monitoring baleen whale abundance and distribution are available and regularly implemented. These methods include a) distance sampling which consists of visual counts of whales from aircrafts, boats, or land to then assess absolute abundance of animals on the surface of the water, (Buckland et al. 2001); and b) mark-recapture methods that uses photography, video and / or genetic samples from vessels or aircrafts to assess population abundance (Best 2000; Cato et al. 2001; Calambokidis & Barlow 2004; Tiemann et al. 2006; Clark et al. 2010; Irvine et al 2014). Passive acoustic monitoring (PAM) techniques normally use distance sampling methods to monitor relative numbers of vocalising animals or to estimate parameters for use in estimating absolute abundance (Marques et al. 2009; Mellinger et al. 2009; Küsel et al. 2011; Marques et al. 2011; Marques et al.

2012; Risch et al. 2012; Marques et al. 2013; Martin et al. 2013; Mellinger et al 2014). Visual or acoustic counts used in distance sampling can result in presence/absence information as well as estimates of relative abundance. Relative abundance represents a proportion of individuals at a particular place, while absolute abundance is the total number of individuals at a particular place. For instance, relative abundance may be the number of whales observed at the surface of the water at a site during one day, while absolute abundance would be the total number of whales (at and below the surface of the water) at that site during one day. Absolute abundance estimates can be undertaken through various approaches, but all of these attempt to estimate the proportion of individuals that were missed during a sampling occasion (e.g. Buckland et al. 2001). When applied to monitoring animal abundance, the collection of photographs follows a “mark-recapture” approach. In this method, the absolute abundance of individuals present in an area is estimated based on the proportion of individuals that are sampled in the initial and subsequent surveys (e.g. Calambokidis & Barlow 2004; Barlow et al. 2011). Similarly, PAM can provide presence/absence information, relative abundance, and indices of relative abundance. Methods for absolute abundance estimation are also being developed for acoustic applications. PAM achieves this by using detections of species-specific vocalisations as ‘proxies’ for the presence of individuals of that species.

Each of the methods described above has its strengths and limitations; which may vary with species, location and season. Some methods have a relatively short detection range from the survey platform but a broader region can be covered during surveys (e.g., vessel-based surveys), while others can have a relatively long detection range but only cover one particular region near the coast (e.g., high-elevation land-based visual observations). Most visual-based methods, or those requiring good visual conditions (photography and videography), cannot be undertaken in poor weather or low light conditions. The collection of genetic samples requires close approaches to whales from a vessel, thus good weather conditions are required for the vessel to operate. Furthermore, methods that use aircrafts and vessels as survey platforms tend to be relatively expensive. As a result of the limitations in visual-based surveys, PAM has increasingly become popular as a technique for monitoring whales and their environment. PAM is often relatively cheap and easy to implement for long-term monitoring programs (Marcoux et al. 2011; Salgado Kent, Gavrilov et al. 2012; Erbe 2013; Nowacek et al. 2013; McCauley et al. 2017), and it is also capable of autonomous data collection across large areas and in remote locations, regardless of weather conditions. Additionally, in contrast to vessel-based surveys it does not influence a species' behaviour through disturbance. These characteristics have led to the development of long-term passive acoustic monitoring (PAM) programs (e.g. Integrated Marine Observation System (IMOS) in Australia; Erbe et al. 2016).

However, to implement effective acoustic monitoring programs, there must be knowledge of species-specific vocal cues and behaviours. Additionally, as sound propagation changes as a result of varying environmental conditions, there is also a need to understand detection capabilities. The best programs should have the capability to estimate densities, species distributions, and population trends, whilst remaining cost effective (Milner-Gulland & Rowcliffe 2007). Although a range of monitoring protocols for birds and mammals have been developed to provide those estimates using visual methods, protocols for PAM data are still in their early stages of development (Van Parijs et al. 2007; Browning et al. 2017). Monitoring protocols for visual methods are often standardised, and may include the number of surveys to be undertaken, their duration and intervals between surveys, survey routes and locations, times and season of surveys, number of point counts or transects in the study area, the distance between points and transects, among other factors (Conway 2011; Tozer et al. 2016). In comparison, many acoustics-based programs designed for monitoring population trends, distribution or the presence and absence of particular species are still under development. This is due to PAM's relatively recent application to measuring more complex population parameters. In addition, few have focused on imperfect detection of acoustic cues or estimate the proportion of vocally active individuals to assess the probability of detecting animals of a given species under varying biological and/or environmental conditions (Kellner & Swihart 2014). Detectability is an important factor in the design of monitoring programs and surveys, because it evaluates biases on ecological estimates (e.g. abundance, species richness), and the comparative likelihood of detecting common as well as rare, cryptic or threatened species (McCarthy et al. 2013).

Studies on the topic of acoustic detection of whales have mostly focused on the development and performance of automated detectors for faster and more accurate extraction of counts of known cues (e.g. vocalisations of whales; for a review on detection algorithms see Bittle and Duncan 2013) from acoustic recordings. Studies focusing on detection bias and the probability of detecting a whale based on its vocalisations are by far less common. This is most likely due to the fact that estimating the probability of detecting whale vocalisations is complex. The probability of detecting vocalisations produced by individual whales depends upon a range of parameters including: the characteristics of its acoustical repertoire, rates at which individuals vocalise, the physical and environmental characteristics of the study site (e.g. sound propagation characteristics), and the background noise at the area of study, among other attributes. Of these, vocalisation rates and their variability under different conditions are considered one of the key research priorities (Marques et al. 2013). A better understanding of vocalisation rate patterns will help to reduce and adjust for sampling bias and imperfect detection by designing the survey methodology according to vocal rate parameters. Knowledge of the vocal rate can inform how, when and how long an acoustics survey should be conducted, which vocal cues are best to use, and which will be the main cohort(s) of animals detected during a particular survey (Marques et al. 2013). This thesis focuses on examining vocal repertoires, vocal rates under different environmental and anthropogenic conditions, and how these conditions might be used to estimate detection probability. In addition, this thesis compares commonly-used acoustic energy metrics as proxies for relative abundance to simultaneously-collected visual relative abundance metrics.

This is accomplished through examination of the acoustic behaviour of two baleen whale species: pygmy blue whale (*Balaenoptera musculus brevicauda*) and humpback whale (*Megaptera novaeangliae*), which migrate through waters off the southwest coast of Western Australia. Specifically, this thesis describes their acoustical repertoire, investigates what influences the vocalisation rates of these sounds, and determines how this information can be used in the estimation of detection probabilities and design of monitoring protocols.

To set the scene for this thesis, a general background on communication, calling behaviour and vocal repertoire of baleen whales is given below; followed by a brief review of the current status of research on vocalisation rates, vocal energy metrics as proxies for whale densities, and detection probability estimation. Finally, there is a review of current monitoring protocols with emphasis on acoustical monitoring programs. The main body of the introduction is concluded by the identification of key knowledge gaps and the overall objectives of the thesis.

1.1. Communication in marine mammals

Communication is a process that allows the exchange of information between individuals or groups of individuals. On land, animals communicate using visual, acoustic, chemical or tactile signals (Dudzinski et al. 2009). Of these, visual strategies are often much less effective for aquatic species because they spend most of their lives in low-visibility underwater environments. Thus, many aquatic species, such as marine mammals, have specialised to use acoustics as the principal mode of communication because underwater sounds can be transmitted over long distances (Dudzinski et al. 2009).

In marine mammals, acoustical communication can be divided into vocal and non-vocal (Tyack & Miller 2002). 'Non-vocal' communication makes reference to the sounds produced by moving or striking parts of the body against one another, when animals jump, slap the water with flukes or flippers, or when emitting bubbles (Tyack & Miller 2002; Dudzinski et al. 2009). For large baleen whales, some of these sounds can propagate over several kilometres and are likely to be used as agonistic behaviours (i.e. breaching or tail slapping in competitive humpback whale groups) and for acoustical contact (e.g. simultaneous tail or pectoral slapping in groups of right whales). Other sounds propagate over shorter distances and may be a result of expressions of excitement or associated with capturing prey (i.e. different types of leaps undertaken by dusky dolphins (*Lagenorhynchus obscurus*), or other activities (Dudzinski *et al.* 2009). In some cases, low-frequency non-vocal communication may be used instead of vocal communication when ambient noise levels are high, as these can dominate the mid-frequency spectrum of frequencies (Hildebrand 2009; Dunlop et al. 2010).

In contrast, 'vocal' communication makes reference to phonation or sound production by vibration of vocal folds in the larynx (Herbst 2016). Vocalisations are used in reproduction, group cohesion, locating prey, navigation, and echolocation among other contexts (Marques et al. 2013). The sounds produced by different marine mammal groups (mysticetes, odontocetes, sirenia and pinnipeds) vary greatly in structure and frequency, but little in their function. Each species produces a wide range of vocalisations, and in some cases, their uniqueness among individuals can be useful for identifying individuals (e.g. signature whistles in bottlenose dolphins or manatee vocalisations; Sousa-Lima et al. 2002; Tyack & Miller 2002).

In general, marine mammal sounds can be broadly described by the following features: whether they are frequency-modulated (FM), amplitude-modulated (AM), or both FM and AM. Sounds that are not FM may be constant wave (CW) tones with harmonic overtones, or broadband pulses that lack tonal characteristics (Erbe et al. 2017). Regardless of the particular characteristics of sounds produced, each marine mammal group vocalises in a particular frequency range and each species (or sometimes population) has a unique repertoire. For example, pinnipeds produce pulses and FM sounds (Stirling & Thomas 2003; Erbe et al. 2017) and sirenians emit broadband click-like sounds and tonal vocalisations in frequencies between 1 and 25 kHz depending on the species (Anderson & Barclay 1995; Sousa-Lima et al. 2002; Nowacek et al. 2003; Parsons et al. 2013). Odontocetes (dolphins and toothed whales) can emit whistles, burst-pulse sounds and clicks (Erbe et al. 2017) with frequency ranges from 0.8 kHz up to at least 200 kHz (Au 1993; Boisseau 2005; Erbe et al. 2017). Finally, mysticetes (baleen whales) produce a range of FM and AM vocalisations in low to medium frequency ranges. Blue whale *Balaenoptera musculus* and fin whale *Balaenoptera physalus,* produce sounds below 200 Hz (McCauley et al. 2001; Širović et al. 2004; McDonald et al. 2006; Oleson, Calambokidis, Burgess et al. 2007; Boisseau et al. 2008; Gavrilov et al. 2011; Recalde-Salas et al. 2014, see Chapter 2), whilst right whales vocalise in a higher range between 100 and 400 Hz (Clark 1982; Gillespie 2004; Parks et al. 2011; Dombroski et al. 2016). Humpback whales are the most broadband among the baleen whales with vocalisations between 40 Hz and 24 kHz (Silber 1986; Au et al. 2006).

Similar to humans, marine mammal species have a repertoire of sounds that are produced in a particular sequence. The characteristics of these repertoires can be specific to particular populations and so, in some cases, allow population-level differentiation. For example, blue whale song is divided into regional types, with each region displaying specific sound types that are stable over long periods of time (McDonald *et al.* 2006). A similar characterisation is observed in humpback whales, where the seasonal song is specific for each population and sung by males during the breeding season (Winn et al. 1981; Garland et al. 2011; Darling et al. 2014); although there are some similarities in the sounds used to compose the song among different populations (Garland et al. 2011; Darling et al. 2014). In other marine mammal groups, there are specific sounds that allow recognition of specific population cohorts. For example, in some pinnipeds, mothers and pups have unique sounds that allow recognition between pairs (Charrier & Harcourt 2006; Sauvé et al. 2015). Finally, the use of signature whistles in dolphins permits the identification of individuals during communication within conspecific groups (Sayigh et al. 2007; Dudzinski et al. 2009; Lima & Le Pendu 2014).

1.2. Vocal repertoire of baleen whales

Baleen whales are widely known for the intense and often complex vocalisations they produce (Edds-Walton et al. 1997; Gavrilov et al. 2011; Stafford et al. 2011). In general, baleen whale vocalisations can be divided into "song" and "non-song" sounds. "Song" is defined as a regularly patterned sequence of notes or units (McDonald et al. 2006; Cholewiak et al. 2013) that is different for each species and population, and thought to be produced only by males (Frankel et al. 1995; McDonald et al. 2006; Garland 2011). Singing behaviour has been reported for several baleen whale species, including bowhead *Balaena mysticetus*, Omura's *Balaenoptera omurai,* minke *Balaenoptera acutorostrata*, humpback, blue, fin whales (Edds-Walton et al. 1997; Gedamke et al. 2001; McDonald et al. 2006; Garland et al. 2011; Mellinger et al. 2014, Cerchio et al. 2015; Stafford et al. 2018). The repertoire of sei (*Balaenoptera borealis*) and Bryde's (*Balaenoptera brydei*) whales is less known (Edds-Walton 1997) and therefore, it is uncertain if they produce song.

Sounds that do not follow a pattern and are vocalised as single units are described as 'non-song' vocalisations (Dunlop et al. 2007; Oleson, Calambokidis, Burgess et al. 2007). These vocalisations have been associated with feeding, foraging, social interactions or to maintain group cohesion; and are produced by adults and calves of both sexes (Dunlop et al. 2007; Zoidis 2008; Oleson, Calambokidis, Burgess et al. 2007). In this study, all non-patterned sounds were classified as 'non-song' sounds because it was not possible to define their specific use and context.

Here, current knowledge of song and non-song vocalisations for the focal species of this study, humpback and blue whales, is briefly described. Humpback whales are one of the most vocal of baleen whale species and have one of the most complex vocal repertoires. They vocalise in a broad frequency range, with most units having a fundamental frequency below 3 kHz. Vocalisations have been reported to have source levels between 123 and 192 dB re 1µPa @ 1m (Thompson et al. 1986; Au et al. 2006; Dunlop et al. 2013; Fournet et al. 2018). Humpback whale song is composed of a variety of structured sound patterns called phrases, several of which make up themes of a song, that are then repeated in a cyclical manner for more than an hour (Payne and McVay 1971; Mercado 2003; Cholewiak et al. 2013). Humpback whale song structure is specific to each population in the world and evolves annually (Payne and Guinee, 1983; Payne et al. 1983; Cerchio et al. 2001; Garland et al. 2011; Cholewiak et al. 2013; Darling et al. 2019). During a particular season, males within the same population mostly produce the current version of the song (Payne and McVay 1971; Garland et al. 2011). Song is reported to mainly be produced on breeding grounds and less frequently on feeding grounds (Clark & Clapham 2004; Vu et al. 2012).

Humpback whale non-song vocalisations (often called social sounds and feeding calls in the literature) are characterized as being unpredictable, non-patterned, and produced in a frequency range from 50 Hz to over 10 kHz (Silber 1986). Feeding calls have been reported to occur within a frequency range of 20 Hz to 2 kHz (Thompson et al. 1986), with peak frequencies generally less than 1 kHz and a duration of less than 1 s (Stimpert et al. 2011). In general, non-song sounds appear to be produced by all cohorts and sexes (Silber 1986; Edds-Walton 1997; Dunlop et al. 2007). These sounds are associated with social interactions and agonistic behaviour, as well as with feeding or foraging behaviours (Thompson et al. 1986; Richardson et al. 1995; Edds-Walton 1997; Stimpert et al. 2011).

While much research has been conducted on quantifying and understanding song and non-song vocalisations produced by humpback whales in particular populations, relatively little is known about blue whale vocalisations. Blue whale song has been described for different populations (McDonald et al. 2006; Gavrilov et al. 2011; Stafford et al. 2011), but there is limited information about the full acoustic repertoire of this species, and even less on non-song vocalisations (Oleson, Calambokidis, Burgess et al. 2007; Recalde-Salas et al. 2014, see Chapter 2). Blue whale vocalisation are among the most powerful (188 dB re 1µPa @ 1m) and the lowest of frequencies (16-200 Hz) produced by marine mammals (McDonald et al. 2001; Oleson, Wiggins & Hildebrand 2007; Gavrilov et al. 2011; Erbe et al. 2017). In terms of non-song calls, the most common have been reported to be downsweeps (“D” vocalisations) and FM and AM vocalisations described as "growls" (Mellinger & Clark 2003; Oleson Calambokidis, Burgess et al. 2007; Gavrilov et al. 2011; Recalde-Salas et al. 2014, see Chapter 2). Non-song calls reported so far have been associated with certain behaviours such as feeding or foraging (Oleson, Calambokidis, Barlow, et al. 2007).

1.3. Conditions influencing vocalisation rates in baleen whales

Vocalisation rates of whales vary widely among species, biological conditions (sex, age, social context, period within the reproductive cycle, etc.), environmental conditions (including the soundscape and human activities, etc.), geographical location, and the function of vocalisations produced (Frankel et al. 1995; Au et al.

2000; Croll et al. 2001). Many PAM studies have used some measure of ‘vocalisation rate’ to investigate seasonal occurrence, diel patterns, responses to noise pollution or anthropogenic activities, and behavioural patterns of whales, or as part of general monitoring programs.

To inform these studies, ‘vocalisation rate’ has been measured in different ways, thus the exact definition itself also varies (Table 1.1). For instance, vocalisation rate can be used to refer to the number of vocalisations per unit time, regardless of the number of individuals producing them (VR-1 in Table 1.1; e.g. vocalisations per minute). Vocalisation rate can also be measured as the number of vocalisations per individual per unit time (VR-2 in Table 1.1; e.g. vocalisations per individual per minute). It has also been measured as the number of individuals vocalising per unit time (VR-3 in Table 1.1; e.g. number of individuals vocalising per minute). Finally, vocalisation rate has been defined and measured as the rate of occurrence of vocalisations (VR-4 in Table 1.1). Rates of occurrence have been reported either as the average duration with at least one vocalising individual in the recording (Clark & Clapham 2004; Monnahan et al. 2014) or as a ratio of time calls are present in a recording with respect to the total time sampled (Melcón et al. 2012). Vocalisations per unit time (VR-1) and rates of vocal occurrence (VR-4) do not account for the number of individuals producing the sounds. In summary, multiple definitions of ‘vocalisation rate’ exist, with the definition used usually based on study-specific objectives and data collection methods.

Table 1.1. Different definitions of the term 'vocalisation rate'

ID	Definition	Example
VR-1	Number of vocalisations per unit time	15 vocalisations hour^{-1}
VR-2	Number of vocalisations per individual per unit time	15 vocalisations individual^{-1} hour^{-1}
VR-3	Number of individuals vocalising per unit time	15 individuals hour^{-1}
VR-4	Rate of occurrence of vocalisations	15% of recordings

To examine how these different definitions of vocalisation rate are used throughout the literature, a review of papers describing baleen whale vocalisations, with emphasis towards humpback, blue and right whales, was undertaken and presented here. To be eligible for consideration, papers needed to meet the following criteria. They needed to (1) be published in a peer-reviewed journal, (2) aim to measure vocalisation rates quantitatively, and (3) clearly state their definition of ‘vocalisation rate’. Because the sample size for papers fulfilling these criteria was small, papers that at least fulfilled criteria 1 and 3 above were included. As a result of these search criteria, 52 papers were selected. Of these, the most common definition of vocalisation rates used was VR-1: vocalisations per unit time (Figure 1.1). This metric does not account for the number of individuals that may be producing the sounds, or variability in vocal rates among individuals. The rate is defined as the number of calls detected per hour, day, week, or month (e.g. Helweg & Herman 1994; Croll et al. 2001; Matthews et al. 2001; Stafford et al. 2009; Clark et al. 2010; Di Iorio & Clark 2010; Hofmeyr-Juritz & Best 2011; Marques et al. 2011; Morano et al. 2012; Mussoline et al. 2012; Vu et al. 2012; Gavrilov & McCauley 2013; Helble 2013; Matthews et al. 2014; Bort et al. 2015; Erbe et al. 2015). This metric is common in studies that use remote underwater recorders, thus do not have access to information on the individuals vocalising.

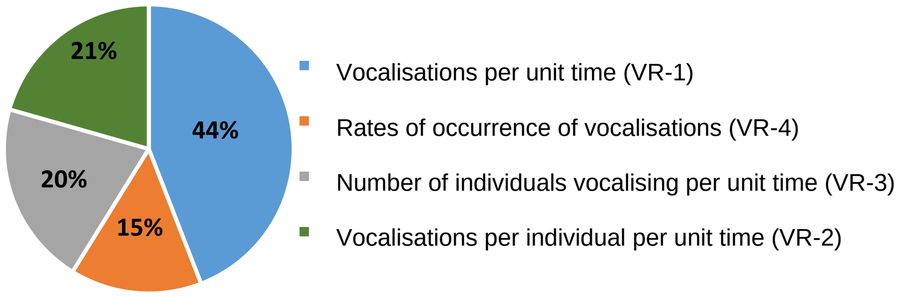


Figure 1.1. Percentage of peer-reviewed papers using different units of measurement for vocalisation rate.

Approximately a fifth of the studies reviewed used definition VR-2, and measured vocalisation rates of individuals (or in some cases vocalisations per group) by counting the number of calls, sounds or phrases vocalised by individuals per unit time (Helweg & Herman 1994; Cato et al. 2001; Charif et al. 2001; Clark & Clapham 2004; Boisseau et al. 2008; Dunlop et al. 2008; Hofmeyr-Juritz & Best 2011; Parks et al. 2011). Often this information is used to document the number of vocalising individuals present, but can also be used in ‘presence-only’ distributional type models where non-vocalising animals are not measured (Charif et al. 2001; Clark & Clapham 2004; Hofmeyr-Juritz & Best 2011). In other studies, this information was used to inform VR-3. In one study, the information was used to estimate the proportion of animals vocalising versus the total number of animals present in an area (Cato et al. 2001). VR-3 is particularly useful for surveys aimed at capturing information on vocalising and non-vocalising animals (Salden 1988; Oleson, Calambokidis, Barlow et al. 2007). Less than a fifth of studies reviewed used definition VR-4: rates of occurrence of vocalisations as a metric of vocal rate (Norris et al. 1999; Kumar 2003; Clark & Clapham 2004; Melcón et al. 2012; Monnahan et al. 2014).

While metrics used in studies measuring vocalisation rates vary, those studies that have used them to investigate the influence of biological and environmental conditions on whale vocalisations have identified certain comparable patterns. For instance, vocalisation rates may vary according to group composition. For example, humpback whale males are more vocally active and produce song over long periods (Tyack 1981; Frankel et al. 1995), while mothers and their calves generally produce sound less frequently than other group types (Dunlop et al. 2008; Zoidis et al. 2008). Conditions such as wind, primary productivity, presence of vessels and the presence of operating seismic surveys have also been reported to be associated with either an increase or a reduction in vocalisation rates for certain species (i.e. Parks et al. 2007; Doyle et al. 2008; Stafford et al. 2009; Dunlop et al. 2010; Melcón et al. 2012; Cerchio et al. 2014). For example, humpback whales may replace vocal activity for surface behaviour (e.g. tail slap, breach) under increased wind conditions (Dunlop et al. 2010), while right whales may reduce their calling rate under high noise conditions (Parks et al. 2007). The presence of vessels and other human activity has been reported to increase the calling rate of blue whales (Croll et al. 2001; Di Iorio & Clark 2010) and reduce the number of humpback whales singing (Cerchio et al. 2014).

While these studies achieved their aims by measuring vocalisation rates for vocalisations detected, many questions regarding the acoustic ecology and social behaviour of whales also require information on non-vocalising individuals (Stanistreet et al. 2013). For instance, knowledge of the proportion of whales vocalising allows an estimation of abundance that includes vocalising and non-vocalising cohorts.

1.4. Sound energy as an index of relative abundance

As vocalising fauna produce sound in species-specific frequency bands, a commonly used technique for determining an acoustic index of relative abundance is to measure the acoustic energy (in the form of sound levels) in corresponding frequency bands (Au et al. 2000; Gedamke et al. 2007; Rowell et al. 2012; Mellinger et al. 2014). This approach has been used in a range of studies as an indicator of densities for fish (Rowell et al. 2012); humpback, fin and blue whales (Au et al. 2000; Širović et al. 2004; Gedamke et al. 2007; Mellinger et al. 2014; Seger et al. 2016); and to define peaks in whale migrations at particular locations (McCauley et al. 2001; Erbe et al. 2015). The approach is based on the idea that increasing numbers of individuals present in an area will be associated with an increase in acoustic energy in the bandwidths they communicate in (Seger et al. 2016). The effectiveness of this approach depends upon the accuracy of this relationship. Thus, the methods are generally used for highly vocal species whose vocalisations are frequent, prolonged, of unvarying sound levels, and that dominate the acoustic environment (Mellinger et al. 2014). More complex models can be developed to account for variability in vocal behaviour in populations; however, they require knowledge on the demographics of the population and their vocal behaviours (Rowell et al. 2012).

In most studies, the relationship between sound energy and relative abundance (and/or density) of vocalising animals is assumed to be monotonic or close to linear (Au et al. 2000; Gedamke et al. 2007). However, the relationship between the number of whales counted visually and acoustic energy measured does vary, with one study reporting a best fit explained by a quadratic equation (Ponce et al. 2012). In other studies, ambient noise levels (which include whale vocalisations in addition to other biological and environmental noise) have often been used as indices of relative population size (Seger et al. 2016). Only a few studies have quantitatively assessed whether acoustic energy levels are linearly related to the number of vocalising individuals. Comparisons of acoustic energy and numbers of vocalising individuals of humpback whales in Hawaii resulted in a positive linear relationship (Helweg & Herman 1994), while other studies have reported a linear relationship only under specific environmental conditions (e.g. high tide) and behavioural states (e.g. spawning) (Rowell et al. 2017). Thus, a greater understanding of the relationship between acoustic energy (and its metrics) and relative abundance of different species of whales in varying environmental conditions is required to accurately interpret results from studies using acoustic energy as indices.

1.5. Estimating detection probabilities of baleen whale vocalisations

Key parameters required from a standard whale monitoring program include distribution, abundance and overall trends. An accurate estimate of these parameters, in turn, requires accurate estimates of whale detectability. For PAM surveys, detection is limited to those individuals that are vocalising and excludes silent animals. Moreover, even when vocalising, not all may be detected by the personnel conducting the survey due to conditions such as high background noise levels (low signal-to-noise ratios), or observer fatigue. This “imperfect detection” of all individuals present in a study area introduces biases in abundance and density (Amundson et al. 2014). Therefore, accurate abundance estimates that include all cohorts of the population require estimates of detection probabilities that account for imperfect detection.

There are a range of sampling methods that allow for adjustments of counts of individuals where there is imperfect detection. These methods include: distance sampling (Buckland et al. 2001), time removal (Farnsworth et al. 2002), repeated counts (Royle et al. 2004), double observer (Riddle et al. 2010) or double sampling (Thompson 2002) for use in mark-recapture approaches (Laake et al. 2011) of reconciled observations, double observer for unreconciled observations (Riddle et al. 2010), or a combination of these such as time removal and distance sampling (Sólymos et al. 2013; Amundson et al 2014). Survey designs within a study region commonly involve surveying multiple line-transects or conducting multiple point-counts. In acoustic surveys, point-counts are the most common. In acoustic point count surveys, a standard approach is for a person to count the number of individual animals based on the number of calls detected over a sample period (for example, over 5 minutes). This approach is commonly used for avian surveys in which vocalising birds can be easily distinguished by a person present at each point-count study site. In many of these studies, the proportion of individuals is assumed to be constant over all point-count study sites within a study region and over the period required to survey them all (Thompson 2002). However, it is likely that this assumption is violated since the probability of detection varies among habitats within a study region, over time within a survey, and among species if the study includes multiple species (Alldredge et al. 2007). In an example of humpback whales, Seger et al. (2016) assumed that the number visually observed during the day was directly proportional to the number of whales singing during the night. Thus, vocalisation rates and movement patterns of whales were assumed to remain constant throughout diurnal periods. However, diel patterns have been identified in which more singing occurs during the night than during the day (Au et al. 2000).

Regardless of which sampling design is applied to estimate the abundance of animals, the probability of acoustic detection of individuals is required to account for non-vocalising individuals and individuals vocalising but not detected. Thus, the probability of detection is a result of the product of two probabilities: the probability that the individual is available to be detected and the probability of being detected given it is available. In acoustic surveys, an individual that is available to be detected is one that is producing sound. An individual's detectability (given it is producing sound) is dependent on the observer listening or sound recording (Farnsworth et al. 2005; Amundson et al. 2014). Estimates of availability bias are often difficult to obtain accurately, and adjustments for heterogeneity in availability over time, space, and among individuals are only recently being made (Farnsworth et al. 2005).

Several sampling approaches have been developed with the aim of reducing availability bias. For instance, rather than an instantaneous count of vocal detections in an area, some surveys use cumulative counts over a given period of time to estimate individuals. When the cumulative count curve reaches a plateau (Figure 1.2), the probability of misdetections is assumed to be null or close to null (McCallum 2005a, McCallum 2005b). This method assumes that all individuals will vocalise at some point in time during the survey period. Thus, the cumulative count (C) is equal to the number of individuals present (N) at that time (Bart & Earnst 2002). This approach is commonly used for bird surveys where an observer can identify and distinguish among vocalising individuals.

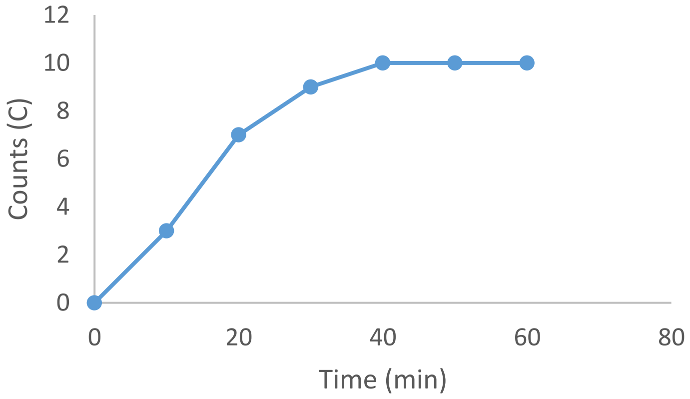


Figure 1.2. Hypothetical accumulation curve (based on McCallum 2005b).

In addition to requiring that an individual vocalises at least once during the survey period, several other conditions are required for accurate counts of individuals present. These conditions include: 1) the distance of the vocaliser and environmental factors (such as background noise levels) must be such that detection of the vocalisation is possible, 2) the recorder (or the person listening) must have the sensitivity to detect the vocalisation, and 3) the person reviewing the recordings (or listening *in situ*) must have the attentiveness to detect the vocalisations (or if auto-detection algorithms are used they must have a high detection rate). To assess whether the first of these conditions is met, vocalisation rates and their variability under ecological, behavioural and environmental conditions occurring in the area must be known. If vocalisation rates are high, detection biases that cause false negative (missed) detections (such as partial masking from intermittent noise) may be reduced because the sound is available for a longer period of time or present at a higher rate (McCallum 2005b). In contrast, if vocalisation rates are low, and background intermittent noise is frequent, detection bias may be high. In this example, the survey protocol may need to be adjusted to include longer sampling periods.

While the method above increases the probability of detecting individuals that are available, accurate counts are still conditional on the individuals being available for detection at some point during the survey period. An approach that accounts for animals that do not vocalise during the survey period (and are not available to be detected) is to estimate the probability that an individual will be vocalising (denoted as P_s in McCallum (2005b)). By multiplying the probability that they will be vocalising (i.e. available) by the probability that the animal will be detected when vocalising ($P_{d/s}$), the overall detection probability can be estimated (Equation 1.1; Farnsworth et al. 2002).

$$p = P_s P_{d/s} \qquad (Eq.\ 1.1)$$

To estimate the probability that individuals are vocalising (i.e. available), double sampling methods such as simultaneous visual and acoustical surveys have been suggested and implemented successfully (Wang et al. 2005; Akamatsu et al. 2008; Kimura et al. 2009; Riddle et al. 2010; Richman et al. 2014). While many studies have estimated detection probabilities in birds (e.g. Bart & Earnst 2002; Farnsworth et al. 2002; Thompson 2002; McCallum 2005a, McCallum 2005b; Alldredge et al. 2006; Riddle et al. 2010; Sólymos et al. 2013; Amundson et al. 2014), there are limited studies that estimate the probability of acoustic detection by combining visual and acoustic methods in cetaceans (Akamatsu et al. 2008; Ponce et al. 2012; Richman et al. 2014). These studies have generally combined either a towed array of hydrophones behind a vessel with visual observations from the same vessel (Akamatsu et al. 2008; Richman et al. 2014), or a stationary array with land and vessel-based visual observations (Ponce et al. 2012; Seger et al. 2016). While the most cost-effective PAM approach is to use a single stationary acoustic recorder, to the author’s knowledge, no studies have yet estimated imperfect acoustic detection of cetaceans using double observer methods with a single stationary recorder.

1.6. Optimal monitoring using passive acoustics

Environmental monitoring plays an important role in conservation and management because it allows for ecological parameters (e.g. abundance, distribution, population growth, etc.) of key species to be tracked over time for the assessment of ecological trends (Pollock et al. 2002; Milner-Gulland & Rowcliffe 2007). By assessing trends, monitoring can evaluate the success of management guidelines and enforce regulations aimed at reducing pressures on target species (e.g. anti-poaching patrols), identifying breaches in regulations (e.g. un-authorized activities in protected areas), and tracking changes in association with increasing pressures (e.g. climate change, industrial activities, etc.). Monitoring programs help decision making processes by providing information required to make adjustments to management strategies so that they are effective (Pollock et al. 2002).

The most successful programs designed for monitoring ecological trends are practical to implement, cost-effective, long-lasting, scientifically-robust, and have the power and longevity to detect trends that inform the required decisions. While designing a monitoring program with all of these characteristics is not trivial, it is considered to be one of the most important aspects of monitoring for conservation (Milner-Gulland & Rowcliffe 2007). In recent decades, monitoring using acoustic sensors has grown because it addresses some of the challenges presented in other approaches. For example, acoustic monitoring can collect reliable data at a lower cost than many other approaches, can be undertaken in areas and times in which visual surveys may not be practical or feasible, in some instances can capture indices of biodiversity and composition more rapidly than visual techniques, and can be used for evaluating impacts of human activities over long time periods (Blumstein et al. 2011).

While acoustic monitoring programs have many benefits, their designs are often optimised for broad objectives on ocean noise. Because PAM is based on species vocalising, the information obtained can be biased towards more vocal species, cohorts or habitats with higher vocal rates. These differences in vocal rates should be considered when developing optimal monitoring protocols for PAM aiming to estimate population parameters of focal species. In general, monitoring programs that consider spatial and temporal variations, and influence of species behaviour on detectability are more informative for population parameter estimation (Pollock et al. 2002; Martin et al. 2007). In particular, monitoring programs that consider the variability in incomplete detection and heterogeneity in detectability in time and space have greater accuracy (Pollock et al. 2002). Thus, monitoring programs that build the estimation of detection probabilities within their designs have been suggested (Pollock et al. 2002) and are increasingly applied (e.g. marsh birds, Tozer et al. 2016). Optimal monitoring protocols for marine fauna using PAM are in early stages of development and are still limited by current knowledge available to inform them (Browning et al. 2017).

1.7. Knowledge gaps

The increase in human activities worldwide has resulted in a growing need for monitoring programs to measure their effects on protected species and their environments. In addition to having the power to detect effects such as changes in abundance and distribution, monitoring programs also need to be cost-effective because of economic constraints that governments, industries or environmental departments face.

PAM can offer cost benefits needed in monitoring programs of marine species including baleen whales. However, for this technique to be most effective in monitoring changes in population parameters, some knowledge gaps need to be filled. The following are some of the current key knowledge gaps:

- **Acoustic repertoire knowledge:** Baleen whales usually vocalise at particular frequencies and produce sounds specific to their species and often populations. This attribute allows species to be identified by the sounds they produce. To attribute sounds to a baleen whale species, the acoustical repertoire of each needs to be known. Thus, verification of sounds produced by the species is required. A number of methods are available to achieve this. Tags that directly attach to the body of a whale and record sound, such as ‘D-tags’, are a reliable way to confidently attribute sounds to the whale producing them. However, these methods are expensive, result in low sample sizes, and affect the overall cost of PAM. Visual observations of individual whales can be combined with acoustic recordings more remotely. This approach requires some knowledge of the vocal behaviour, movement patterns, and distribution of whales to be able to match vocalisations recorded or heard with individuals observed. For some species that have well-studied repertoires, additional new sounds recorded by remote underwater recorders can be attributed to the species when the new sounds are produced with known sounds. However, it is important to note that the acoustic repertoire of most baleen whale species, with some exceptions (i.e. humpback whales), remains unknown. As a consequence the sources of many sounds remain unidentified. Further studies that describe the acoustic repertoire of baleen whales using such techniques would improve our knowledge base for using PAM to monitor whales into the future.

- **Using vocalisations as indices of relative abundance:** Most long-term acoustic monitoring studies use single underwater recorders deployed within a target study site. These studies are cost-effective, but do not allow localising individuals in space. This limitation is partially mitigated by using knowledge of their stereotypical songs and comparing signal-to-noise ratios to distinguish individuals from each other and count them. However, when a large number of whales are vocalising simultaneously, this approach is not possible. Multiple recorders (three or more) or the use of directional sonobuoys can provide acoustic tracking capabilities to identify the direction and/or location of individuals vocalising. In these cases, individuals can be distinguished and counted. However, the use of multiple recorders and sonobuoys increases the cost of a program, often beyond what is affordable. Consequently, studies using a single recorder have either used counts of vocalising whales nearby (within a designated high signal-to-noise ratio limit) or have used acoustic energy as an index of relative abundance. However, the accuracy of using sound energy metrics as proxies for relative abundance has not been adequately explored. For instance, accuracy may be affected by changes in relative distance of vocalising animals from the recorder, with closer animals increasing energy levels more than animals far away. Thus, it is important to understand how energy level metrics correlate with actual numbers of vocalising whales and conditions that may affect this relationship.

- **Biological, environmental and anthropogenic conditions influencing the variability in vocalisation rates:** Vocalisation rates can be influenced by different environmental, biological, ecological and anthropogenic conditions and combinations of these. While some of the conditions that influence variability in vocalisation rates have been investigated on a species-by-species basis, few studies have explored the influence of combinations of these on multiple species at a site. A broader understanding of the conditions influencing baleen whale detectability and vocal behaviour is important for identifying potential sources of bias. This knowledge can then be used to adjust detection probability estimates to improve the accuracy of abundance estimates.

- **Acoustic detection probability:** Finally, abundance estimates (and other population parameters) using PAM that include an estimation of detection probability have a higher accuracy than those that use raw counts. Estimation of the availability component of the overall detection probability is one of the main challenges associated with PAM, because it depends upon knowledge of the vocalisation rates and behaviour of whales at the target study site during the period monitored. For most baleen whale species, information on vocal behaviour and vocalisation rates is scarce or non-existent (Oleson, Calambokidis, Burgess et al. 2007; Marques et al. 2013). Some studies have measured individual vocalisation rates using D-tags, and this information has been used in density estimation by dividing the number of individuals visually observed by cue rates. However, behavioural studies have suggested differences in vocal rates among individuals and cohorts of a population that vary in different environmental conditions. Thus, by estimating detection probabilities using parameters known to influence the variability in vocalisation rates as covariates (observer bias, environmental conditions, distance, technical specifications), and making adjustments based on the probability that the animal is available for detection (an animal is vocalising), both availability and detectability can be further adjusted for and incorporated into abundance estimates or population parameters.

  Availability bias can be approximated using two different survey platforms that count different cues for detection, such as visual and acoustic cues. This approach has been used in a few studies aimed at adjusting for imperfect detection of dolphins (e.g. Akamatsu et al. 2008; Ichikawa et al. 2009; Akamatsu et al. 2014; Richman et al. 2014) and gray and minke whales (Rankin et al. 2007; Van Parijs et al. 2009; Ponce et al 2012). It is important to note that double observations from visual and acoustic platforms approximate estimates of detection probability bias, since animals that are not detected by either platform are not counted. Studies that consider a large number of sources of detectability bias are still under development.

- **Optimal monitoring protocols:** The use of PAM has increased over recent decades because of the development of acoustic sensors that are affordable, non-invasive and can be used for long periods of time. Therefore, PAM has become an important tool used in cost-effective monitoring of species on land and in aquatic environments, and for monitoring anthropogenic impacts on their populations. However, the use of this tool for long-term monitoring of focal species requires knowledge of their biology, behaviour and habitats to optimise the selection of acoustic sensors, survey design and data analysis. Ultimately, the estimation of population parameters of target species can be improved through the development of guidelines for developing optimal monitoring protocols.

1.8. Aims and rationale

To optimise PAM for baleen whale population monitoring (abundance, density, etc.), its biases and limitations need to be measured to adjust and improve population parameter estimates. To achieve this, a greater understanding of baleen whale acoustical ecology is required. This thesis has been prepared with the aim of improving our current knowledge of the acoustical ecology of baleen whales by filling some of the knowledge gaps described above.

In this study, PAM of pygmy blue whales and humpback whales that migrate along the coast of Western Australia using a single, stationary underwater recorder was undertaken as a ‘case study’. Humpback and pygmy blue whales migrate along the Western Australian coast annually during their northern and southern migrations from high-latitude feeding grounds to low-latitude breeding grounds and back. Both species are protected under the Australian Environment Protection and Biodiversity Conservation (EPBC) Act (1999, Australian Government 2018) and are listed on the IUCN Red List of threatened species. Humpback whales are globally listed as least concern (Reilly et al. 2008) and in Australia as vulnerable (Australian EPBC Act 1999), while blue whales are listed as endangered (Australian EPBC Act 1999; Cooke 2018; Department of the Environment 2018a). The coastal movements of both species make them economically important for whale watching activities in the state. However, due to increasing pressure from industrial activities including recreation and tourism, migrating pygmy blue and humpback whales are increasingly being exposed to certain anthropogenic threats throughout their migratory corridor.

Geographe Bay, located in southwestern Australia, was used as the principal study site; however, acoustic data were also available from the waters off Port Hedland in north-western Australia and used to complement the humpback whale repertoire of this study. Geographe Bay was selected as the primary study site because pygmy blue and humpback whales migrate very close to the coast at this location. Thus, observations of both species using simultaneous acoustic and land-based visual techniques were possible. In addition, Geographe Bay is a popular tourist destination and experiences significant recreational boat activity during weekends and holidays (Salgado Kent et al. 2014). Consequently, Geographe Bay offers varied anthropogenic noise conditions for which to assess PAM. Geographe Bay, itself, is recognised for its biological significance. The bay falls within the Commonwealth Marine Reserves Network (Department of the Environment and Energy 2018b), and is a recognised migratory corridor for multiple species of baleen whales (Salgado-Kent et al. 2014).

Monitoring population trends of these whales is required for effective management of this sector of the Commonwealth Marine Reserves Network. Thus, while this thesis has the primary general aim of improving the design of baleen whale PAM programs, it also directly informs pygmy blue and humpback whale monitoring and management programs in an important migratory corridor off Western Australia.

To achieve the aims of this thesis, the work was broken down into a number of steps. Firstly, a description of the acoustic repertoire of each species was required so that sounds produced by whales could be accurately identified and allocated to species. Song for these two species in Western Australia has been described previously (Gavrilov et al. 2011; Murray et al. 2012; CMST and the author’s data unpublished). However, non-song sounds from Western Australia have not. Thus, the first step was to describe non-song sounds. The second step was to use the species’ known vocal repertoires to compare the acoustic energy in frequency bands of their vocalisations with counts of detected whale groups. This comparison allowed for an assessment of how accurately the acoustic-energy indices reflected the relative abundance of groups. The third step was to identify relevant information for consideration in detection probability estimation. This step involved evaluating the biological, environmental, and anthropogenic influences on the variability in the vocalisations rates. The fourth step was to estimate detection probabilities under different environmental and anthropogenic conditions using acoustic and visual data for each species. The fifth and final step was to identify the strengths and limitations of the different approaches to acoustic monitoring of baleen whales using a single stationary underwater recorder and to discuss considerations that must be made when designing optimal monitoring protocols for baleen whale species.

To achieve the objectives described above, this thesis has been organised according to their logical order. The work is presented as a hybrid thesis containing published papers and manuscripts prepared for publication that address the objectives. Therefore, each chapter includes its own introduction, methods, results and discussion. While repetition of information was minimised where possible, because the thesis is in the format of stand-alone papers and manuscripts, there is unavoidable recurrence of some information. The thesis chapters and their goals are briefly described below:

Chapter 1 Introduction: Introduces the topic, knowledge gaps and rationale behind the research presented.

Chapter 2: Non-song vocalisations of pygmy blue and humpback whale populations that migrate off the coast of Western Australia: Describes the non-song acoustical repertoire of humpback and pygmy blue whales for the populations that migrate through Geographe Bay, Western Australia. This chapter consists of two papers; one published in *The Journal of the Acoustical Society of America Express Letters* and the second published in *Frontiers in Marine Science.* The latter opportunistically used acoustic data on humpback whales collected off Port Hedland as well as from Geographe Bay, Western Australia. The Port Hedland data resulted from work required as part of an industry program, thus was integrated into this thesis to fulfil its objectives. Humpback whales that migrate past Port Hedland are from the same population that migrate through Geographe Bay. Verification that non-song sounds described from Port Hedland were the same as those in Geographe Bay was undertaken before proceeding to chapters that only used data from Geographe Bay.

Chapter 3: Variability in vocalisation rates of baleen whales in Geographe Bay, Western Australia: investigating the influence of biological, environmental, behavioural and anthropogenic parameters: Evaluates biological, environmental, and anthropogenic influences on humpback and pygmy blue whale vocalisation rates in Geographe Bay, Western Australia. The chapter has been prepared as a manuscript to be submitted to a peer reviewed journal.

Chapter 4: Can sound energy be used as an indicator of relative density of baleen whales in an embayment?: Evaluates the relationship between acoustic energy levels in frequency bands of whale vocalisations and the number of (i) acoustically detected and (ii) visually observed groups for each species in Geographe Bay, Western Australia. The chapter has been prepared as a manuscript to be submitted to a to a peer reviewed journal.

Chapter 5: Modelling detection probabilities of baleen whales: the influence of imperfect detection and biological variability in monitoring protocols for baleen whales: Estimates detection probabilities under different environmental and anthropogenic conditions using acoustic and visual observation techniques for each species in Geographe Bay, Western Australia. The chapter has been prepared as a manuscript to be submitted to a peer reviewed journal.

Chapter 6: General discussion: Discusses the findings in the chapters, makes recommendations for optimal monitoring protocols for PAM for pygmy blue and humpback whales in Western Australia. The chapter concludes with implications of the thesis findings for baleen whale monitoring worldwide. This chapter is the 'General Discussion' of the thesis.

1.9. Glossary

Term	Definition in this thesis
Availability bias	A systematic tendency of missing certain animals present in a given area during a survey because they are unavailable to be detected. This term was originally defined by Marsh and Sinclair (1989) in reference to animals that were visually concealed from detection by vegetation or because they were submerged under turbid water. The definition has been adapted here to the acoustical context and refers to animals that are present in the area of study but not available for acoustic detection because they are not producing sounds.
Cue	A signal perceived by an observer indicating the presence of an animal or a species in an area. For example, for baleen whales a whale's blow (exhalation), pectoral fin slap, or breach at the surface of the water are cues used for detection by observers surveying an area from a vessel or land visually. For acoustic surveys of baleen whales, cues are sounds produced by whales.
Detectability bias	A systematic tendency to miss counting certain animals present in an area and available for detection during a survey due to a failure to detect them. Detectability bias in acoustic

	surveys can result from the signal being masked by other sounds, lower intensity sounds being missed or low vocalisation rates leading to missed detections.
Parameter estimation bias	A systematic tendency for parameter estimates to be different from the population parameter being estimated due to any one or combination of sources of bias, including sampling bias, detectability bias, availability bias, etc.
Detection probability bias	A systematic tendency to miss counting certain animals present in a survey area due to combined availability and detectability biases.
Sampling bias	A systematic tendency for certain individuals of a population to be sampled either more or less frequently than at random sample.
Vocalisation rate	The number of sounds produced by an individual or group of individuals of a species per unit time. In this thesis, the definition is used as the number of whale groups vocalising in a recording.

Chapter 2.

Non-song vocalisations of pygmy blue and humpback whale populations that migrate off the coast of Western Australia

*This chapter is composed by two papers describing non song vocalisations of pygmy blue (2.1) and humpback whales (2.2) in Geographe Bay and Port Hedland Western Australia.

2.1. Non-song vocalisations of pygmy blue whales in Geographe Bay, Western Australia

Non-song vocalisations of migrating pygmy blue whales (*Balaenoptera musculus brevicauda*) in Western Australia are described. Simultaneous land-based visual observations and underwater acoustic recordings detected 27 groups in Geographe Bay, WA over 2011 to 2012. Six different vocalisations were recorded that were not repeated in a pattern or in association with song, and thus were identified as non-song vocalisations. Five of these were not previously described for this population. Their acoustic characteristics and context are presented. Given that 56% of groups vocalized, 86% of which produced non-song vocalisations and 14% song units, the inclusion of non-song vocalisations in passive-acoustic monitoring is proposed.

2.1.1. Introduction

The identification, description, and quantification of a species' acoustical repertoire are prerequisites to understanding their acoustic behaviour, function, and geographic variation. This information is also important to begin to assess the effects of anthropogenic underwater noise on the species' ability to communicate, and for effectively implementing passive acoustic detection techniques.

Baleen whales are known for the intense and often complex vocalisations they produce. Many of these vocalisations appear to be associated with specific contexts such as feeding, socializing, and breeding (Watkins et al. 1981; Clark 1990; Mellinger & Clark. 2003; McDonald et al. 2006; Gavrilov et al. 2011; Oleson, Calambokidis, Burgess et al. 2007; Oleson, Wiggins & Hildebrand 2007; Stafford et al. 2011). The best-studied of these vocalisations is the "song," defined as a regular, patterned sequence of notes unique to each population of a species (Winn et al. 1981, Clapham and Mattila 1990; Mellinger and Clark 2003; McDonald et al. 2006, Stafford et al. 2018). There is evidence that song in great whales is predominantly produced by males (Clark 1990). Single, non-patterned vocalisations not associated with song have also been documented and described as non-song vocalisations (Clark 1990; Dunlop et al. 2007). Non-song vocalisations have been associated with feeding, foraging or social interactions by both sexes (Clark 1990; Dunlop et al. 2007).

While much research has been conducted to quantify and understand song and non-song vocalisations produced by humpback whales (*Megaptera novaeangliae*), relatively little is known about blue whale (*Balaenoptera musculus*) vocalisations. Blue whale song has been described (Mellinger & Clark 2003; McDonald et al. 2006; Gavrilov et al. 2011; Stafford et al. 2011), however, there is limited information about the full acoustic repertoire of this species, and even less on non-song vocalisations. For blue whales from the North Pacific and Atlantic, downsweeps ("D" vocalisations) and frequency and amplitude modulated (FM and AM, respectively) vocalisations described as "growls" have been attributed to non-song vocalisations (Mellinger & Clark 2003; Oleson, Calambokidis, Burgess et al. 2007) and associated to certain behaviours such as feeding (Oleson, Calambokidis Burgess et al. 2007). The pygmy blue whale (*Balaenoptera musculus brevicauda*) population, present in Western Australian waters (the East Indian Ocean population) is one of nine blue whale populations globally (McDonald et al. 2006). For this population the only non-song sound described is a downsweep, similar to the "D-call" reported for the North Pacific and Atlantic populations (Gavrilov et al. 2011). This study aims to characterize “non-song” vocalisations for the East Indian Ocean population of pygmy blue whales, during two seasons (2011 and 2012), as they migrated through a coastal embayment in southwestern Australia. The proportion of groups producing sound as they passed through this area is described, and the dominant acoustic behaviour of groups of whales (song or non-song vocalisations) is also determined.

2.1.2. Methods

Simultaneous land-based visual observations and underwater acoustic recordings were conducted during November of 2011 and 2012 in Geographe Bay, Western Australia. In Geographe Bay, East Indian Ocean pygmy blue whales migrate as close as 500 m from shore over an approximate six week window in November and December each year towards high-latitude foraging areas. Land-based visual observations were conducted using a surveyor’s theodolite to position surfacing whales for an average for 6–7 h per day from a 50 m hill, approximately 500 m from the water’s edge. The maximum visual detection range for blue whales was 5 km. The theodolite was a TopCon GTS-60#.F Electronic Total Station, and real-time positioning was obtained via a direct link to a laptop running the software Cyclops (v.2.8.04). Surfacing location, group composition, and behaviours were documented during visual observations.

Acoustic recordings were made using a Curtin University acoustic recorder (Curtin University acoustic recorder, 2014), deployed on the seabed, approximately 3 km offshore from the land-based station at 30 m depth (Fig. 1) and scheduled to record 800 s of every 900 s at a sample rate of 12,000 samples/s.

Concurrent real-time visual tracking and acoustic recordings with a single recorder were made. Sound transmission and expected received levels of blue whales producing sound within 2 km of the acoustic recorder were previously modelled for the area (Salgado Kent, Gavrilov et al. 2012). These received levels were used to match groups visually tracked within a 3 km radius of the acoustic recorder with the recorded vocalisations. Thus, four criteria had to be fulfilled to accept a match between the group of whales being visually tracked and the vocalisations recorded: (1) Groups being matched had to be visually confirmed to be within 3 km of the acoustic recorder, and no other whales (humpback or blue) could be within 3 km of the recorder at the time. (2) Only a single group of blue whales could be in the study area so that no confusion could occur in discerning which group produced sounds when multiple groups were present (in all but one case was there one group in the study area at a time). (3) The time the sounds were recorded had to coincide with the time a group was being visually tracked through the study area. (4) The sounds recorded had to have received levels corresponding to the distances of the groups from the position of the acoustic recorder at the time the sounds were recorded. The distances of the groups from the acoustic recorder were measured using the theodolite track. The expected received levels at range from the noise recorder were based on transmission loss estimates calculated previously (Salgado Kent, Gavrilov et al. 2012).

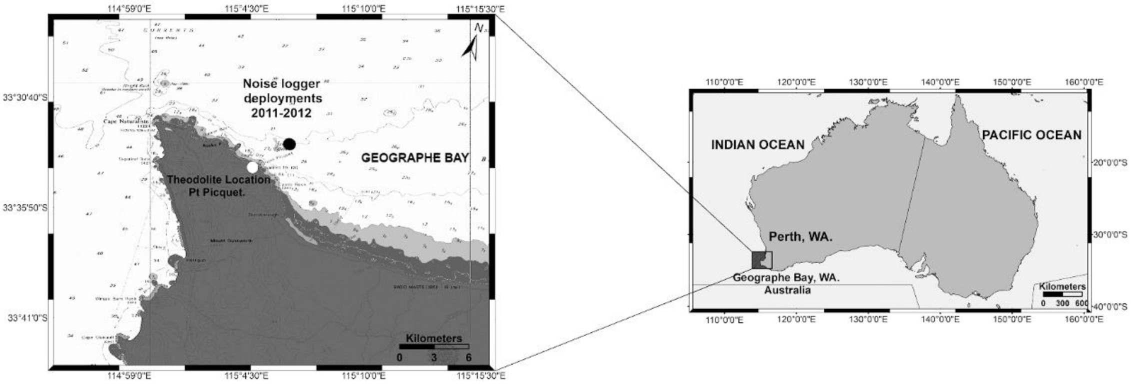


Figure 2.1.1. Location of acoustic recorder (black circle) and land-based theodolite platform (white circle), in Geographe Bay, Western Australia. The inset shows the location of the study area (highlighted in black) within Australia.

While there is a possibility that there were visually undetected groups of whales in the study area, the likelihood is assumed to be small given that the average time for a group of whales to traverse the area (within visual detection range of 5 km) was approximately an hour, giving multiple opportunities for sighting when surfacing.

Acoustic data were analysed using Curtin University's, custom-designed Characterization of Recorded Underwater Sound (CHORUS) toolbox providing a MATLAB graphical user interface. Once features of interest had been identified, spectrograms were produced for inspection using a 1024-point Hanning window with 95% overlap over a frequency range of 5 Hz to 4 kHz. Pygmy blue whale vocalisations were identified by visual scrutiny of spectrograms, based on their similarity in frequency and duration to previous reports (Mellinger & Clark 2003; McDonald et al. 2006; Oleson, Calambokidis, Burgess et al. 2007; Oleson, Wiggins & Hildebrand 2007; Gavrilov et al. 2011; Stafford et al. 2011).

While humpback whales were present during the study period, pygmy blue whale vocalisations were easily distinguished by their patterns, frequencies, and descriptions for the 2011 and 2012 seasons (Salgado Kent, Gavrilov et al. 2012). As stated above, comparison of signal received level with that expected for a whale at a given range corroborated matching a sighted whale to a recorded sound.

2.1.3. Results

A total of 27 groups of blue whales passed within acoustic detection range during the 107 h of visual tracking in this study. Blue whales were present in the study area for 11 h and 6.5 h within 3 km of the noise recorder. During this period, six types of vocalisations that were not repeated in a pattern or a particular sequence, nor produced in association with song, were attributed to blue whale groups. These vocalisations were identified as non-song vocalisations. Five of these comprised new non-song vocalisations for the East Indian Ocean (EIO) population of blue whales (Fig. 2.1.2), plus a previously reported downsweep. All call types comprised acoustic energy under 200 Hz, with the exception of an EIO2 which extended to 750 Hz [Fig. 21.2. (b)]. In each call type the peak of the spectral content was below 100 Hz, the exception was EIO3 producing the lowest peak frequency at approximately 20 Hz [Fig. 2.1.2. (c)]. EIO1 [Fig. 2.1.2. (a)], EIO4 [Fig. 2.1.2. (d)], and EIO5 [Fig. 2.1.2. (e)], call types all contained at least two spectral peaks of which the highest were at approximately 50 and 100 Hz (Table 2.1.1). All vocalisations included one or more harmonics or overtones, varying in frequency throughout the individual call. Durations ranged between approximately 0.9 and 4.4 s, and EIO2 was the longest call type [EIO2, Table 2.1.1; Fig. 2.1.2(b)]. Three vocalisations were observed with different groups [EIO1, EIO4, and EIO5, Table 2.1.2; Figs. 2.1.2. (a), 2.1.2. (d), and 2.1.2 (e)], while the remaining two were produced by only one group each [EIO2 and EIO3, Table 2.1.2. and Figs. 2.1.2 (b) and 2.1.2. (c)].

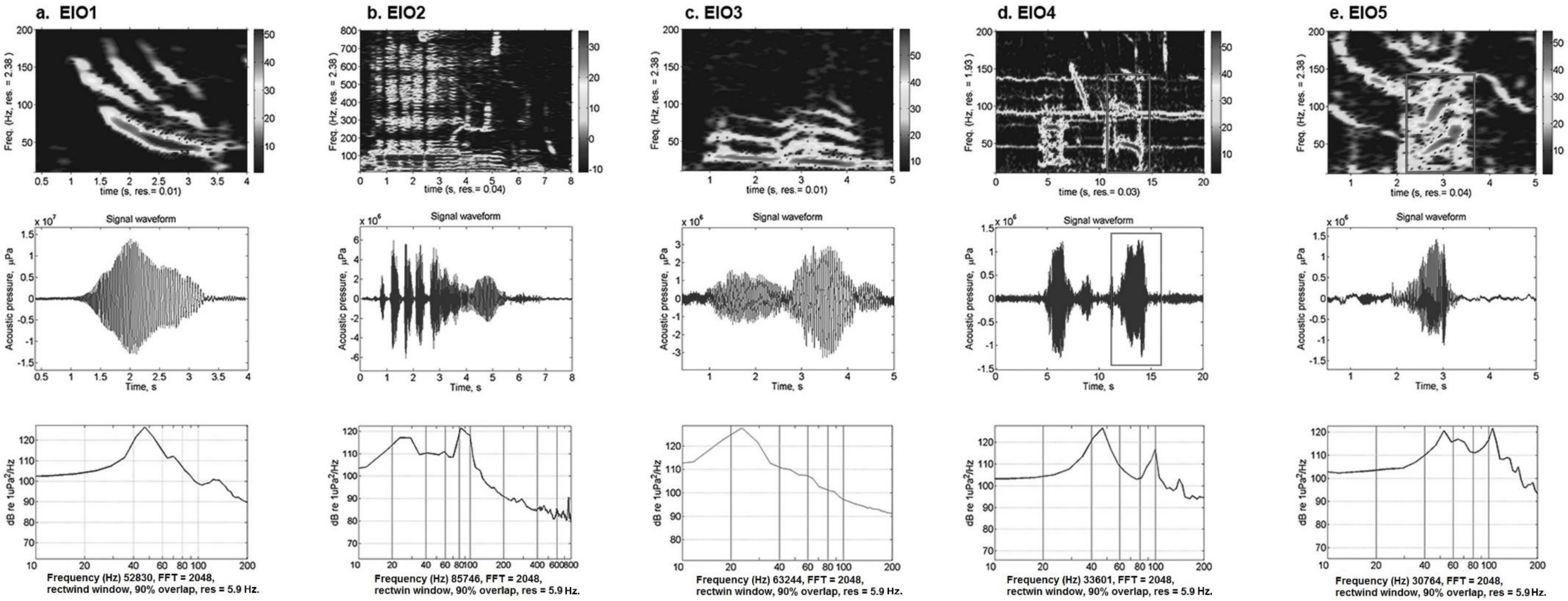


Figure 2.1.2. Spectrogram (top panels) of (a) EIO1, downsweep with non-harmonic overtones; (b) EIO2, broadband, pulsed AM growl with harmonics; (c) EIO3, grunt with harmonics; (d) EIO4, short FM tone with harmonics (highlighted in the square); and (e) EIO5, upsweep with harmonics (highlighted in the square). Medium and bottom panels present the waveforms and power spectrum density plot (PSD) for each signal, respectively (Colour image in online publication).

Of the 27 gro555ups visually tracked, 56% (15) emitted sound and of these 14% (2) produced song or song units while 86% (13) produced non-song vocalisations. On average, 10.25 non-song vocalisations per group were detected (max=38, min=1). Of the non-song vocalisations, 10 groups produced the previously described downsweep, and five produced the new non-song vocalisations described here. The total number of new non-song vocalisations detected was 15. Given that group transit times across the study area are ~1 h, approximately three new non-song vocalisations an hour were detected, per group the average estimated was 2.6 (min=1, max=6). A summary of the group composition associated with the vocalisations is presented in Table 2.1.2. All groups were observed traveling in the same general direction.

Table 2.1.1. Characteristics of new non-song vocalisations recorded in Geographe Bay, Western Australia. Frequency characteristics were extracted from the power spectrum density plot.

Call	**Feature Measure**				**# of analysed vocalisations***	**# of times recorded**
	Approximate frequency range of all energy (Hz)	**Peak frequency (Hz)**	**Frequency band 10 dB of peak (Hz)**	**Duration (s)**		
EIO1	20-200	Peak 1:~52 Peak 2:~102	30-105	1.62 ± 0.29	6	6
EIO2	10-750	86	13-105	4.42	1	1
EIO3	10-120	~21	11-31	3.42	1	1
EIO4	20-150	Peak 1: ~43 Peak 2: ~99	Peak 1: 33-51 Peak 2: 82-107	2.96 ± 0.83	2	4
EIO5	20-120	Peak 1: ~51 Peak 2: ~102	40-120	0.92	1	3

**Vocalisations analysed were selected based on high signal-to-noise ratio and low levels of background noise (i.e. no humpback whales or vessels in the area).*

Table 2.1.2. Association between compositions of groups tracked in Geographe Bay and vocalization type (including song units and downsweeps similar to the 'D' call. Downsweep = downsweep similar to the 'D' call, and (x) = the identification (ID) letter for groups producing the sound types (three groups produced multiple sound types).

Group Type	Vocalisation Type
Singleton	Downsweep $^{(\text{Bw1112})}$, Song units$^{(\text{Bw0311})}$
Two adults	EIO1$^{(\text{Bw0112})}$, EIO2$^{(\text{Bw0112})}$, EIO3$^{(\text{Bw0112})}$, EIO4$^{(\text{Bw0112,Bw0212})}$, EIO5$^{(\text{Bw0112})}$, Downsweep$^{(\text{Bw0411, Bw0112, Bw0212, Bw0512, Bw0612,Bw1212 })}$, song units$^{(\text{Bw0211})}$
Mother-calf	EIO4$^{(\text{Bw0812})}$, Downsweep$^{(\text{Bw0912})}$
Mother-calf-additional adult	Downsweep$^{(\text{Bw1512})}$
More than 2 adults	EIO5$^{(\text{Bw1312})}$, Downsweep$^{(\text{Bw0412,Bw1312, Bw0712})}$

2.1.4. Discussion

Five vocalisations not previously described for the East Indian Ocean pygmy blue whale population have been attributed to blue whales in Geographe Bay. Their characteristics were different from those of song for this species (Gavrilov et al. 2011), and because of their non-patterned and variable nature, these are described here as non-song vocalisations. A sixth non-song sound was also detected and identified as a previously reported downsweep (Gavrilov et al. 2001). While the new non-song vocalisations are unique in their modulation and duration, some have minor similarities with vocalisations reported from other populations.

First, EIO2, is similar to an AM sound in the North Pacific reported for blue whales (Oleson, Calambokidis, Burgess et al. 2007) in that it is pulsed and has comparable frequency range and bandwidth; however, it is approximately half the duration. Consistent with the AM sound recorded here (EIO2), the growl in the North Pacific was not identified as part of song. Second, EIO4 [see Fig. 2(d)] recorded here has a weak resemblance to unit three of the East Indian Ocean blue whale song (McDonald et al. 2006). However, the new signal described here is significantly shorter in duration and does not have the exact frequency range as song unit three. Also, no song or song units were evident in the recordings here, prior to, or after, these vocalisations were produced. Third, EIO5, is very similar to the one reported as the second unit of the blue whale song of the Sri Lankan population (Stafford et al. 2011). However, both are very different in duration (almost 2 s for the non-song unit reported in this study vs 1 s for the Sri Lanka song unit) and frequency (fundamental ranging from ~30–40 Hz vs 30–80 Hz, respectively). Fourth, the vocalization EIO1 reported here comprises simultaneous tones at different frequencies that are not harmonics [see EIO1, Table 2.1.1 and Fig. 2.1.2 (a)]. This is of particular interest and is a characteristic also identified in the last unit of song from the East Indian Ocean population of pygmy blue whales (Gavrilov et al. 2011). The structure of the non-song sound here may be the result of multiple sources of sound production in the whale's vocal apparatus as has been suggested for production of the last unit of their song (Gavrilov et al. 2011). The prevalence or lack of this type of sound production across baleen whale species also remains un-quantified. Last, the most prevalent non-song sound, the variable downsweep with harmonics recorded here and described previously for this population (Gavrilov et al. 2011), has a striking similarity to “call type D” from North Pacific and Atlantic blue whale (*Balaenoptera musculus*) populations (Mellinger & Clark 2003; Oleson, Calambokidis, Burgess et al. 2007; Oleson, Wiggins & Hildebrand 2007; Gavrilov et al. 2011). However, unlike the findings from the North Pacific, where vocalisations were produced by groups exhibiting feeding dive behaviour in a foraging area (Oleson, Calambokidis, Burgess et al. 2007), in Geographe Bay the surface behaviour was that of traveling in one general direction, indicative of migratory behaviour. Geographe Bay is not considered a feeding ground, but it is worth noting that there is a known foraging area 150 km to the north in the Perth Canyon and perhaps in the region of the Mentelle Basin westward. It is unclear whether the downsweep recorded in this study has a different function, or whether it is associated with the presence of foraging grounds nearby.

During this study, there was one instance of multiple groups in the area. This period was the occasion when the broadband, pulsed EIO2 was recorded, and there was a significant increase in repetition of downsweeps (7.0/800s ± 4.24 vs 4.18/800s ± 62.64). Increased signal complexity, repetition and variability has been speculated to correlate with activity type in southern right whales (*Eubalaena australis*) (Clark 1982) and bowhead whales (*Balaena mysticetus*) (Würsig et al. 1985), and agonistic interactions among fin whales (*Balaenoptera physalus*) (Edds 1988). Further research is required to disentangle the social and behavioural context of increased repetition and complexity of non-song vocalisations. In this study, EIO4 and EIO2 were produced mostly by groups containing two animals and no calves (although the EIO4 was also observed in mother-calf pairs). This paper presents evidence of the production of non-song vocalisations by pairs of adults as well as mother-calf groups, thus provides support for the possibility of fulfilling a similar role to social vocalisations described for other species of mysticetes, such as humpback whales (Dunlop et al. 2007).

The high proportion of groups traveling through Geographe Bay producing sound (>50%), and the majority of which produced non-song vocalisations (almost 90%) as compared to song or song units (just over 10%) suggests that non-song communication serves an important function at this location. Given that non-song vocalisations dominated in the numbers of groups producing them in Geographe Bay, we suggest that at locations with the same level of non-song sound proliferation, the inclusion of non-song vocalisations in passive acoustic detection censuses will significantly increase counts (rather than basing methods solely on song). Furthermore if social context for the different vocalisations is verified, an even more powerful tool for population studies will be available.

2.1.5. Acknowledgments

This research was funded in part by the Australian Geographic Society and the International Fund for Animal Welfare (IFAW). Much gratitude is owed to Eric Kniest (University of Newcastle) for provision of the CYCLOPS software, Dunsborough Sea Rescue for assisting in acoustic recorder deployments and retrievals, Curtin University's Department of Spatial Sciences, the Southwest Whale Ecology Study (SouWEST) partners: Chris Burton (Western Whale Research), Ron Glencross (Dunsborough Coast and Land Care), to Ian and Glenys Wiese for providing in kind support in accommodation during fieldwork, and the many volunteers that have been involved in the collection of data over the years. The authors would also like to thank to Alec Duncan, Alexander Gavrilov, Malcolm Perry, and Frank Thomas from the Centre for Marine Science and Technology for their technical support and advice.

2.2. Non-song vocalisations of humpback whales migrating off the coast of Western Australia

This study presents non-song vocalizations of humpback whales (*Megaptera novaeangliae*) from two migratory areas off the Western Australian coast: Geographe Bay and Port Hedland. A total of 220 sounds were identified as non-song sounds in 193 hours of recordings reviewed. Of those, 68 were measured and qualitatively classified into 17 groups using their spectral features. One group (HW-02) had a high level of variation in terms of spectral slope. However, further classification using statistical classification methods was not possible because of the small sample size. Non-song sound frequencies varied from 9 Hz to 6 kHz, with the majority of sounds under 200 Hz. The duration of non-song sounds varied between 0.09 and 3.59 s. Overall, the use of spectral features allowed general classification of humpback whale sounds in a low sample size scenario that was not conducive to using quantitative methods. However, for highly variable groups, quantitative statistical classification methods (e.g., random forests) are needed to improve classification accuracy. The identification and accurate classification of a species' acoustic repertoire is key to effectively monitor population status using acoustic techniques and to better understand the vocal behaviour of the species. The results of this study improve the monitoring of humpback whales by standardizing the classification of sounds and including them in the species' repertoire. The inclusion of non-song sounds in passive acoustic monitoring of humpback whales will add females and calves to the detection counts of otherwise only singing males.

2.2.1. Introduction

Passive Acoustic Monitoring (PAM) is used worldwide as a technique to estimate relative abundance and distribution of marine faunal species. It is applied in basic ecology as well as for monitoring fauna before, during and after anthropogenic activities with potential impacts. PAM relies on the accurate identification of species, based on the acoustic characteristics of the sounds they produce. Therefore, the characterisation of acoustical signals and repertoires for different species is a significant component of their monitoring.

The humpback whale is considered to be one of the most vocal of the cetaceans and, is the species whose behaviour and vocalisations have been most studied. Humpback whale call repertoire is diverse in frequency range and duration, with most units exhibiting a fundamental frequency below 3 kHz. However, the general frequency range can vary between 50 Hz and 24 kHz (Silber 1986; Au et al. 2006). Song is the best-studied form of communication for humpback whales and is defined as a sequence of sounds that is repeated over time (Payne 1978). It is typically unique for each population, evolving from year to year, but can also be transmitted between populations (Garland et al. 2011). Song is documented to be produced only by males, occurring primarily on breeding grounds (Payne 1978; Frankel et al. 1995, Darling et al. 2006) and less frequently in feeding grounds (Clark & Clapham 2004).

In addition to song, humpback whales emit other less-studied sounds described as social sounds. Social sounds are unpredictable and produced erratically, are not patterned, and range from 50 Hz to over 10 kHz (Dunlop et al. 2007, Zoidis et al. 2008) with source levels between 123 to 183 dB re 1 μPa @ 1 m (Dunlop et al. 2013). These sounds can be song or non-song units vocalised in a social context (Dunlop et al. 2008, Rekdahl et al. 2013). Social sounds have been recorded in association with agonistic behaviour or other individual interactions between adults (males and females; Silber et al. 1986; Richardson et al. 1995; Edds-Walton 1997; Dunlop et al. 2008), and within groups with calves (e.g. mother-calf or mother-calf-escort(s), Dunlop et al. 2008; Zoidis et al. 2008). In this study, social sounds are referred to as non-song sounds because the behaviours associated with the sounds were not identified and it was not possible to determine whether these sounds served a social function.

According to spectrographic features, baleen whale sounds can be classified as constant-wave (CW), frequency-modulated (FM) and amplitude-modulated (AM) (Erbe et al. 2017). However, in the literature, these are frequently named and grouped according to how they are perceived by the listener (and are given onomatopoeic names, such as grunt, growl, moan, wop, etc.). While most of the published studies that describe humpback whale vocalisations use onomatopoeic names, this type of classification may be problematic because different authors may give different names to the same signals, making a direct comparison difficult (Cholewiak et al. 2013; Erbe et al. 2017). Spectral features, however, are more standard and facilitate comparison among different signals, although some variation in categorisation can occur as a result of recording and analysis settings (Erbe et al. 2017).

Few studies have described non-song sounds of the different humpback whale populations around the world. A repertoire of 34 social sounds and their social context have been described for the population that migrates along the east coast of Australia (Dunlop et al. 2007, Dunlop et al. 2008; Rekdahl et al. 2013), and another 24 have been described for the North Pacific population (Silber et al. 1986; Cerchio & Dahlheim 2001; Zoidis et al. 2008). Only a few non-song sounds have been described for the Western Australian humpback whale population (Videsen et al. 2017) and a repertoire is yet to be developed.

The population of humpback whales off Western Australian (Breeding Group D) migrates from high-latitude feeding grounds in Antarctica to low-latitude breeding grounds off northwestern Australia. During migration, whales travel past Port Hedland (in the northwest) between approximately June and August on their way north, and between approximately August and November on their way south. During the southern migration they travel through Geographe Bay (in the southwest of Australia) between September and January, before undertaking the remainder of their journey to sub-Antarctic and Antarctic waters. The period of migration at each location (Port Hedland and Geographe Bay) occurs over several months as different cohorts of the population migrate in a temporally staggered manner. This structured migration has been termed ‘temporal segregation’ (Dawbin 1997), where the first whales departing foraging grounds on their way north to breeding grounds include a mix of females in late stages of lactation or with their yearly offspring. This cohort is followed by juveniles (males and females), then by resting females and mature males, and finally females in late pregnancy (Dawbin 1997; Craig et al. 2003). The migration back to foraging grounds from breeding grounds has been reported to be first a mix of resting females and females in early stages of pregnancy, followed by immature males and females, then mature males and finally, females in early stages of lactation and mothers with newly born calves (Dawbin 1997, Craig et al. 2003).

The aim of this chapter is to describe non-song sounds for the humpback whale population that migrates along the coast of western Australia using: (1) qualitative descriptions of spectral features (CW, FM, AM, contour shape, and number of subunits), (2) qualitative onomatopoeic names for comparability with other studies, and (3) quantitative measures of spectral features. Sounds were recorded in two areas: Geographe Bay in the southwest of Australia and off Port Hedland in the northwest of Australia.

2.2.2. Methods

2.2.2.1. Study site

Underwater acoustic recordings were obtained in two areas off the coast of Western Australia: Port Hedland and Geographe Bay (Figure 2.2.1). In Port Hedland, the northern and southern migrations of the 2011 migratory season were captured with recordings made between June 2011 and January 2012, while in Geographe Bay, the southern migrations of 2011 and 2012 were captured between November and December. Consequently, all recordings from Port Hedland in 2011 and 2012 and recordings in Geographe Bay in 2011 were from the same migratory season, while recordings made in Geographe Bay in 2012 were from southbound animals in the subsequent migratory season.

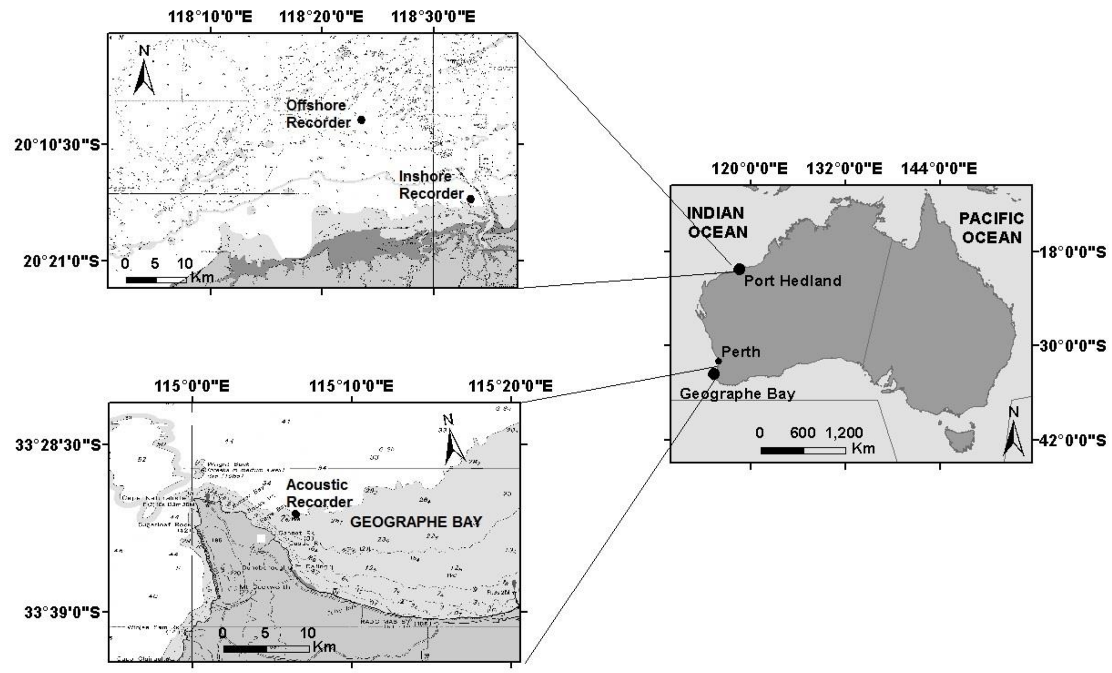


Figure 2.2.1. Geographic locations of noise recorder deployments in Port Hedland and Geographe Bay, Western Australia.

Geographe Bay is an important tourist destination in southwestern Australia, with recreational boating and whale watching being key attractions that bring economic value to the region. Therefore, high levels of vessel traffic and interactions with whales occur at this site. As a result, a long-term whale monitoring program has been underway since 2010, in which visual observations from multiple platforms have been collected to complement acoustic data.

Geographe Bay was selected as the principal study site as more data were available from this monitoring program. Humpback whales migrating between September and January through Geographe Bay have peak migratory periods that vary among seasons (Salgado Kent, Gavrilov et al. 2012). However, monitoring has been focused on the period after the peak of migration. This is important as it facilitates identification of non-song sounds because they are not masked by humpback whale song vocalised by a large number of whales passing through the area.

The area off the coast of Port Hedland was selected as a secondary study site to increase the geographical scale of the study. As indicated above, waters off Port Hedland are used by the same population of humpback whales migrating northward towards recognised calving grounds in the Kimberley, Dampier Peninsula and

Camden Sound, before returning from breeding grounds to Antarctica during the southern migration (Jenner et al. 2001). As these animals migrate further offshore at this site than in Geographe Bay and, as a result no visual observations were available. Port Hedland is the second-largest town in the Pilbara region of Western Australia and is also the location of the highest tonnage port in Australia (Western Australia Planning Commission, Department of Planning 2011).

2.2.2.2. Acoustic recordings and data processing

In Geographe Bay, a single stationary underwater acoustic recorder was deployed on the seabed at 33°32'52.38"S and 115°6'39.18"E, approximately 2.5 km from the coastline in 30 m water depth (Fig 2.2.1). The recorder was scheduled to record 13 minutes every 15 minutes. The recordings used corresponded with a subsample selected for comparing visual and acoustic whale detections in Geographe Bay (see Chapter 3).

In Port Hedland, two underwater recorders were deployed: one offshore at 20°8'19.32"S and 118°23'34.92"E, at 20 km from the coastline and one inshore at 20°15'25.62"S and 118°33'22.74"E, at 5 km off the coast (Figure 2.2.1). Recorders were deployed at 16 m and 6 m depths respectively, and scheduled to record 5 minutes every 15 minutes. The offshore location was expected to capture sounds produced by a range of different cohorts of the whale population, while the inshore location was expected to capture a comparatively larger proportion of mothers and calves that typically migrate closer to the coast (Smultea 1994; Ersts & Rosenbaum 2003; Rasmussen et al. 2012; Guidino et al. 2014; Oña et al. 2016; Irvine & Salgado Kent 2017). All recordings were used (no subsampling occurred).

Both areas used acoustic recording systems developed by the Centre for Marine Science and Technology (CMST) and the Defence Science and Technology Organisation (DSTO) (McCauley et al. 2017) fitted with a calibrated, omni-directional HTI 90-U hydrophone (HighTech Inc., MS, USA). Recording systems were calibrated with a white noise generator at -90 dB re 1 V^2/Hz. Recorder settings for Port Hedland and Geographe Bay recorders are summarized in Table 2.2.1.

Table 2.2.1. Acoustic recorder settings for Port Hedland (PH) and Geographe Bay (GB) deployments.

Area	Date of recording	Total gain (dB)	Sample frequency (kHz)	Anti-aliasing filter (kHz)	High-pass filter	Low-pass filter	Duty cycle
PH Offshore	Jun 2011-Jan 2012	40	10	4	8 Hz	4 kHz	5 minutes every 15 minutes
PH Inshore	Jun 2011-Jan 2012	40	10	4	8 Hz	4 kHz	5 minutes every 15 minutes
GB	Nov-Dec 2011	40	12	5	8 Hz	5 kHz	13 minutes every 15 minutes
GB	Nov-Dec 2012	40	12	5	8 Hz	5 kHz	13 minutes every 15 minutes

Acoustic data were first processed and reviewed using the Characterisation Of Recorded Underwater Sound (CHORUS) toolbox built in the software MATLAB (The MathWorks, Inc., v.2012a) which provides a Graphical User Interface (GUI) (Gavrilov & Parsons 2014). Data were visually inspected by plotting spectrograms with 2948-point Fast Fourier Transforms (FFTs), 70% overlap, and using a logarithmic frequency scale of 8 to 4000 Hz. Colour scale of the spectrograms was fixed at 60 to 110 dB re 1 $\mu Pa^2/Hz$.

Non-song sounds were identified as either: (1) sounds that were not part of humpback whale song, or (2) song units that did not follow the sequence characteristic of the song (Dunlop et al. 2007). Song described for each season in each area was referred to for this assessment. Of those non-song sounds identified in recordings, only sounds without overlapping signals (e.g. other humpback whale vocalisations, vessel, etc.) were selected for description. In addition, only sounds with fundamental frequency sound pressure level (SPL) higher than 90 dB re 1 μPa and signal-to-noise ratio calculated by CHORUS of at least 8 dB were selected. Non-song sounds that met these criteria were described qualitatively and quantitatively. Sounds were qualitatively described: (1) as CW, FM, AM, or a combination, (2) according to their contour shape, and (3) by the number of subunits present in the non-song sound, based on spectral features. Subunits were defined as a component of a sound distinguished by discontinuities in frequency and were referred to as parts A, B, and so on (Pace et al. 2010; Cholewiak et al. 2013); a unit was identified as the shortest continuous sound (Payne & McVay, 1971). When a sound was made of only one unit, it was considered to have no subunits and marked as zero (0) (Cholewiak et al. 2013). Sounds were attributed onomatopoeic names based on how they were perceived by the listener (e.g. wop, cry, thwop, etc.), and according to names used in other studies for comparability (Silber 1986; Dunlop et al. 2007; Zoidis et al 2008, Rekdahl et al. 2013).

Quantitative description of non-song sounds included measures of call duration (in seconds), maximum and minimum frequencies (Hz) (Table 2.2.2). Furthermore, a mean spectrum was computed over the duration of each call and the peak frequency was then picked as the frequency of peak power. Then, 3-dB and 10-dB bandwidths were computed as the frequency bands around the peak frequency in which the peak power dropped by 3 dB and 10 dB respectively. Because some literature described fundamental frequencies of sounds (i.e., the lowest frequency component of the sound, specifically for harmonic sounds), the maximum frequency of the fundamental was measured as well for these sounds.

Table 2.2.2. Quantitative metrics used to describe non-song sounds of humpback whales in Geographe Bay and off Port Hedland, Western Australia.

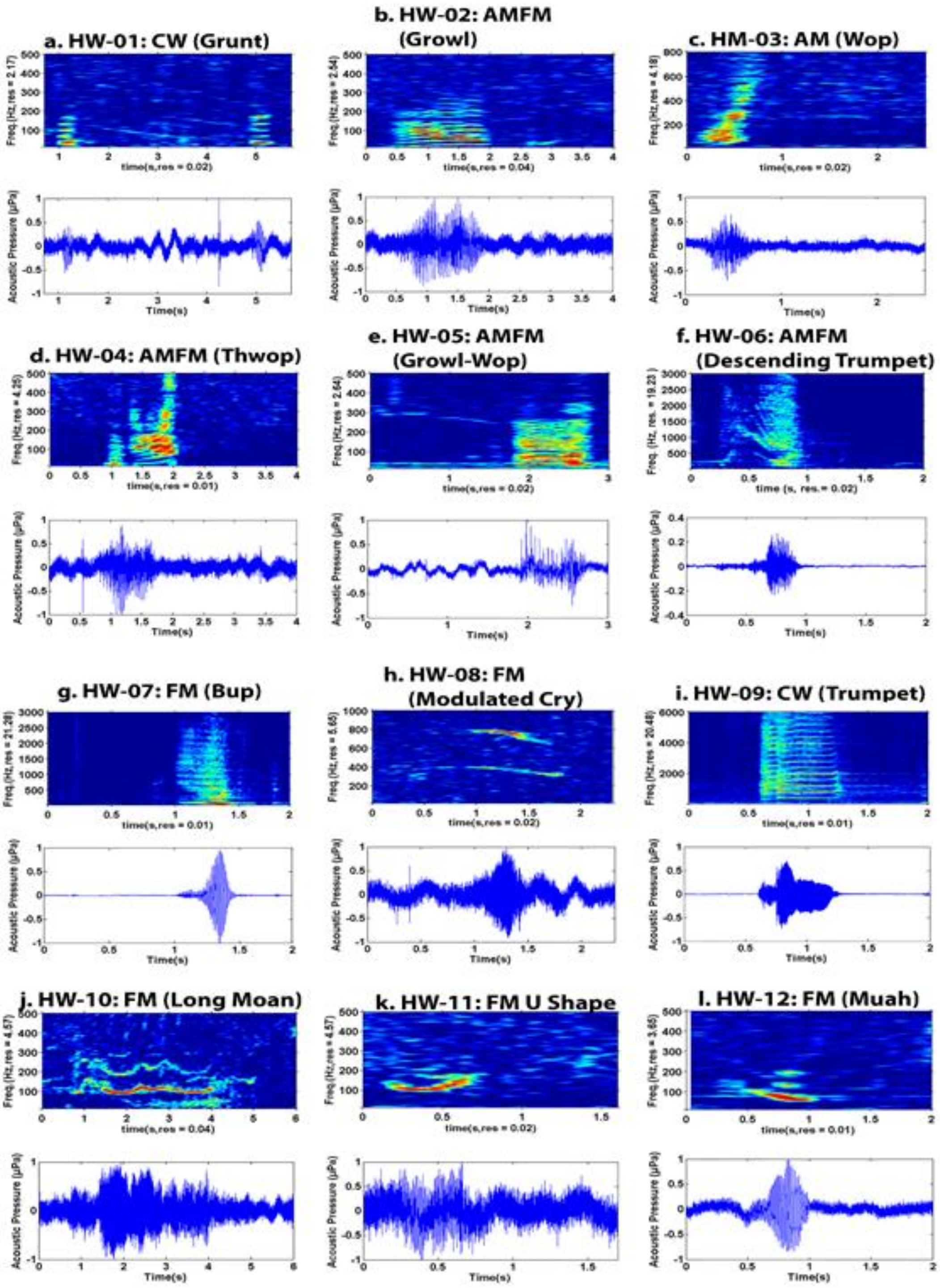
Variable	**Description**
Maximum Frequency	Maximum frequency of the sound
Maximum Frequency of the fundamental (f0)	Maximum frequency of the lowest frequency component of the sound
Minimum Frequency	Minimum frequency of the sound
Peak Frequency	Frequency of peak power
10-dB Bandwidth	Frequency band in which the peak power dropped by 10 dB
3-dB Bandwidth	Frequency band in which the peak power dropped by 3 dB
Duration	Sound duration

Quantitative measures were undertaken using a code developed in MATLAB (The MathWorks, Inc., v.2015a). All analyses were carried out by two experienced analysts. Under the SPL and SNR criteria used in this study, there were too few samples for classification using approaches such as Random Forest Decision Trees as done in other studies (Rekdahl et al. 2013). Thus, statistical summaries, spectrograms and wave forms are presented for visualisation of the range and variability of non-song sounds from the humpback whale population off the coast of Western Australia.

2.2.3. Results

A total of 107 (November – December 2011, 2012) and 84 hours (June 2011 – January 2012) of recordings were analysed for Geographe Bay and off Port Hedland, respectively. A total of 220 sounds were identified as non-song sounds (197 in Geographe Bay and 23 off Port Hedland). Of those, 68 were selected for qualitative and quantitative description (53 from Geographe Bay and 15 from Port Hedland). These discernible sounds occurred within 28% of recordings in Geographe Bay and 0.3% of recordings off Port Hedland. Off Port Hedland, any clearly discernible non-song sounds that might have been present were only identified from inshore recordings before and after the peak migratory period. The offshore recordings had no discernible non-song sounds before and after the peak of the migration. During the peak period, any non-song sounds were likely masked due to the high number of song sounds present in recordings. In the inshore recordings, sounds were not clearly discernible in Port Hedland during the peak of humpback whale migration between early August and late October for the same reason. However, there were discernible non-song sounds in the inshore recordings early in the migration in mid-July (two non-song sounds were identified) and late in the migration in mid-November 2011 (15 non-song sounds were identified). The non-song sounds recorded in November were identified one month after the last singer was recorded. In contrast with results from Port Hedland, non-song sounds were more easily discerned in recordings from Geographe Bay. This is likely due to less masking of non-song sounds due to fewer singers recorded at any one time at this location. However, it is possible that when multiple singers were present in Geographe Bay, some non-song sounds may have been miss-identified as song units.

Sounds fell into one of 17 non-song sound types (referred to here as non-song sounds HW-01 to HW-17) based on their qualitative spectral features (Figure 2.2.2, Table 2.2.3). Of the different non-song sound types described, most were FM (n = 7) followed by AMFM (n = 5), CW (n = 4) and AM (n = 1) (Figure 2.2.2). These non-song sound types included the following onomatopoeic descriptors: grunt, growl, wop, thwop, trumpet, bup, cry, moan, muah and boop (Figure 2.2.2). Sounds composed of subunits had in some cases combinations of these descriptors. These appear in Table 2.2.3 with the names adjacent to each other (such as ‘Growl-Wop’). In cases where two onomatopoeic descriptors made up a sound composed of different subunits, the descriptors are separated by a dash (such as “Growl-Wop”). The first of the descriptors (such as “Growl” in “Growl-Wop”) describes the sound the signal commenced with, while the second descriptor (such as “Wop” in “Growl-Wop”) describes what the sound ended with.



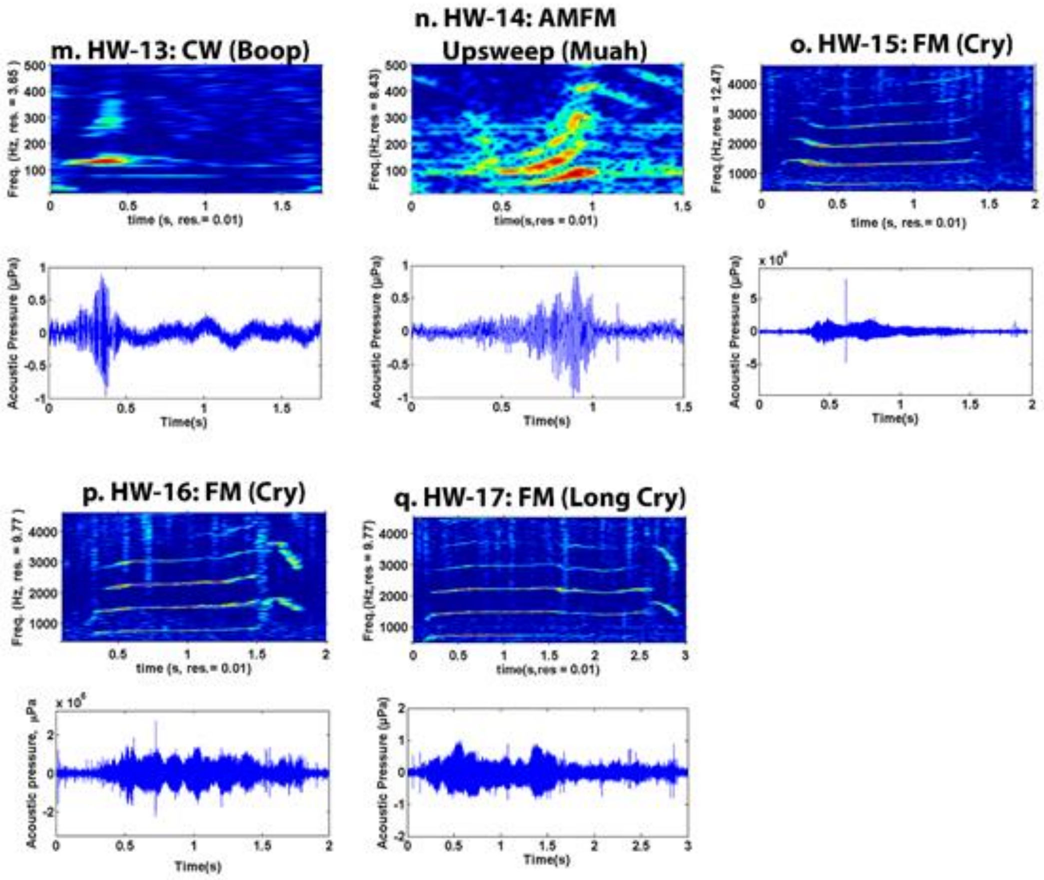


Figure 2.2.2. Spectrograms of unique non-song sounds recorded off Geographe Bay and Port Hedland, northwestern Australia. Names are organised by number (e.g. HW-01), spectral feature (e.g. FM) and onomatopoeic name in parenthesis (e.g. Growl)).

Variation was observed in some sound types, particularly in HW-02, HW-05 and HW-07 (Figure 2.2.3). Although, these sound types showed greater variation in spectral features than other sound types, variability was not so great as to result in different groupings. Variability for sounds HW-02 was the greatest, as sounds varied in upsweep shape that on one occasion appeared as an inverted U (as shown in Figure 2.2.3.a). Variation in sound type HW-05 was based on variable bandwidth with some sounds having much more energy at higher frequencies (see HW-05 variations in Figure 2.2.2e and Figure 2.2.3.b).

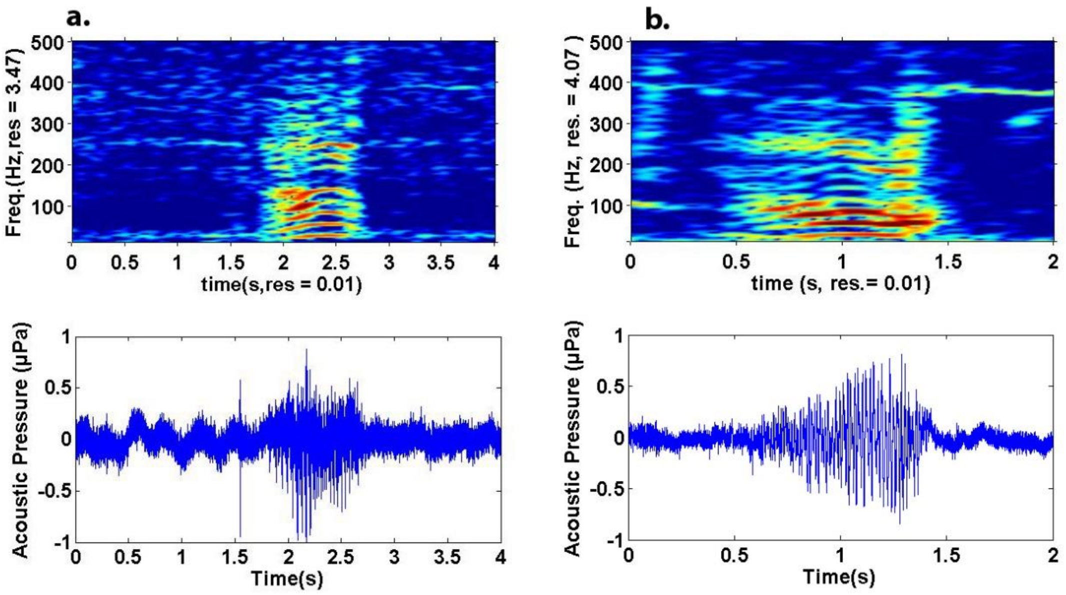


Figure 2.2.3. Example of spectrograms showing variability for non-song sounds: a.HW-02 and b. HW-05.

Two sound types were recorded in both areas (HW-02 and HW-05), 12 were exclusive to Geographe Bay (HW-01, HW-03, HW-04, HW-06 to HW-14), and three were exclusive to Port Hedland (HW-15, HW-16, HW-17). Only one sound type was identified as a unit used in a song context (HW-12). Of the 17 non-song sound types, 23.8% were HW-02 ‘Growl-Wop’, 13.4% were HW-07 ‘Bup’, 11.9% were HW-15 ‘Cry’, with all other sound types having fewer than 10% of the total number of sounds discerned in recordings.

Table 2.2.3. Summary of spectral features and onomatopoeic names for non-song sound types recorded in Geographe Bay and off Port Hedland.

Sound Category	Type	No. of Subunits	Subunit description	Contour shape	Sample size	Onomatopoeic name
HW-01*	CW	0	--	--	5	Grunt
HW-02*▲	AMFM	0	--	Up	17	Growl
HW-03*	AM	0	--	Pulse	3	Wop
HW-04*	AMFM	3	A: similar to HW-01	--	4	Thwop
			B: similar to HW-02	Up		
			C: similar to HW-03	Up		
HW-05*▲	AMFM	2	B: similar to HW-02	Up	5	Growl-Wop
			C: similar to HW-03	Pulse		
HW-06*	AMFM	0	--	Down	1	Descending Trumpet
HW-07*	FM	0	--	--	9	Bup
HW-08*	FM	0	--	Down	1	Modulated Cry

HW-09*	CW	0	--	--	1	Trumpet
HW-10*	FM	0	--	Sine	1	Long Moan
HW-11*	FM	0	--	U	1	--
HW-12*	FM	0	--	Down	2	Muah
HW-13*	CW	0	--	--	2	Boop
HW-*14*	AMFM	2	A: Upsweep B: similar to HW-03	Up Pulse	3	Muah
HW-15▲	FM	2	A B: similar to part B HW-16 and HW-17	Inverted U Up	8	Cry
HW-16▲	FM	2	B: similar to part B HW-15 C: similar to part C HW-17	Up Down	4	Cry
HW-17▲	FM	3	B: similar to part B HW-15 C: similar to part C HW-16 D	Up Down U	1	Long Cry

CW = constant wave, FM = frequency modulated, AM = amplitude modulated, ▲Non-song sounds identified in Port Hedland, *Non-song sounds identified in Geographe Bay

Non-song sound frequencies varied between 9 Hz and 6 kHz. The most common sound type (HW-02) had a mean peak frequency under of 56 Hz, 3-dB bandwidth of 41 Hz and 10-dB bandwidth of 111 Hz (Table 2.2.4). Only two sound types (HW-15 and HW-16) had mean peak frequencies higher than 1 kHz and 10-dB bandwidth over 100 Hz (Table 2.2.4). All non-song sound types had a mean duration of less than 4 s, with 11 having a mean under 1 s, and two with mean duration over 2 s (Table 2.2.4). Some variability in spectrogram parameters was expected for each sound category. The largest variation was observed for the 3-dB bandwidth in all sounds. HW-15 and HW-16 also showed high variability for the parameters peak frequency and 10- dB bandwidth (Figure 2.2.4).

Table 2.2.4. Mean spectrogram parameters of non-song sounds recorded in Geographe Bay and Port Hedland. Values of Standard Deviation (SD) are in brackets. NA: Sounds with no replicate, therefore SD is not calculated.

Sound type	**Onomatopoeic name**	**Max freq. [Hz]**	**Max freq. [Hz] (Fundamental)**	**Min freq. [Hz]**	**Peak freq. [Hz]**	**10-dB Bandwidth [Hz]**	**3-dB Bandwidth [Hz]**	**Duration [s]**
HW-01	Grunt	230.5	40.9	20.9	49.2	107.5	20.6	0.3
		(20.5)	(4.2)	(4.3)	(44.9)	(59.0)	(2.6)	(0.1)
HW-02	Growl	347.9	--	19.3	56.4	111.5	40.7	1.1
		(133.5)		(9.7)	(25.0)	(44.2)	(21.4)	(0.3)
HW-03	Wop	2255.8	--	54.8	180.7	178.7	36.4	0.3
		(1693.6)		(24.3)	(83.6)	(70.0)	(23.6)	(0.1)
HW-04	Thwop	1980.4	--	19.0	144.5	81.8	20.8	1.0
		(493.9)		(2.5)	(113.8)	(18.3)	(8.0)	(0.3)
HW-05	Growl-Wop	491.8	--	27.7	64.5	115.1	29.8	0.8
		(267.2)		(11.2)	(25.5)	(35.3)	(11.6)	(0.1)
HW-06	Descending Trumpet	5941.4	--	165.9	843.8	90.9	54.8	0.5
		(NA)		(NA)	(NA)	(NA)	(NA)	(NA)
HW-07	Bup	4170.6	--	59.8	109.4	64.3	25.4	0.3
		(2007.9)		(NA)	(29.3)	(26.8)	(6.9)	(0.1)
HW-08	Modulated Cry	2000.0	815.8	649.3	761.7	74.0	26.9	1.1
		(NA)	(NA)	(NA)	(NA)	(NA)	(NA)	(NA)
HW-09	Trumpet	5976.6	--	288.9	785.2	37.3	19.5	0.8
		(NA)		(NA)	(NA)	(NA)	(NA)	(NA)
HW-10	Long Moan	316.0	177.3	60.7	105.5	35.1	14.7	3.6
		(NA)	(NA)	(NA)	(NA)	(NA)	(NA)	(NA)
HW-11	--	222.7	164.1	93.8	117.2	91.1	23.8	0.6
		(NA)	(NA)	(NA)	(NA)	(NA)	(NA)	(NA)
HW-12	Muah	304.7	125.5	51.4	41.0	56.1	29.9	0.6

		(116.0)	(4.6)	(12.6)	(41.4)	(12.7)	(8.5)	(0.1)
HW-13	Boop	509.8	99.6	64.6	140.6	47.8	29.0	0.3
		(174.0)	(16.5)	(8.3)	(16.6)	(23.3)	(21.6)	(0.0)
HW-14	Muah	820.3	--	38.5	74.2	77.3	23.8	0.8
		(40.6)		(8.5)	(44.4)	(56.3)	(17.0)	(0.1)
HW-15	Cry	3540.0	741.8	634.8	1052.2	86.6	35.3	1.1
		579.2)	(76.8)	(9.0)	(349.7)	(46.1)	(30.7)	(0.1)
HW-16	Cry	4555.7	871.6	634.8	2648.9	1136.5	52.9	1.4
		(817.1)	(78.7)	(58.6)	(2235.9)	(1132.2)	(36.1)	(0.3)
HW-17	Long cry	4472.7	781.2	703.1	732.4	224.0	27.5	2.8
		(NA)	(NA)	(NA)	(NA)	(NA)	(NA)	(NA)

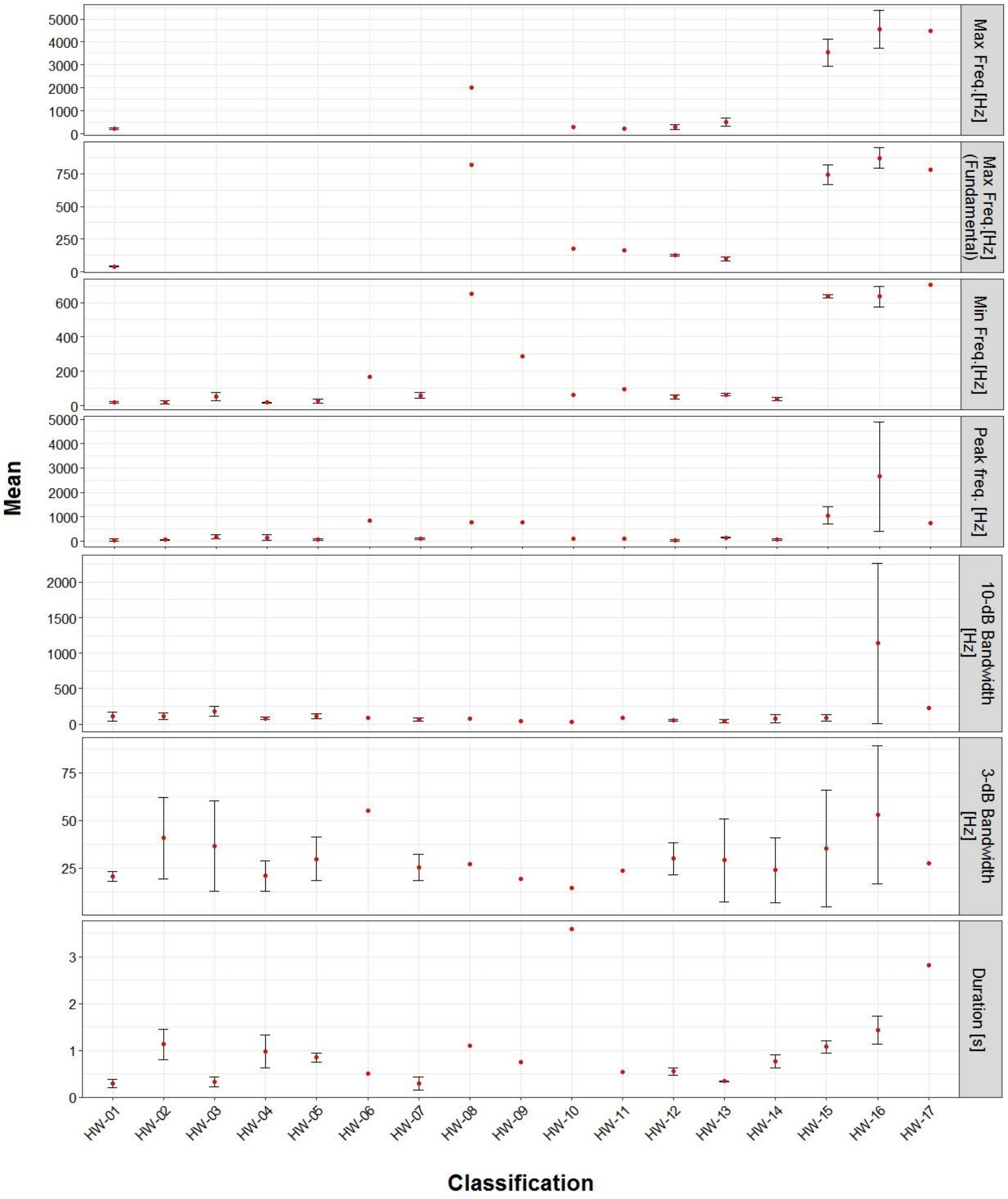


Figure 2.2.4. Mean (± SD) metrics for the spectrogram parameters of each sound type recorded in November 2011 and 2012 in Geographe Bay and between June and January 2012 off Port Hedland, Western Australia.

2.2.4. Discussion

While humpback whales are recognized for the complexity of their songs, the results in this study suggest that non-song sounds are also highly variable in structure. This study showed that the non-song repertoire can be composed of a variety of sounds including CW, FM and AMFM with frequencies ranging from 9 Hz to up to 6 kHz. This is similar to other studies that have reported non-song sound repertoires ranging in frequencies from 30 Hz to 2.5 kHz (Dunlop et al. 2007). In this study, it is likely that additional non-song sounds were present in the recordings, but not identified. In total, non-song sounds from Port Hedland were detected in 3 days over 6 months of data analysed and in Geographe Bay in 5 over 20 days analysed in 2011, and 17 out of 25 days in 2012. Thus, the variability in non-song sounds produced off Western Australia is likely to be even greater than that described here. This is particularly true for non-song sounds in recordings off Port Hedland, as song dominated the recordings during the peak period of migration and precluded discerning non-song sounds from song. It is important to clarify that this information should not be used to describe or compare vocal activity and acoustical ecology of the species between areas because of differences in habitat use, ecology and behaviour in each site. In addition, the study design also differed and does not allow a direct comparison between areas.

Only one (7.7%) of the non-song sound types reported in this study was identified as a song unit in song of the same year (HW-12). In contrast, 23.2% of the non-song sounds identified from the population of whales that migrate along the east coast of Australia (Breeding Stock E) were considered to be similar to song units from the same or previous years (Rekdahl et al. 2013). However, one of the sounds reported here (HW-08) has characteristics similar to a “cry”, which is reported as a non-song sound used as a song unit by the population off the east coast of Australia (Rekdahl et al. 2013). Whether the other non-song sounds identified in this study have been used as part of song off Western Australia in previous years, or will be in future years, is yet to be established.

Many non-song sounds not used as song units have been reported as ‘stable’. This means that the same non-song sounds are produced over multiple years (Rekdahl et al. 2013). Examples of stable non-song sounds reported include “wops” and “thwops” in the humpback whale population off the east coast of Australia (Dunlop et al. 2008, Rekdahl et al. 2013), which are similar to HW-02 identified in this study. HW-02 was identified in 2011 and 2012 in Geographe Bay, which suggests that it is stable in this population.

Complex sounds (those with multiple subunits) seem to be typical within the humpback whale repertoire (Cholewiak et al. 2013). The definition of subunits and units has been used in classification of humpback whale song and bird song analysis (Isaac & Marler 1963; Payne & McVay, 1971), but less frequently in the classification of humpback whale non-song sounds (Winn et al. 1979). Here, the number of subunits in non-song sounds proved to be valuable for describing non-song sounds and allowed the separation of certain sound types (e.g. HW-15, HW-16 and HW-17).

Some of the identified sounds here appear similar to social sounds or feeding calls reported elsewhere. For instance, HW-15 is similar to a series of “cries” reported as feeding calls in Alaska (Cerchio & Dahlheim 2001). In Alaska, the “cry” was observed as a train of units, here we also found multiple cries one after the other. However, because it was observed only in one recording, it is not possible to establish if these sounds are vocalised as independent units or a train of sounds as observed in Alaska. The feeding “cry” in Alaska was described as formed by three sections: i) a short upsweep or downsweep, ii) the main section of the call represented in a non-frequency modulating portion, and iii) a short trailing portion, usually a downsweep (Cerchio & Dahlheim 2001). A similar composition was observed for the population off Western Australia and sounds had similar shapes at the beginning and end of contours to “cries” reported in Alaska. However, the cries here were classified based on the combination of parts (here described as subunits). Cries were classified into three groups: HW-15 formed by the short up or downsweep (subunit A) and the CW portion (subunit B), HW-16 composed of subunit B and a short downsweep (subunit C) and finally a longer cry (HW-17), formed by subunits B and C connected by an additional subunit (subunit D). Further divisions were made based on variation in the duration of “cries” (e.g. HW-17 was two times longer than other cry types). These differences indicate a variability in the spectral characteristics of “cries” as previously reported. However, the small sample size prohibited confirmation of whether each variation was produced consistently enough for them to be defined as separate non-song sound types; or whether variations simply reflected variability among individual whales producing the same sound type, as suggested in previous studies (Cerchio & Dahlheim 2001).

One of the few studies on non-song sounds for humpback whales migrating along the coast of Western Australia deployed D-tags on mother-calf groups (Videsen et al. 2017). The study identified grunting sounds that are similar to HW-03 identified here. Sounds in group HW-03 were recorded in Geographe Bay, an area that, according to visual observations, has a significant number of mother-calf groups during the time of recordings. It is likely that these sounds are also vocalised by mother-calf groups in the area. However, additional analyses that match visual and acoustical observations are needed to confirm this.

Many studies use onomatopoeic names to describe sounds. This method can be problematic for comparison because sounds may be assumed as similar or different depending on the perception of the analyst (Dunlop et al. 2007; Erbe et al. 2017). Here, a comparison of spectrograms showed similarities among multiple sounds in different studies, some of which were given a different onomatopoeic name (Table 2.2.5). The use of spectral features to qualitatively describe sounds is suggested as a more accurate approach to overcome this problem. However, it is important to consider differences in recording and analytical settings used (e.g. FFT, overlap, etc.) to plot the spectrograms as these can also influence comparisons (Erbe et al. 2017). For example, in this study, HW-07 was suspected to be similar to a variety of different sounds reported in previous studies off Hawaii and the east coast of Australia. However, because of the variability within the group, it was not possible to confirm whether these sounds were the same as those reported in other studies using visual comparisons due to differences in spectrogram settings.

Table 2.2.5. Summary of similarities in non-song sound types identified for humpback whales off Western Australia and those reported elsewhere based on spectral feature comparison. Minimum frequency and duration are reported as a range or a mean value depending on the available information.

Non-song sound type	**Description in literature**	**Min freq. [Hz]**	**Duration [s]**	**Humpback whale population**	**Reference**
HW-03	Yup	40-95	0.13-0.29	north Atlantic	Winn et al. 1979
	Grunt	-	-	western Australia	Videsen et al. 2017
HW-04	Thwop	42.2	0.949	eastern Australia	Dunlop et al. 2007
HW-05	Pulsed Moan	25-50	1.69-5.70	north Atlantic	Winn et al. 1979
	Wop	43	0.748	eastern Australia	Dunlop et al. 2007
HW-09	Violin	548	0.312	eastern Australia	Dunlop et al. 2007
HW-10	Moan	90-105	0.63-4.55	north Atlantic	Winn et al. 1979
	Groan	139	1.262	eastern Australia	Dunlop et al. 2007
HW-14	Upsweep Grunt	369	0.74	north Atlantic	Stimpert et al. 2011
HW-15, HW16	Cry	236 - 1219	2.6	north Pacific	Cerchio and Dahlheim 2001

A qualitative analysis of spectral features of non-song sounds may have some limitations, particularly when there is high variability in sound types. Even when spectral features are used to describe sounds, there are some variations that occur as a result of the analyst’s visual perception of spectral features. For example, in this study both analysts agreed with spectral descriptions for almost all sounds, but there was a discussion on whether to divide some sounds classified in group HW-02. While a larger sample size would likely dissipate much of the uncertainty, classification and similarity analyses of quantitative metrics in spectral features are helpful in confirming groupings. Some of the analytical approaches that have been used include Random Forests (Rekdahl et al. 2013; Risch et al. 2013; Stowell & Plumbley 2014), Principal Component Analysis (Dunlop et al. 2007) or machine-learning techniques (Halkias et al. 2013) for a variety of animal vocal repertoires including birds, bats and cetaceans. The use of these methods requires a sufficiently large sample size for reliable results (Morgan et al. 2003).

For instance, many studies have used classification methods with over 200 sounds, with all sound types recorded more than once (e.g. Cerchio & Dahlheim 2001; Dunlop et al. 2008; Rekdahl et al. 2013; Halkias et al. 2013). In this study, the overall sample size was less than 70, and six of the sound types were recorded only once. The effectiveness of grouping of sound types using qualitative spectral features is supported by similarities reported between aural and visual inspection of spectrograms and quantitative classification in other studies (Dunlop et al. 2007; Rekdahl et al. 2013). However, for highly variable sound types (HW-02 and HW-15), quantitative classification using a large sample size is suggested to improve their classification.

In this study there was some regional spatial variation in detections of non-song sounds, in that they were only identified in the inshore recordings off Port Hedland. Humpback whales have habitat preferences related to social organization, where mother and calves show strong preference to shallower inshore waters (Ersts & Rosenbaum 2003; Irvine & Salgado Kent 2017). It is not possible to identify whether the non-song sounds recorded in inshore waters were produced by mother-calf groups, but those recorded in November (e.g. HW-15, HW-16) correspond with the end of the southerly migration in mother-calf groups from breeding grounds (Dawbin 1966; Craig et al. 2003). Considering that humpback whales have a structured migration in which females in early stages of lactation and mothers with newly born calves are the last to depart from breeding grounds (Dawbin 1997, Craig et al. 2003), it is likely that the sounds recorded in November in Port Hedland were vocalised by a mother-calf group.

Finally, this paper has improved current knowledge on the vocal repertoire of humpback whales, which improves the basis for PAM in behavioural and ecological studies. Attributes, such as differences in timing between the presence of song and non-song off Port Hedland observed here, extend the use of PAM to cohort-specific studies. However, the use of sound types in PAM must consider its potential limitations, such as difficulties in discerning sounds during peak periods for highly-vociferous species such as humpback whales. Thus, consideration of the range of PAM approaches available is suggested, with selection of an optimal approach based on the objectives of a study and how the focal species behaves in its habitats.

2.2.5. Acknowledgments

The authors would like to thank to Dr. Alec Duncan, and Malcom Perry from Centre for Marine Science and Technology for the technical support and advice. To Melinda Rekdahl from Wildlife Conservation Society (WCS), Ellen Garland from St Andrews University and Elisa Girola from the Cetacean Ecology Acoustics Laboratory (CEAL) at the University of Queensland for their advice. Finally, we would like to acknowledge BHP Billiton Iron Ore for funding this research, through the community engagement program.

Chapter 3.

Variability in vocalisation rates of baleen whales in Geographe Bay, Western Australia: Investigating the influence of biological, environmental, behavioural and anthropogenic parameters

This study aimed to identify conditions influencing the vocalisation rates of pygmy blue (*Balaenoptera musculus brevicauda*) and humpback (*Megaptera novaeangliae)* whales migrating through Geographe Bay, Western Australia. Specifically, the association between the number of vocalising groups detected in underwater recordings for each species and a combination of biological, environmental, behavioural, temporal and anthropogenic conditions was investigated. Simultaneous visual and acoustic observations were made during the month of November in 2010, 2011, 2013, and 2014 when whales migrated through Geographe Bay. Vocalisation rate was modelled comprehensively using a GEE framework by producing three separate models: one global model including both baleen whale species and one model for only humpback or pygmy blue whales. Vocalisation rate was species specific, with humpback whale vocalisations detected more frequently than pygmy blue whale vocalisations. Vocalisation rates varied with the type of sound recorded (song versus non-song), with song more frequently detected than non-song for humpback whales and vice versa for pygmy blue whales. Vocalisation rate also varied among years, but only for humpback whales; and with Julian days for both species with higher number of whales recorded at the beginning of the month. Unlike humpback whales, pygmy blue whales were detected more often during the morning than in the afternoon. Environmental (i.e. sea state, cloud cover) and anthropogenic (i.e., vessel presence) factors did not influence vocalisation rates for either species. This study identified that baleen whale species have different communication and reproductive strategies that may explain the differences in their vocal rates even when they have a similar habitat use. Understanding the variability in the vocal behaviour of different species will contribute to improve species specific models of detection that will reduce bias in population trends estimations using passive acoustic data.

3.1. Introduction

The use of remote sensing technologies for monitoring aquatic populations and mitigating human impacts has significantly increased over the last decade. Passive acoustic monitoring (PAM) has become popular because it is relatively cheap, can be used over long periods varying from months to years, and can be undertaken in remote areas independent of weather conditions. However, the use of PAM to measure population parameters (such as presence, distribution and animal movements) relies on animals being vocally active and on their vocalisations being detected. Most populations monitored will have some animals that are not vocalising. Thus, knowledge on vocal ecology and how likely animals are to be detected using PAM (i.e. the detection probability) will allow inferences to be made about the entire population (vocalising and non-vocalising cohorts).

In general, the probability of acoustic detection is dependent on a combination of parameters. These include animal vocalisation rates, the physical characteristics of the study area and how sound propagates through it, and environmental conditions during the study period. Of those parameters, vocalisation rate and its variability are often poorly known (Oleson, Wiggins & Hildebrand 2007; Marques et al. 2013).

The variability in vocalisation rates has been evaluated for several terrestrial taxa, including Carnivore (Laundre 1981; Bender et al. 1996), Avian (Conway et al. 1993; Lucas et al. 1999; Rehm & Baldassarre 2007; Odom & Mennill 2010; Belinsky et al. 2012) and Amphibia (Sinsch & Joermann 1989; Lingnau & Bastos 2007). These studies have found that variability in vocalisation rates is species specific but can increase as a function of specific conditions such as increased group size in coyotes, *Canis latrans* (Laundre 1981; Bender et al. 1996), food limitation in Carolina chickadees, *Poecile carolinensis* (Lucas et al. 1999), social interactions in marsupial frogs of the species *Gastrotheca marsupiata* (Sinsch & Joermann 1989), or decreasing temperature in frogs of the species *Hylodes heyeri* (Lingnau & Bastos 2007). Some conditions influence vocalisation rates of highly diverse species in the same way, such as some birds and frogs that increase vocal activity at sunset and/or sunrise (Sinsch & Joermann 1989; Lingnau & Bastos 2007; Odom & Mennill 2010; Belinsky et al. 2012) or have similar seasonal patterns in vocal activity (Conway et al. 1993; Rehm & Baldassarre 2007; Odom & Mennill 2010).

Studies on vocalisation rates of marine fauna are far fewer because often are logistically challenging and costly due to species' remote occurrence in oceanic habitats. However, studies that have been carried out on marine species have identified seasonality, food availability and lunar cycles as the most common causes of variability in vocalisation rates (e.g. Radford et al. 2008; Staaterman et al. 2014; Parsons et al. 2016). For instance, for many fish species vocalisations are detected more frequently at sunrise and/or sunset (McCauley 2012; Parsons et al. 2016) or during new and full moons (McCauley 2012; Staaterman et al. 2014).

Studies on cetaceans have identified diel patterns in vocalisation rates that vary among species, areas and seasons. For pygmy blue whales (*Balaenoptera musculus brevicauda*), fewer song sounds were detected during the day than at night but the difference was not large (Gavrilov & McCauley 2013). In contrast, southern right whales (*Eubalaena australis*) had similar vocalisation rates during day and night-time periods (Hofmeyr-Juritz & Best 2011). In others studies, humpback whales (*Megaptera novaeangliae*) have been reported to be more active at night (Cholewiak et al. 2008) and to have significant diel pattern when combined with moon phases (Sousa-Lima & Clark, 2008, Cerchio et al. 2014). For other species, the rate of whistles and echolocation bouts of bottlenose dolphins (Tursiops truncatus) reportedly changed among geographic locations (Jones & Sayigh 2002), and the presence of spinner dolphin vocalisations in Hawaii may be related to prey occurrence and distribution (Lammers et al. 2008).

In general, identification of variables such as behavioural and social contexts, environmental conditions (apart from diurnal patterns), and anthropogenic effects that may influence vocalisations has been more limited for cetaceans. Despite this, some examples on how environmental, behavioural and anthropogenic variables can influence vocalisation rates of whales and dolphins have been reported. For example, a previous study identified the location of the southern boundary of the Antarctic circumpolar current as a predictor of blue whale's (*Balaenoptera musculus*) D and Z call rates, and temperature, primary productivity, location and wind speed, were predictors of overall vocal rates for blue whales in the Southern Ocean (Shabangu et al. 2017). The later has also been linked to changes in vocal behaviour of humpback whales (Dunlop et al. 2010) and ice coverage has been found to be directly correlated with vocalisation rates of beluga whales (*Delphinapterus leucas*) in the Pacific Arctic region (Garland et al. 2015). In addition, studies in areas with high levels of anthropogenic activity have showed that North Pacific right whales (*Eubalaena* *japonica* lower their vocalisation rates when there are high vessel noise levels (Parks et al. 2007), and seismic surveying has been associated with a significant reduction in the number of humpback whale singers (Cerchio et al. 2014). Furthermore, it has been suggested that males change their song structure in the presence of other singers (Cholewiak 2008). However, whether a male starts or stops singing because other singers are in the vicinity is not known.

While the studies on cetaceans provide insight into conditions that influence vocalisation rates, wide knowledge gaps remain for a large number of species. In addition, most studies have focused on one set of factors of interest that can be environmental, behavioural or anthropogenic and specific sound types (generally song). To fill some of the existing knowledge gaps, this study evaluated multiple influencing conditions on vocalisation rates of two species of whales that occur concurrently in the same location, humpback and pygmy blue whales. Conditions included a combination of environmental, behavioural and anthropogenic factors.

Specifically, the study investigated vocalisation rates as a function of species (humpback and pygmy blue whales), type of acoustical cues produced (song and non-song), social context (as the number of whale groups of the same species present in the area), temporal scale (time, day, and year), vessel presence, and environmental conditions (sea state, cloud cover and glare) in Geographe Bay (GB), Western Australia (WA). Vocalisation rate in this study was defined as the number of groups detected vocalising per recording (with a duration of 13 or 23 minutes), given they were known to be present. A group was defined as individuals travelling within approximately 100 m of each other and displaying a coordinated behaviour and direction (Morete et al. 2007). Only recordings at times when whales were confirmed to be present, either acoustically or via simultaneous visual observations, were used.

GB is a notable location in that it is one of few known locations worldwide where pygmy blue whales migrate within a few hundred metres of the shore and can be observed and tracked from land. GB is also an important tourist destination in the south-west of Australia. Whale watching and recreational fishing are among the principal attractions, and in recent years such activities have been increasing. Understanding vocal variability over time in relation to social, anthropogenic, and environmental conditions is essential to understanding the behaviour of whales and assessing anthropogenic impacts. In addition, knowledge on how the number of vocalising groups may vary under different conditions is required for developing passive acoustic methods to estimate population parameters that use detection probabilities. Through monitoring whale populations and underwater noise levels, regional management guidelines and species conservation policies can be improved.

3.2. Methods

3.2.1. Study area

GB is located in the south-west of Australia, about 220 km south of Perth (Figure 3.1). The bay's coastline extends from Cape Naturaliste located at the south-western tip of Australia to Bunbury (from 33° 18' 32'' S and 115° 38' 6'' E to 33° 32' 6'' S and 115° 0' 29'' E). Geographe Bay's coast is predominantly sandy, comprised of a thin offshore sand-sheet and a series of parallel ridges that are part of the Quindalup system (Damara 2011). The southern area of GB is fringed by hills up to approximately 50 m high, while the seafloor depth ranges between 20 and 50 m. The seafloor of GB is part of the Yallingup shelf (Borissova 2002) and composed of Holocene sediments, tamala limestones and clays.

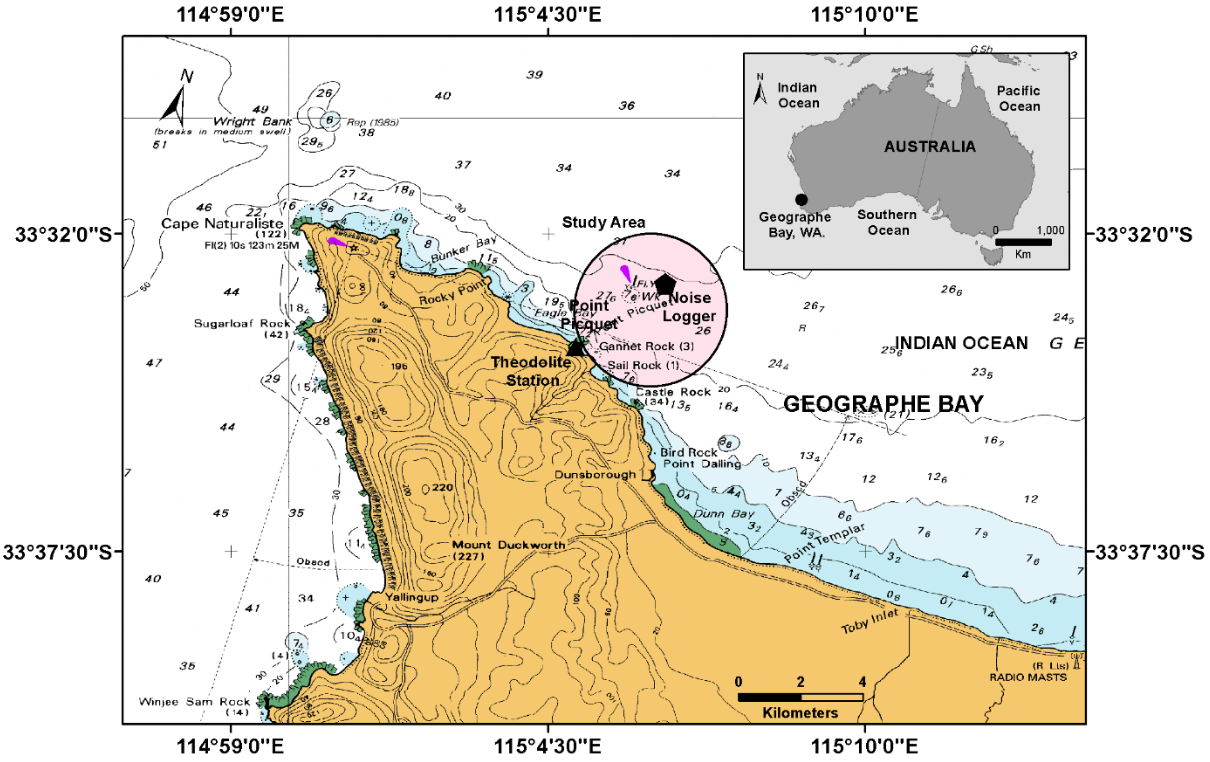


Figure 3.1. Location of study site, including the position of the acoustic recorder, the land-based theodolite station, and the study area (shaded in pink) in Geographe Bay, Western Australia.

Humpback and pygmy blue whales migrate through GB while on route to feeding grounds in Antarctica from northerly breeding grounds. Thus, humpback whales are present in GB between approximately August and December, and pygmy blue whales between approximately October and January. The exact peak periods in migration for these species vary among years (Salgado Kent et al. 2014).

The region near Pt. Piquet in GB was selected as the study area for several reasons (Figure 3.1). Firstly, a relatively large number of pygmy blue and humpback whales pass very close to the shore at Pt. Piquet (as close as ~200 m). The close proximity allows for simultaneous acoustic and land-based visual surveys to be undertaken at this location. Secondly, the physical characteristics influencing acoustic transmission at this location (including a relatively flat seabed depth of 30 m) allow for pygmy blue whale vocalisations to be detected within approximately 6-10 km, and humpback whale vocalisations within around 20-30 km but not beyond (Salgado Kent, Gavrilov et al. 2012). Thirdly, hills just behind Pt. Piquet with 180° field of view from a height of ~50 m allowed a maximum visual detection range of 15 km. Thus, the characteristics of the region near Pt. Piquet allowed for simultaneous visual and acoustical monitoring of the area near land.

Consequently, the 'Study Area' was defined as a 19.7 km^2 circular area off Pt. Piquet (Figure 3.1) with a radius up to 3 km in range. The circular shape corresponded to the decreasing detection in all directions as a function of distance from an omnidirectional hydrophone fitted to the stationary acoustic recorder used in this study. The stationary underwater recorder was placed at 2.5 km from Pt. Piquet. The 3 km maximum radius (in all directions away from the logger position) corresponded with vocalisation signal-to-noise ratios (SNRs) of 8 dB (regardless of species; Salgado-Kent, Gavrilov et al. 2012). This SNR allowed sounds to be distinguished easily from background noise. Visual observations within the Study Area were undertaken from the 50 m hill called Hill 50 in Meelup Regional Park, 293 m behind Pt. Piquet. From Hill 50, whales could be confidently tracked from a range of approximately 3 km while still having relatively good detection out to 6 km.

Because the area in which whales were detected by each survey platform varied in range and shape, observations from each platform were truncated for data analysis to correspond with the Study Area. Because there were no features to demarcate the boundaries of the Study Area in the field, visually tracked whales beyond 6 km were removed from the dataset. Similarly, acoustically detected whales with SNRs less than 8 dB were removed. Thus, all observations were standardised to the Study Area.

3.2.2. Study period

The study was conducted during the month of November in 2010, 2011, 2013 and 2014 as part of the Southwest Whale Ecology Study (SouWEST: https://souwest.org/). November is known to be the peak of the pygmy blue whale migration (Burton, unpublished data), and while humpback whale numbers begin to drop in the area they continue to be high in November (Salgado Kent et al. 2014). The period just after the peak of migration for humpback whales was chosen to facilitate the differentiation of multiple vocalising groups, since recordings during the peak period can be saturated with humpback whale song.

3.2.3. Survey methodology

The geographical location where land-based visual observations were undertaken on Hill 50 was 33° 36’ 7.48’’ S and 115° 4’ 46.55’’ E (Figure 3.1). The stationary underwater acoustic recorder was located at approximately 33° 32’ 48’’ S and 115° 06’ 24’’ E (Figure 3.1; see Table 3.1. for exact positions of each recorder).

3.2.3.1. Visual observations

Land-based visual observations were collected using a TopCon GTS-603AF Electronic Total Station theodolite connected to a computer running a real-time positioning software called CYCLOPS (v.2.8.04 for 2010-2011 data - Erick Kniest, University of Newcastle) or VADAR (for 2013 – 2014 data, Erick Kniest, University of Newcastle). Observations were conducted by a team of at least three observers over 6-7 hours per day, depending on weather conditions. Observations were undertaken in Beaufort conditions of less than 5 to reduce bias and error in sightings due to whitecaps. Observer teams rotated at midday to reduce error caused by observer fatigue. The first team undertook a shift commencing at 07:30 and finishing at approximately 11:00 to avoid the midday heat. The second team undertook an afternoon shift commencing at 14:00 and finishing at 17:45.

The observations were collected continuously following a protocol to obtain numbers of whales sighted, spatial distribution, group composition and general information on local movements, behaviour and direction of travel over time. Additionally, presence and location of vessels and weather conditions were recorded. Weather conditions were collected on site every 30 minutes, and included: qualitative estimates of wind speed (knots), wind direction (relative to magnetic north), swell height (m) and direction (relative to magnetic north from its origin), sea state using the Beaufort scale (Barua 2005), cloud cover (in octaves), glare (on a scale of 0 to 3, with 0 corresponding to no glare and 3 to intense glare), and the presence or absence of haze. All conditions were estimated by an experienced observer.

3.2.3.2. Acoustic recordings

The underwater acoustic recorders were built at the Centre for Marine Science and Technology (CMST, Curtin; McCauley et al. 2017). Acoustic recorders were positioned on the seafloor with a mooring configuration consisting of an anchor, ground line and acoustic release, as described in McCauley et al. (2017). Deployment positions of acoustic recorders varied in geographical location and depth from year to year only by a few meters (Table 3.1).

Table 3.1. Geographic positions and depths of underwater acoustic recorders deployed in Geographe Bay, WA in 2010-2011 and 2013-2014.

Year	Latitude (S)	Longitude (E)	Seafloor depth (m)
2010	33°32'51.66"	115° 6'29.28"	29.0
2011	33°32'52.38"	115° 6'39.18"	29.0
2013	33°32'33.00"	115° 6'39.42"	32.3
2014	33°32'45.72"	115° 7'0.90"	30.0

The recorders were calibrated before and after deployment using white noise of known level in series with the hydrophone. The received signals were amplified using a pre-amplifier of 20 dB gain and a channel amplifier of 20 dB gain. Signals were high-pass filtered at 8 Hz so as to reduce the naturally high levels of low-frequency noise in shallow water and increase the dynamic range of the recording system. The signals were anti-aliasing filtered and digitised by a 16-bit analogue-to-digital converter (ADC). Sampling schedules, sampling frequencies, anti-aliasing filters and duty cycles for all years are given in Table 3.2. Schedules of recording were either 13 minutes every 15 minutes or 23 minutes every 30 minutes over a period ranging from 30 to 80 days (depending upon year). Individual recordings of 13 or 23 minutes are called *samples* (in the statistical sense) in this study.

Table 3.2. Acoustic recorder settings and recording schedules for each year of study.

Year	Total Gain (dB)	Sampling frequency (kHz)	Anti-aliasing filter (kHz)	Duty cycle	Underwater recording period
2010	40	12	5	13 minutes every 15 minutes	14/11/2010 to 13/12/2010
2011	40	12	5	13 minutes every 15 minutes	10/11/2011 to 15/12/2011
2013	40	6	1.8	23 minutes every 30 minutes	14/11/2013 to 05/02/2014
2014	40	6	1.8	23 minutes every 30 minutes	31/10/2014 to 15/01/2015

3.2.4. Data processing

Because visual observations were limited to shifts conducted during daylight hours on good weather days, all data from the two platforms were made comparable by only including acoustic data from times with corresponding visual observations. Of these data, only those with acoustical and/or visual whale detections were included in the analysis, so the analysis included only times when whales were present in the Study Area.

For acoustic analyses, whale vocalisations were manually extracted from recordings using the MATLAB (The MathWorks Inc.) toolbox 'CHORUS' (Characterisation Of Recorded Underwater Sound) developed by CMST (Gavrilov & Parsons 2014). Spectrograms were computed using Hamming windows of 1 or 0.5 s, with 50 or 90% overlap. All spectrograms were displayed with a frequency range of 6 Hz to 4 kHz for consistency amongst recording settings. Spectrograms and waveforms were displayed in 50-s windows and longer (Figure 3.2). Segments of this length allowed song phrases produced by different groups to be distinguished since song phrases have an average duration of between 7 s and 1 minute (Payne et al. 1983; Guan et al. 1999).

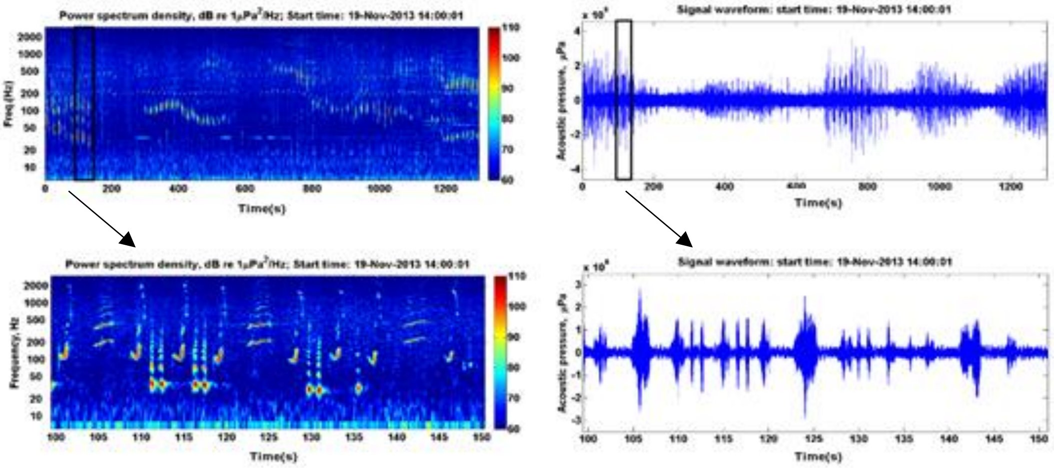


Figure 3.2. Example of spectrograms and waveforms used in the acoustic recording review process, including those for the full recording (top panel) and for the 50-s clips (bottom panel). Spectrograms were plotted using the following settings: a. Top panel, fs = 6 kHz, NFFT = 6000, Hamming window and overlap = 50%; b. Bottom panel, fs = 6 kHz, NFFT = 3000, Hamming window, and overlap = 90%.

Humpback and blue whale sounds were marked and classed as either song or non-song. Songs produced by humpback and blue whales are recognized for its regular and patterned sequences of notes or units (McDonald et al 2006; Cholewiak et al. 2013, Figure 3.3). Because humpback whale song is highly complex and can evolve seasonally, it was qualitatively described for each season following the methods by Garland et al. (2011). In contrast, non-song vocalisations for both species are identified as single units that do not follow a pattern (Payne et al. 1983; Dunlop et al. 2007; Oleson, Calambokidis, Burgess et al. 2007).

Humpback whale non-song vocalisations are sounds that either are completely different from those used in song, or are used in song but not in a patterned sequence, or appear as sequences of sounds. In the latter two cases, non-song sounds can be difficult to distinguish from song units. Thus, the description of song for each season was used to identify non-patterned units produced outside of song patterns (see Chapter 2). To ensure that sequences of non-song sounds were not erroneously identified as song as a result of clipping of the sequence in the recording, recordings with the entire sequence (unclipped) were used to compare to song sequences. If after full comparison it was not possible to categorize the sequence as a non-song sequence or as a song phrase, the sample was not included in the analysis. This was done to reduce error. Non-song vocalisations described for humpback whale populations elsewhere were used to aid identification (Silber 1986; Cerchio &

Dahlheim et al. 2001; Simao & Moreira. 2005; Dunlop et al. 2007; Zoidis et al. 2008; Rekdahl et al. 2013; Fournet et al. 2015; Videsen et al. 2017, Chapter 2).

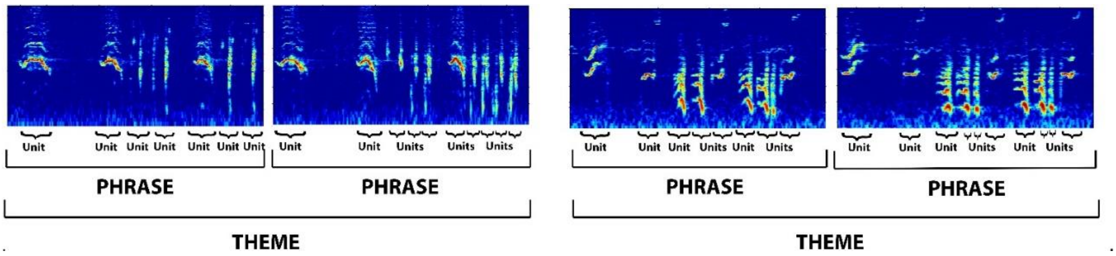


Figure 3.3. Example of humpback whale phrases and themes that are typically placed in particular combinations and repeated to make up song.

Pygmy blue whale song was identified using previous descriptions for the population (McDonald et al. 2006; Gavrilov et al. 2011) since pygmy blue whale song structure evolves over long time periods of decades, rather than annually as does humpback song (Gavrilov et al. 2011). Pygmy blue whale non-song sounds were distinguished from humpback song by their simpler patterns and their characteristic frequencies between 14 and 300 Hz, previously documented in Geographe Bay (Salgado Kent, Gavrilov et al. 2012; Recalde-Salas et al. 2014; Chapter 2 of this thesis). In some cases, unpublished sounds (not described in Mellinger & Clark 2003; Oleson, Calambokidis, Burgess et al. 2007; Stafford et al. 2011; Recalde-Salas et al. 2014) were suspected to be from pygmy blue whales. In these cases, sounds were attributed to pygmy blue whales if: (1) at least one pygmy blue whale group was observed (visually) in the Study Area, and (2) no humpback whale group was sighted in the Study Area between 10 minutes before and 10 minutes after the sound was recorded. This 20-minutes period meant that any humpback whales that might have been in the region were likely approximately 1 km outside the Study Area, based on an average migratory speed of 3 km hr^{-1} (unpublished data from the Study Area).

Once the species and vocalisation types were identified in a recording, the number of groups producing them was determined. A group of whales was defined as whales traveling within 100 m of each other, moving in a coordinated direction and exhibiting the same behaviour (Morete et al. 2007). A *group* can be a singleton or multiple animals. The number of groups rather than the number of individuals vocalising per sample was assessed because it was not possible to identify which individuals within a group were vocalising using a single stationary underwater acoustic recorder.

However, the number of groups vocalising could be assessed based on the rationale described below.

Firstly, song is thought to be produced by males (Frankel et al. 1995; Darling et al. 2006; McDonald et al. 2006; Oleson, Calambokidis, Burgess et al. 2007; Garland et al. 2011) and has been reported to be produced mostly by solitary animals (Payne et al. 1983, Frankel et al. 1995; Darling et al. 2006; McDonald et al. 2006). In humpback whales, it has been reported that singers stop singing in the presence of other males or adults (Tyack 1981). Some studies have also reported that males can start singing after joining a mother-calf group (forming a mother-calf-escort group), or can have interactions with other group types such as dyads or competitive pods (Smith et al. 2008). According to visual observations, there were relatively few mother-calf-escort groups in the area (i.e. an average of 4 groups per season, with a minimum of 0 and maximum of 7) and even fewer single individuals joining mother-calf groups (i.e. this was reported on two occasions for all seasons) or other group types. Consequently, for humpback whales, song was assumed to be produced mainly by groups of one individual. Consequently, bias caused by singers in mother-calf-escort groups was expected to be low. However, this bias should be considered when a survey begins before and occurs during the peak of migration since the number of singers escorting mother-calf groups may be greater. While the same evidence is not available for blue whales, song was associated with groups of two individuals only twice; on all other occasions, potential blue whales singing travelled singly. Thus, for blue whales, song was also assumed to be produced by groups of one individual.

Non-song sounds were assumed to be produced by groups different from those producing song based on the rationale given above. When multiple non-song sounds were observed in a recording, then these were assigned to different groups when signal SNRs in spectrograms clearly differed from visual inspection. Often this occurred together with overlapping units (Figure 3.4). If SNRs were similar and units were not overlapping, non-song sounds were assumed to be produced by the same group. However, there is the possibility of underestimating the number of groups vocalising non-song sounds when multiple vocalising groups are located at similar distances from the hydrophone and therefore present similar SNR values. The current data does not allow for this bias to be corrected as acoustical tracking is the only option to reduce it. Although this bias will be considered in the results and discussion of this study for non-song sounds, it was considered highly unlikely for song. When multiple singers are at similar ranges, all groups should be vocalising the same phrase simultaneously and units will need to be overlapping in the entire recording so it is not possible to distinguish individual song phrases. It was possible to distinguish individual song units and phrases in this study because the sampling was carried out after the peak of migration when the number of singers is lowering.

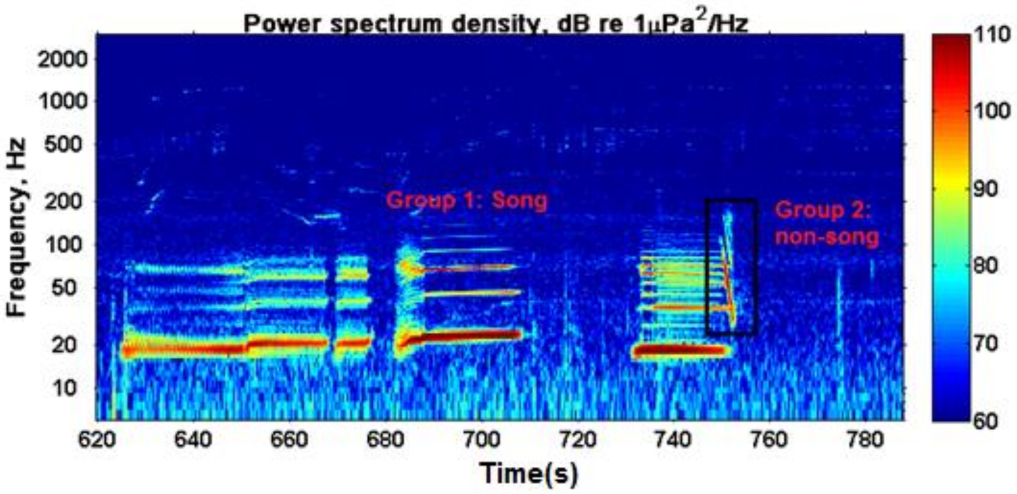


Figure 3.4. Example of count of pygmy blue whale groups detected acoustically based on multiple sounds observed in a sample spectrogram (overlapping units attributed to different whale groups shown with the black rectangle). The spectrogram has the following settings: fs = 6 kHz, NFFT = 6000, Hamming window and overlap = 90%.

For each recording, the minimum, maximum and best estimates of the number of groups producing song and non-song sounds were assessed.

3.2.5. Statistical analyses

Generalized Estimating Equations (GEE) were used to investigate the influence of factors such as species (humpback and pygmy blue whales), vocalisation type produced (song and non-song), social context measured as the number of whale groups of the same species visually observed in the area, temporal scales (time of day, day, and year), vessel presence, and environmental conditions (wind speed, sea state, cloud cover and glare) on vocalisation rates (numbers of groups vocalising per sample) in the Study Area in GB. Temporal explanatory variables included year, Julian day and period of the day (either AM or PM). A temporal scale finer than AM or PM (such as hours) was not possible because of temporal autocorrelation. The response variable was the best estimate of the number of groups vocalising per recording, given they were known to be present in the Study Area.

Three GEE models were fitted, including: (1) a global model that included both species (called M1), (2) a model that only included humpback whales (M2), and (3) a model that only included pygmy blue whales (M3). The first of these models included all explanatory variables and their interactions with species. The species-specific models (M2 and M3) included all explanatory models (except for species) and included all two-way interactions that were identified as biologically relevant. By fitting species-specific models, the complexity of 3-way interactions that captured species-specific effects was avoided.

Models were fitted using RStudio Version 3.2.1 (© 2015 RStudio, Inc.) and the following R (R Development Core Team 2016) packages: MRSea (Scott-Hayward et al. 2013), doBy (Højsgaard 2006), stringr (Wickham, 2012), geepack (Halekoh et al. 2006) and lattice (Sarkar 2014). GEE models were preferred over other methods as they account for autocorrelation of residuals when the structure is not identified (Dormann et al. 2007), they allow for non-normally distributed responses (Zuur et al. 2009) and model the average population effect of covariates instead of individual-specific effects (Oedekoven 2013). GEE were also chosen for its flexibility to manage unbalanced datasets without having to discard data or reduce the number of observations (Ballinger 2004). Because of variability in start and end dates of seasonal observations among years, data were subsampled so that all observations were from the month of November (between Julian days 315 and 335).

Temporal autocorrelation in residuals resulting from the same groups detected acoustically and visually in the study area in consecutive samples was confirmed using the *runACF f*unction of the MRSea R package (Scott-Hayward et al. 2013). Thus, an autocorrelation structure was included in the models. Tracking data from visual observations in this study indicated that groups of whales could be expected to take up to approximately 2-3 hours to cross the Study Area. Thus, samples within a morning (AM) period and samples within an afternoon (PM) period for each day could be considered to be autocorrelated (as these observations were over a period of 2-3 hours). The autocorrelation test confirmed that autocorrelation within each AM and PM 'block' decayed until it was negligible towards the end of each block. Thus, 'AM/PM blocks' for each day were used as the blocking structure for the *waves* argument in geepack. Within each AM/PM block, samples were numbered according to their temporal spacing and these values allocated to an 'ID' vector used as an argument for the autocorrelation structure.

Geepack allows for AR-1, unstructured, independence, and exchangeable autocorrelation structures in models. An AR-1 correlation structure was initially selected as this is suggested as the most appropriate structure for datasets with time order (Zuur et al. 2009). However, GEEs were fitted with different structures to confirm the stability of the model (Hardin & Hilbe, 2012), and the best fit correlation structure selected based on the lowest Quasi likelihood under the independence model (QIC) values (Pan 2001).

Because the response variable consisted of count data, a Poisson family and log-link function were used in the model. Explanatory variables, including species, presence of vessel, year, period of the day (AM/PM) and vocalisation type, were considered as factors. Beaufort, wind speed, glare, cloud cover and number of visually tracked groups were included as numeric variables. As these explanatory variables were not necessarily expected to vary linearly with the response variable, a smooth fit was tested with knots selected using the *makesplinesParams* and *runSALSA1Dwithremoval* functions of the MRSea package (Scott-Hayward et al. 2013). The best fit, smoothed or linear, was chosen based on the Bayesian information criterion score (BIC). BIC is based on a likelihood function that compares non-nested models by comparing posterior to prior probabilities of two models in the model selection process (Redfern 2006). All variables were tested for collinearity to ensure that no collinear variables were included in the same model. If adjusted Variance Inflation Factors (VIFs) exceeded 2, variables were considered to be collinear. As Beaufort and wind speed were collinear, and Beaufort was considered to more directly affect detection of whales, wind speed was excluded from analyses.

To fit the models, first, a full-model was constructed which included all explanatory variables and factors. Step-wise model selection occurred by comparing constructed sub-models that step-wise excluded non-significant explanatory variables with the previous larger model using QICu and ANOVAs (Pan 2001; Halekoh et al. 2006). The most parsimonious model that reduced the QICu by more than 2 units (Hardin & Hilbe 2013) and showed no significant differences between models (using ANOVAs) was selected as the better of the two models. Models were validated and checked by plotting fitted values versus scaled Pearson´s residuals and by comparing observed and fitted values. Finally, scatter plots, boxplots, and summary statistics such as means and standard deviations were used to describe and visualise patterns in numbers of groups as a function of different conditions and over time.

3.3. Results

3.3.1. Effort

A total of 48 days were sampled; i.e., 15, 12, 12, and 9 days during 2010, 2011, 2013 and 2014, respectively.

Acoustic recordings: The 48 days consisted of 126.6 hours in 482 acoustic samples. Of the total 126.6 hours, 40.2 hours (181 samples) were from 2010 and 28.0 hours (126 samples) were from 2011. These had an acoustic recording duty cycle of 13 minutes every 15 minutes. Slightly less effort was associated with the longer acoustic recording duty cycle of 23 minutes every half hour; which included 33.7 hours (101 samples) from 2013 and 24.7 hours (74 samples) from 2014.

The number of samples reviewed in the morning and afternoon of each day were comparable (AM period: $\bar{X}$ = 15.17 samples day^{-1}, SD = 7.41; PM period: $\bar{X}$ = 14.80 samples day^{-1}, SD = 5.39). However, on several days, samples were collected only during the morning or afternoon, but this unbalanced sampling occurred haphazardly throughout the season (i.e. it was not clustered; Figure 3.5).

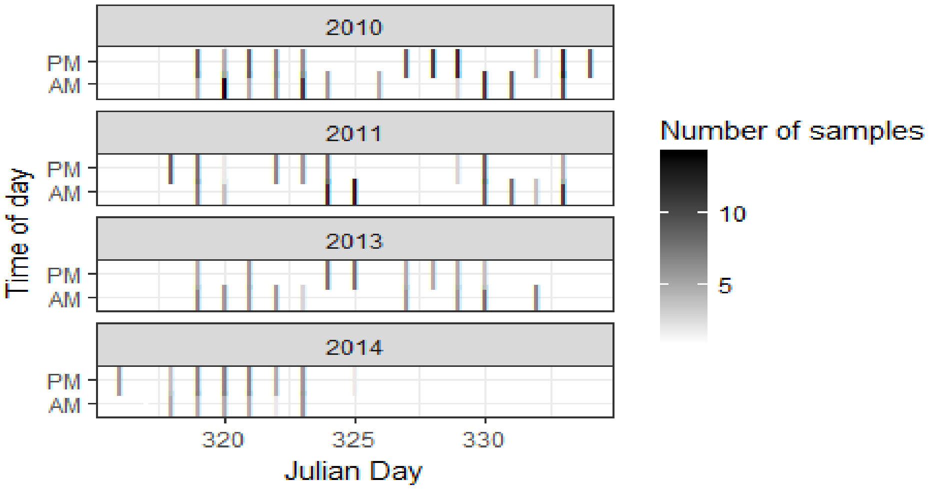


Figure 3.5. Number of acoustic samples collected during AM and PM periods over Julian days in the Study Area in Geographe Bay during 2010-2011 and 2013-2014.

Visual observations: Visual observations during the 48 days were conducted over a total of 190.4 hours. This effort was greater than acoustic effort because it was collected continuously rather than on a duty cycle. Of the total effort, 55.0 hours were conducted in 2010, 39.4 in 2011, 53.6 in 2013, and 42.4 in 2014 (Figure 3.6).

Differences in effort between AM and PM periods varied from as little as 0.24 hours in 2010 to 6.9 hours in 2014 (Figure 3.6).

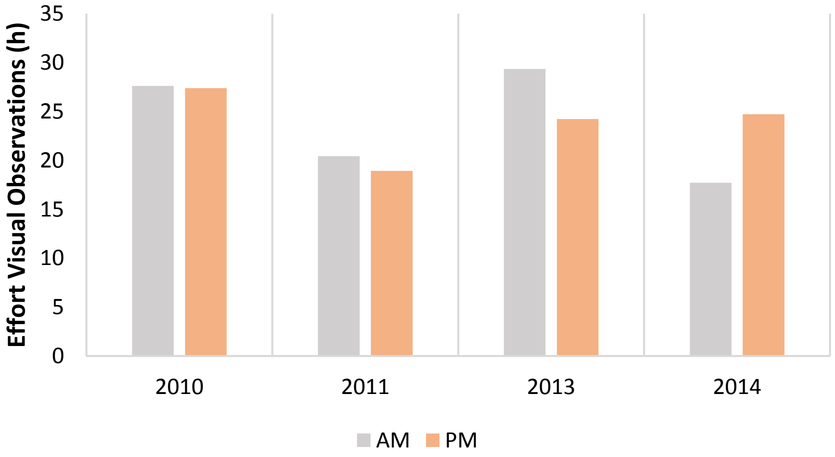


Figure 3.6. Visual observation effort (hrs) during AM and PM periods in the Study Area in Geographe Bay during 2010-2011 and 2013-2014.

3.3.2. Environmental conditions and vessel presence

A range of environmental conditions and vessel presence occurred throughout the study period (Figure 3.7). These conditions varied from sea state conditions of 0 to 5, cloud cover from 0 to 8, glare from 0 to 3, and a large sample size of vessels present and absent.

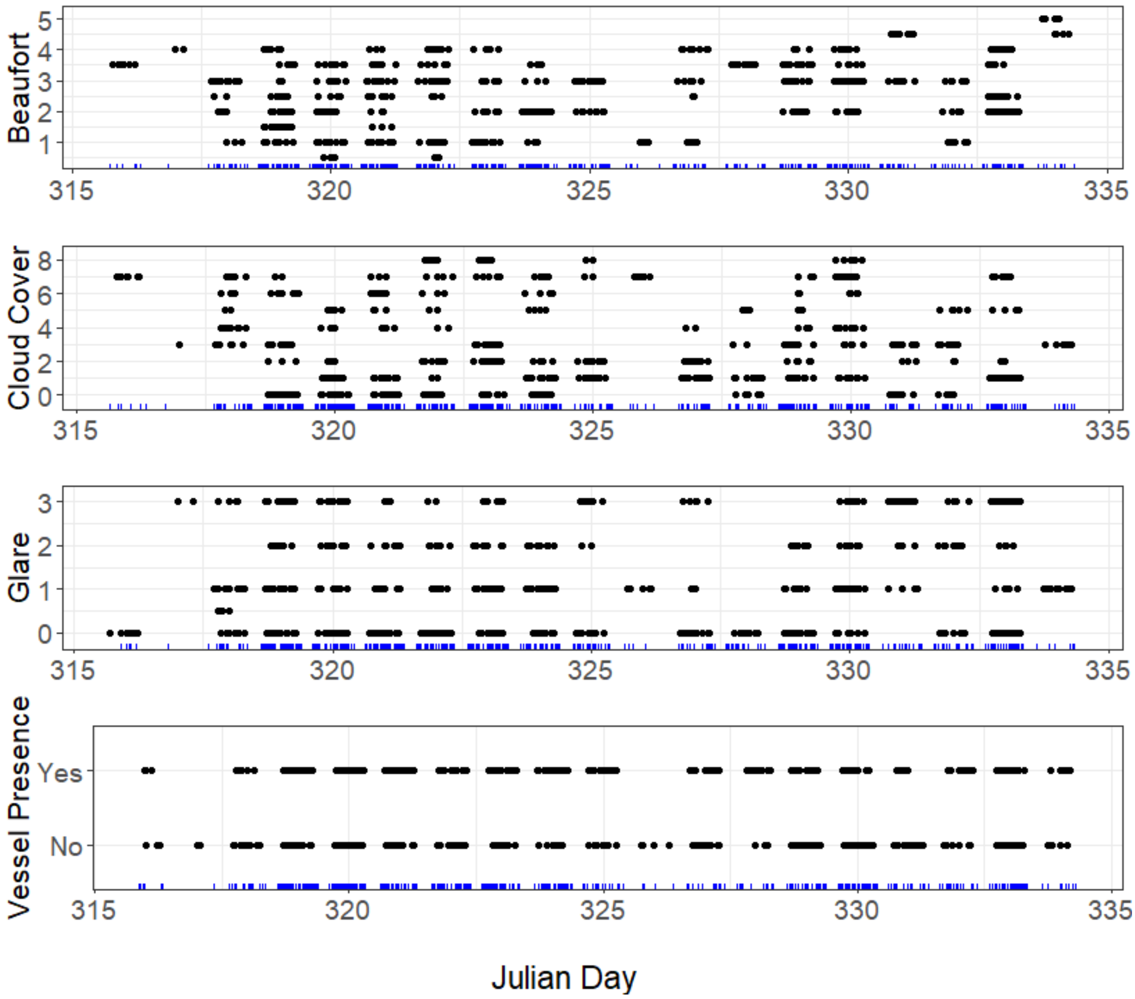


Figure 3.7. Summary of variability for environmental and anthropogenic variables over the study period.

3.3.3. Number of vocalising whale groups

The number of whale groups reported here represents the number of groups vocalising per sample. Consequently, groups counted in adjacent samples within an AM or PM period within any one day may include some of the same whale groups in adjacent samples. Thus, the total sum of count over all samples represents the total number of vocalising groups in the area rather than the total number of whale groups present in the area (vocalising and not vocalising). However, the number of groups per sample is a measure of the relative number of groups in the area during the duration of the sample.

On average, one group of baleen whales was vocalising per sample (Max = 7, Min = 0, Var = 1.48, SD = 1.22). Differences between species were observed, with more humpback than pygmy blue whale groups vocalising per sample (Figure 3.8).

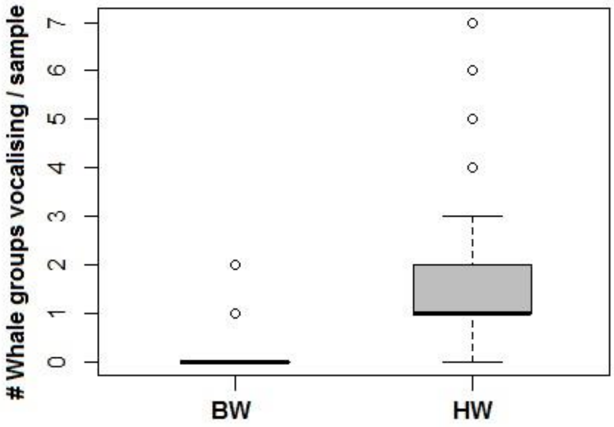


Figure 3.8. Boxplots (95% confidence intervals) for the number of vocalising blue whale (BW) and humpback whale (HW) groups in Geographe Bay.

The mean number of vocalising baleen whale groups per sample varied among years, with a decrease in number of humpback whales over the years from a mean of 1.33 (SD = 1.48) in 2010 to a mean of 0.78 (SD = 0.96) in 2014 (Figure 3.9).

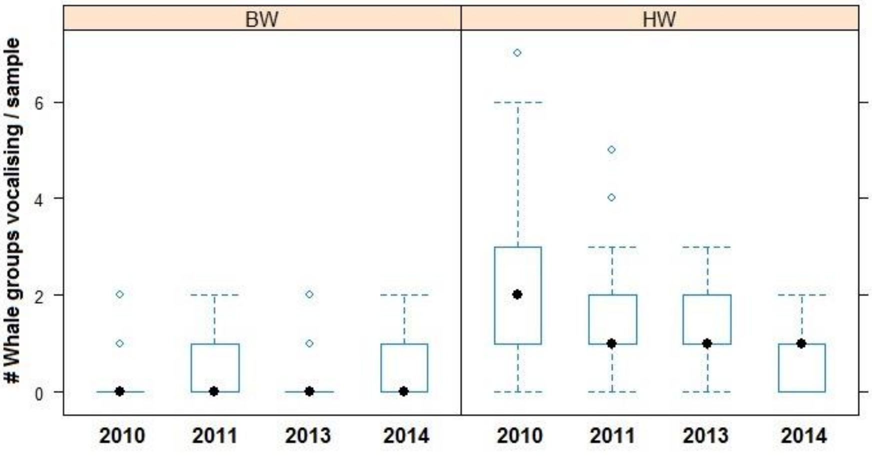


Figure 3.9. Boxplots (95% CI) of cumulative number of pygmy blue whale (BW) and humpback whale (HW) groups vocalising per sample in 2010, 2011, 2013 and 2014. HW.

For acoustic recordings, 828 groups produced song, and 244 groups produced non-song sounds; with an average of 1.86 detections per sample (SD=1.30) from groups producing song and an average of 0.25 detections per sample (SD=0.52) from those producing non-song sounds (Figure 3.10.a).

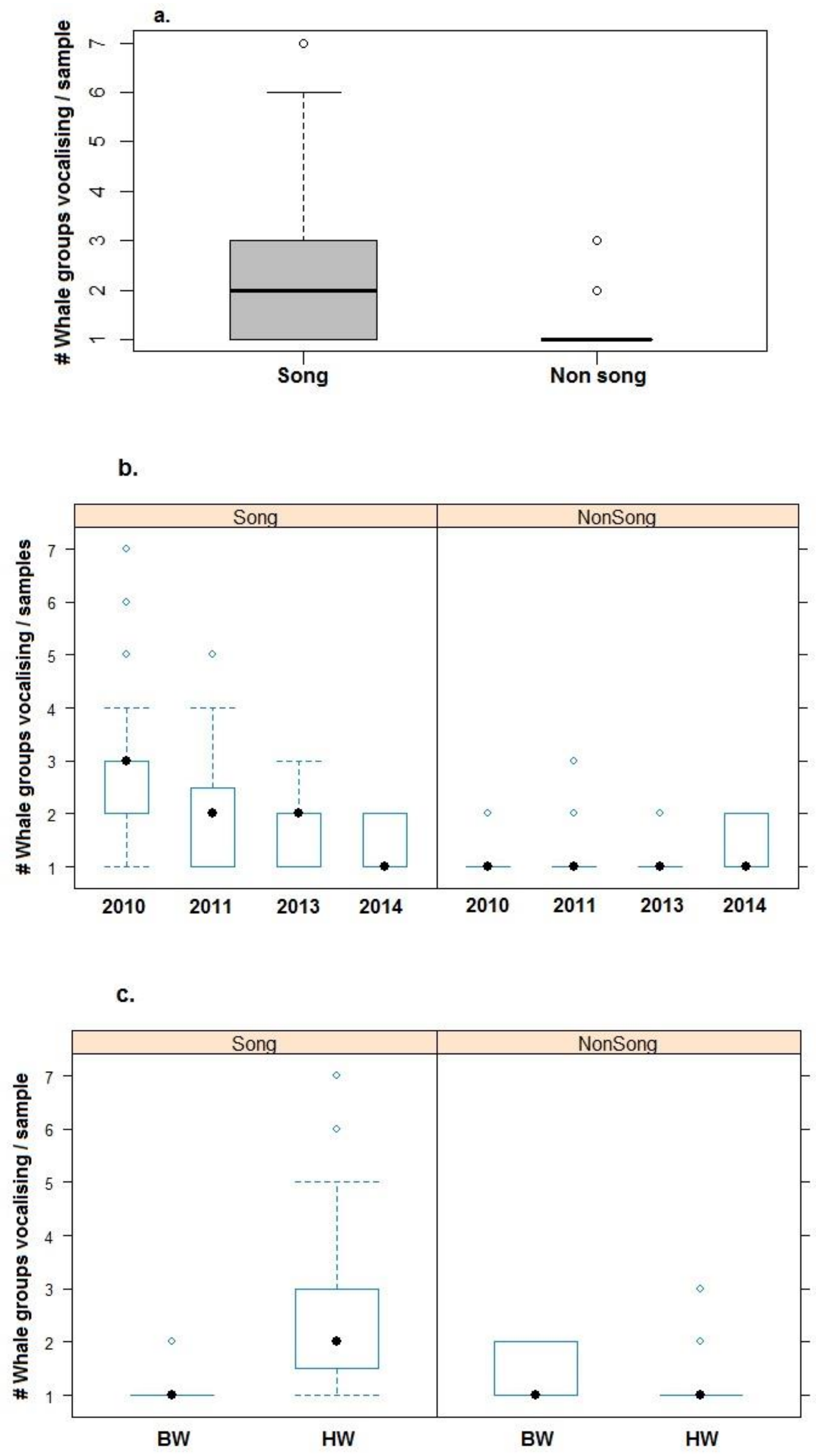


Figure 3.10. Boxplots (95% CI) of the mean number of whale groups vocalising song and non-song sounds per sample per hour for: a. for each type of vocalisation category (song and non-song), b. for type of vocalisation split by year, and c. for type of vocalisation for each whale species (blue whale (BW) and humpback whale (HW).

While groups producing song and non-song sound were recorded for both species during all years (Figure 3.10.b), there was a decrease in number of vocalising humpback whale groups between 2010 and 2014 (Figure 3.9), which is probably driven by the number of groups vocalising song (Figure 3.10.b). Differences were observed between species in that the mean number producing song per sample was larger for humpback whales ($\bar{x}$ = 2.30, SD = 1.13) than pygmy blue whales ($\bar{x}$ = 1.04, SD = 0.21), and was larger than either species producing non-song sounds (humpback whale non-song: $\bar{x}$ =1.13, SD = 0.37; pygmy blue whales: $\bar{x}$ =1.29, SD = 0.45) (Figure 3.10.c).

3.3.4. Conditions influencing the number of vocalising baleen whale groups within Geographe Bay

Biological, behavioural, and temporal conditions influencing the number of vocalising groups per sample were similar in all best models (Table 3.3, Table 3.4 and section 3.6. Supplementary Material). Environmental conditions had very little influence in all models. Anthropogenic conditions, measured in terms of vessel presence, had no influence in any of the models.

Biological variables: The global model that included both whale species (M1) indicated a marked difference in number of vocalising groups between species, with greater numbers of humpback whales than blue whales detected reflecting the patterns in raw means presented above (Table 3.4).

Behavioural variables: All models (M1, M2 and M3) indicated that sound type influenced the number of vocalising groups detected per sample, with a greater number of song-producing than non-song producing groups detected in the case of humpback whales and the opposite in the case of blue whales (Figure 3.11.c; Figure 3.12.c; Figure 3.13.b). For humpback whales, the interactions between sound type and year was significant, with song decreasing over years as indicated in raw detections in the section above. For blue whales, the interaction between sound type and AM/PM indicated and decreased from AM to PM periods. The global model (M1) and the model for humpback whales only (M2) indicated that the number of groups visually tracked through the area per sample was associated with the number detected acoustically; however, this was not the case for blue whales (M3). The difference in species is further corroborated by the interaction between species and sound type and between species and number of groups visually tracked in the global model (M1). In addition, for humpback whales, the association between the number of acoustic detections and the number of visually tracked groups of whales was dependent upon year (evidenced by the interaction in M2), and dropped in 2014.

Temporal variables: The number of groups detected acoustically decreased with increasing Julian day in all models (M1, M2, and M3; Table 3.4; Figure 3.11.a, Figure 3.12.a, Figure 3.13.a). The number detected was associated with year only in the global and humpback whale models, showing decreasing numbers with increasing year (M1 and M2, respectively; Table 3.4; Figure 3.11.b, Figure 3.12.b). The difference in species is further corroborated by the interaction between species and year in the global model (M1). On the shortest time scale, there were no significant differences in the number of vocalising groups between AM and PM periods for humpbacks, but AM/PM was a significant parameter in the blue whale model (M3, Figure 3.13.c).

Table 3.3. Best GEE sub-models for predicting the vocalisation rate of baleen whales based on conditions measured at the study site in Geographe Bay.

Model	**Species**	**Response Variable metric**	**Best Model**
M1	Combined	Number of vocalising whale groups	$log\{E(Y_{ij})\} = \beta_0 + \beta_1 Species + \beta_2 SoundType + \beta_3 Year + \beta_4 JulianDay + \beta_5 Species * Year + \beta_6 Species * SoundType + Species * NumGroupsVisTracked$
M2	Humpback	Number of vocalising whale groups	$log\{E(Y_{ij})\} = \beta_0 + \beta_1 SoundType + \beta_2 Year + \beta_3 NumVisDetGroups + \beta_4 JulianDay + \beta_5 SoundType * NumGroupsVisTracked + \beta_6 Year * NumGroupsVisTracked + \beta_7 AM/PM * CloudCover + \beta_8 s(Glare) * JulianDay$*
M3	Pygmy blue	Number of vocalising whale groups	$log\{E(Y_{ij})\} = \beta_0 + \beta_1 SoundType + \beta_2 AM/PM + \beta_3 NumGroupsVisTracked + \beta_4 JulianDay + \beta_5 SoundType * A$

Table 3.4. Summary of biological, behavioural, temporal, anthropogenic, and environmental conditions influencing the vocalisation rate at the study site in Geographe Bay based on best fit GEE sub-models.

Global Model (M1)			
	Conditions	**Terms**	**M1**
Main effects	Biological	Species	🟧
		Num. groups visually tracked	⬜
	Behavioural	Sound type	🟧
	Temporal	Year	🟧
		Julian day	🟧
		AM/PM	⬜
	Anthropogenic	Vessel presence	⬜
	Environmental	Beaufort	⬜
		Glare	⬜
		Cloud cover	⬜
Interactions	Biological * Biological	Species * Num. groups visually tracked	🟧
	Biological * Behavioural	Species * Sound type	🟧
	Biological * Temporal	Species * AM/PM	⬜
		Species * Year	🟧
		Species * Julian day	⬜
	Biological * Anthropogenic	Species * Vessel presence	⬜
	Biological * Environmental	Species * Beaufort	⬜
		Species * Cloud cover	⬜
		Species * Glare	⬜

Species-Specific Models (Humpback Whale = M2, Pygmy Blue Whale = M3)				
	Conditions	**Terms**	**M2**	**M3**
Main effects	Biological	Num. groups visually tracked	🟧	🟧
	Behavioural	Sound type	🟧	🟧
	Temporal	Year	🟧	⬜
		Julian day	🟧	🟧
		AM/PM	⬜	⬜
	Anthropogenic	Vessel presence	⬜	⬜
	Environmental	Beaufort	⬜	⬜
		Glare	⬜	⬜
		Cloud cover	⬜	⬜
Interactions	Biological * Behavioural	Num. groups visually tracked * Sound type	🟧	⬛
	Biological * Temporal	Num. groups visually tracked * Year	🟧	⬛
		Num. groups visually tracked * AM/PM	⬜	⬜
		Num. groups visually tracked * Julian day	⬜	⬛
	Behavioural * Temporal	Sound type * AM/PM	⬜	🟧
		Sound type * Year	🟧	⬜
		Sound type * Julian day	⬜	⬜
	Behavioural * Anthropogenic	Sound type * Vessel presence	⬜	⬜
	Behavioural * Environmental	Sound type * Beaufort	⬜	⬜
		Sound type * Cloud cover	⬜	⬜
		Sound type * Glare	⬜	⬛
	Temporal * Anthropogenic	Julian day * Vessel presence	⬜	⬜
		AM/PM * Vessel presence	⬜	⬜
		Year * Vessel presence	⬜	⬛
	Temporal * Environmental	AM/PM * Beaufort	⬜	⬜
		AM/PM * Cloud cover	🟧	⬜
		AM/PM * Glare	⬜	⬜
		Julian day * Beaufort	⬜	⬜
		Julian day * Cloud cover	⬜	⬜
		Julian day * Glare	🟧	⬛
	Temporal*Temporal	Year * AM/PM	⬜	⬜
		Julian Day * AM/PM	⬜	⬜

🟧 Significant in model
⬜ No significant in model
⬛ Not included in model*

* Terms not included were those with sufficiently low sample size or under-dispersion for the model to converge.

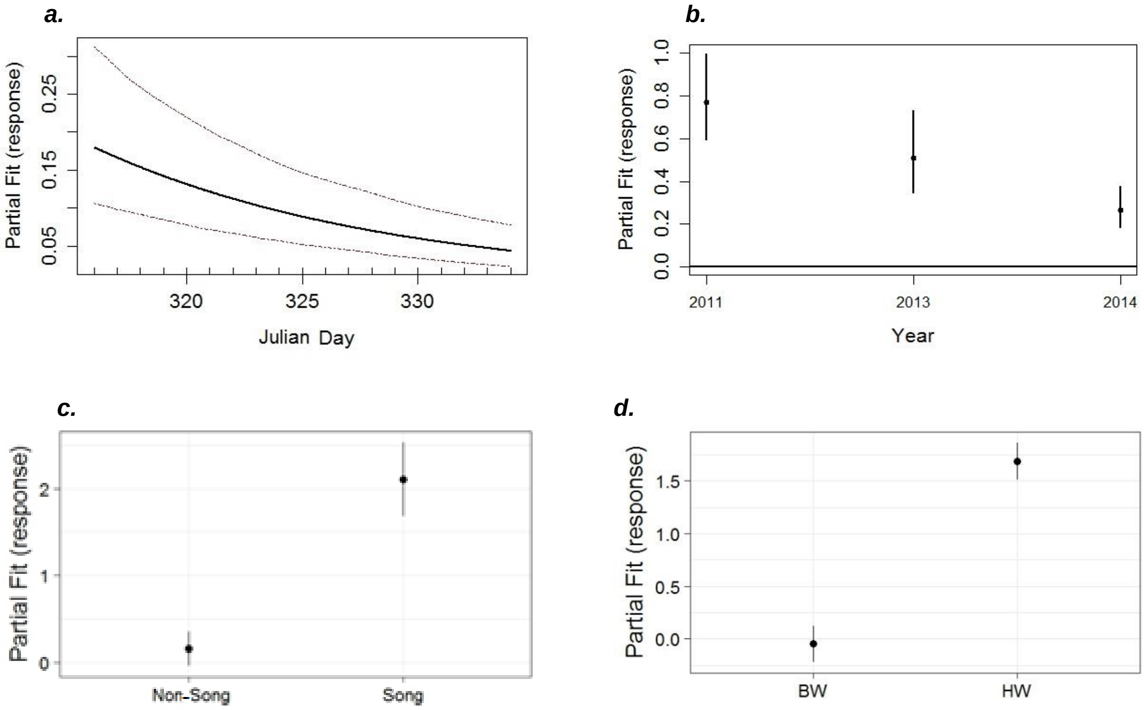


Figure 3.11. Partial plots of significant main effects influencing the number of vocalising baleen whale groups in Geographe Bay for the global GEE model (M1) which includes both baleen whale species (BW = pygmy blue whale and HW = humpback whale).

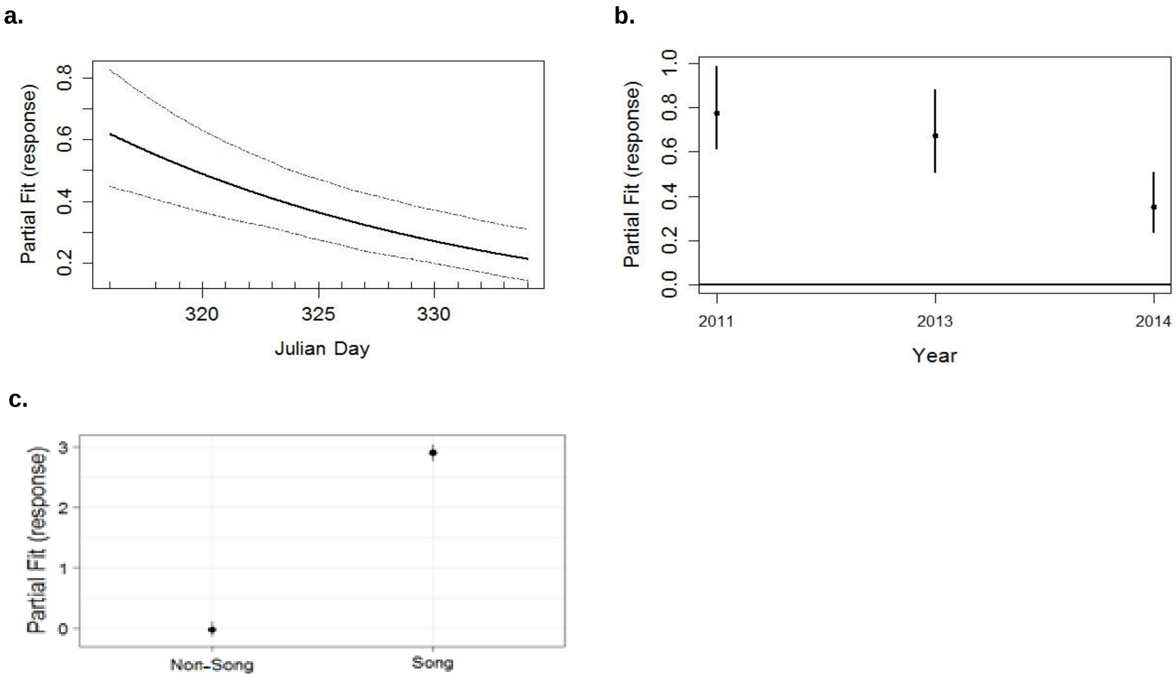


Figure 3.12. Partial plots of significant variables influencing the number of vocalising humpback whale groups in Geographe Bay based on GEE model (M2).

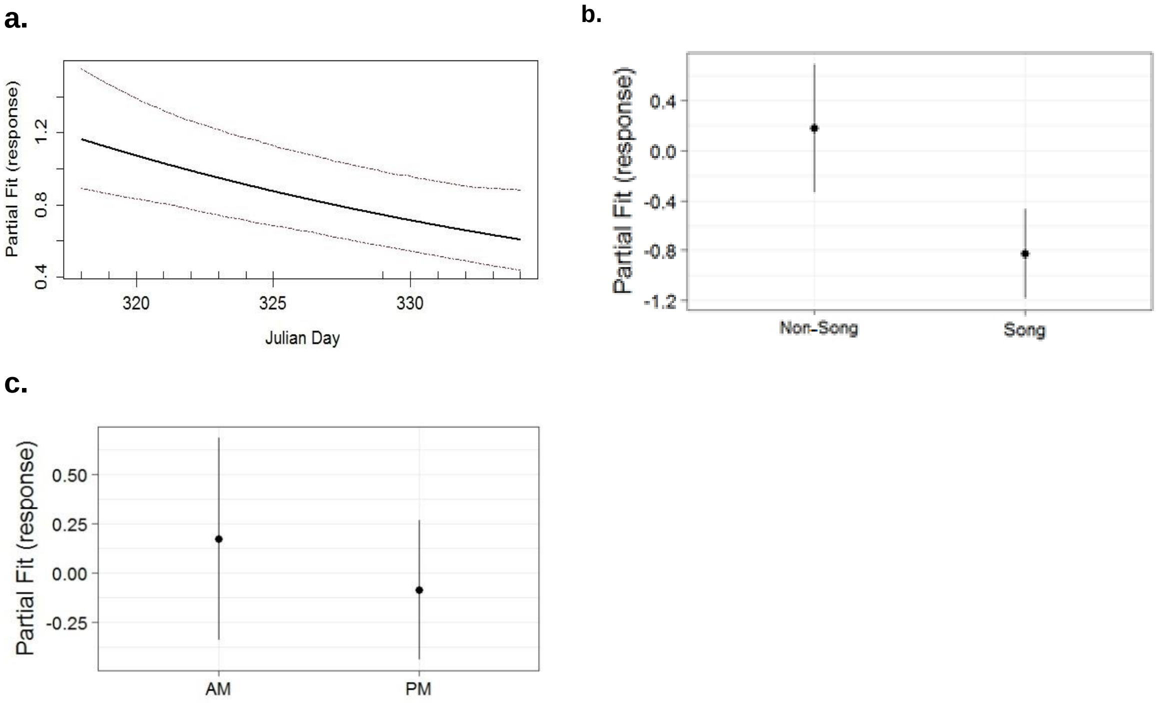


Figure 3.13. Partial plots of significant variables influencing the number of pygmy blue whale groups vocalising in Geographe Bay based on the GEE model (M3).

3.4. Discussion

3.4.1. Baleen whale vocalisation rates in relation to species and their population size

The vocalisation rate of baleen whales in Geographe Bay was different between species, with humpback whale groups vocalising at a much higher rate than pygmy blue whales. The disproportional vocalisation rates were likely linked to the large differences in the species' population sizes. The humpback whale population that migrates along the coast of Western Australia (Breeding Group D) was estimated to be between 26,000 and 31,000 individuals in 2008 (Hedley et al. 2011; Salgado Kent, Jenner et al. 2012) and increasing at ~11% per year (Salgado Kent, Jenner et al. 2012); while the population size of pygmy blue whales was estimated to be between 712 and 1,754 individuals between years 2000 - 2005 (Jenner et al. 2008) with an unknown trend (International Whaling Commission 2018). In addition, within Geographe Bay, the number of humpback whales recorded from visual observations seasonally (to the time of writing this paper) by a land-based volunteer community program (part of '*SouWEST';* souwest.org) has consistently far outnumbered blue whales sighted (Burton, pers. comm.). Also, the simultaneous visual observations in this study indicated that humpback whales were sighted approximately ten times more often than pygmy blue whales. These observations provide strong evidence for there being a larger number of humpback whale groups available to vocalise than pygmy blue whale groups in Geographe Bay during this study.

When comparing with other areas, including breeding grounds in Angola (Cerchio et al. 2014), the British Isles (Charif, Clapham & Clark 2001), Hawaii (Helweg & Herman 1994) and Brazil (Sousa-Lima & Clark 2008), a similar number of vocalising humpback whales per hour were reported here. Considering that vocalisation rates are usually higher on breeding grounds than along the migratory path, a lower rate was expected in Geographe Bay. This high rate may also be explained by the larger population size off Western Australia. All other humpback whale populations were estimated at less than 20,000 individuals in 2007 (International Whaling Commission 2018).

In comparison, the average vocalisation rate per sample was low for pygmy blue whales. Although there are no comparative studies between humpback and blue whales, previous reports have also estimated a low blue whale vocalisation rates in areas of the North Atlantic (Boisseau et al. 2008) and the North Pacific (Stafford et al. 2009). Despite this, the number of individuals vocalising was greater in the North Pacific with 2.06 animals per hour (Oleson, Calambokidis, Barlow, et al. 2007) than in Geographe Bay (with 0.5 vocalising groups per 13 or 23 minutes). The disparity between locations could be related to differences in the population sizes, but the estimates for any of the populations are highly uncertain and comparisons cannot be made (Branch 2007; Branch et al. 2007; McCauley & Jenner 2010, International Whaling Commission 2018). Alternatively, differences could be due to different subspecies occupying the study sites. Blue whales in the North Atlantic and North Pacific are *Balaenoptera musculus musculus,* while those travelling through Geographe Bay are *Balaenoptera musculus brevicauda*.

While vocalisation rates and numbers of visually tracked groups were consistent in that they were both high for humpbacks and low for pygmy blue whales, within species, the vocalisation rate was highly significant for the interaction between the number of visually tracked groups and sound type. For humpback whales the number of visually tracked whales was more strongly associated with non-song than song vocalisation rates. This result may be because non-song sounds can be produced by all whales with varied levels of visual detectability (Félix 2004; Stimpert et al. 2012), while song is only produced by males within the population. Furthermore, singers are often more difficult to detect visually because they can spend long periods of time submerged underwater.

In other studies, low correlations between the number of groups acoustically active and visually tracked have been reported (e.g. Helweg & Herman 1994; Cato et al. 2001; Kimura et al. 2009; Dunlop 2016). Previous studies have associated either song or non-song rates with visually detected groups; but have not combined both sound types. Consequently, these studies have related vocalisation rates of specific cohorts with numbers of all whales visually tracked, which could have resulted in a reduced correlation.

In contrast to humpback whales, pygmy blue whale vocalisation rates were negatively correlated with visually tracked groups. This result is likely due to the overall low number of vocalisations in samples. Previous studies found a high correlation between the number of blue whale groups observed and those acoustically detected especially for non-song sounds (Oleson, Calambokidis, Barlow et al. 2007) and in some studies, the number of singers was higher than the number of whales visually observed (Širović et al. 2004). In the latter study, the recorders were located at more than 100 m depth, and so the difference between acoustic and visual observations could be attributed to the larger acoustic than visual detection range. In this study, the areas were the same, thus results here may not be comparable with those of other studies.

3.4.2. Baleen whales vocalisation rates of song and non-song sounds

While the number of whales available to vocalise was likely the most important factor influencing vocalisation rates, differences in vocal behaviour between species also had an important role in observed variability. While some species of baleen whales have been reported to be more vocally active than others (Edds-Walton 1997) and use a variety of acoustical signals for communication (Sayigh 2014), vocal activity in any species depends upon behavioural context and communication strategies needed in specific situations and/or habitats.

In general, many animal species use sound for different activities including social interactions, communication, feeding or reproduction (Fichtel & Manser 2010). Because baleen whales migrate long distances, their acoustical behaviour is explained by a combination of habitat, behavioural and social contexts (e.g. ‘breeding grounds' where reproduction occurs, 'migratory routes' for travelling, and 'feeding grounds' for foraging, etc.). In this sense, almost all the available information is from either feeding or breeding grounds but there is not much knowledge about vocalisation rates and acoustic behaviour of baleen whales for transit areas such as Geographe Bay. Overall, sound type produced (whether song or non-song) varied widely between the species travelling through Geographe Bay; with higher rates of song observed for humpback whales when compared to those of pygmy blue whales. Considering that the habitat use for both species is similar, the differences observed in the rates may be explained by differences in the specific function of the sounds for each species.

Across many taxa, song has been associated with reproduction (Winn et al. 1973; Tyack 1981; Frankel et al. 1995) and intersexual and intrasexual advertisement (Watkins et al. 1981; Croll et al. 2002; Darling et al. 2006; McDonald et al. 2006; Smith et al. 2008). For example, in yellowthroats (*Geothlypis trichas*), song appears to be used mainly as advertisement of male territory and spacing (Bolus 2013); while for passerine birds, it is used for male-male advertising and male-female attraction (Sasahara et al. 2012). For humpback whales, song function has been associated with male advertising, female attraction as well as spacing (Seger et al. 2016; Noad et al. 2017), and is commonly vocalised on breeding grounds and at a lower rate on feeding grounds and during migration (Clark & Clapham 2004; Stimpert et al. 2012; Stanistreet et al. 2013).

Because there is no information on song vocalisation rates for the species on breeding grounds of Western Australia, it is not possible to define whether this stock follows the same pattern reported for other populations. However, in terms of function and, considering that the data was collected during the end of the southern migration, it is possible that humpback whales are using song to attract female, a last chance to mate before the end of the season, but also for spacing (home range establishment) and intrasexual advertising. Spatial separation between singers is important because it creates an 'acoustic' territory that potentially limits the male-male interaction, advertise the presence to others and maintain their access to females by reducing interference (Herman 2017). This is further supported by visual observations. Although humpback whale song is sung mostly by solitary animals (Payne et al. 1983; Frankel et al. 1995; Darling et al. 2006), singers can also escort females with calves probably to increase their reproductive success (Smith et al. 2008). In Geographe

Bay, groups formed by mother-calf and one additional adult (potential singer) were relatively uncommon (unpublished data).

In contrast to humpback whales, the song rate of pygmy blue whales was very low. Studies on blue whales suggested that song is used for reproductive purposes (Oleson, Wiggins & Hildebrand 2007) but as for most baleen whale species, there is still debate on whether song has an intersexual or intrasexual function, or a combination of both (Sayigh 2014). The low rate of song observed in Geographe Bay confirms that the area may not be used for reproduction and its low rate may be related to population density. Studies in terrestrial species showed that individual home ranges are reduced under increasing population density but individuals have a threshold to limit the contact among neighbours (Sanchez & Hudgens 2015). Under this scenario, song may act as a signal to advertise the presence of an individual, to define home range and to reduce male-male interactions. Because the population density of pygmy blue whales is low, it is possible that there are insufficient whales in the bay to require continuous singing for spacing purposes. Whether pygmy blue whale song is used for spacing or serves an alternative purpose cannot be established with the available data.

In comparison to song, non-song vocalisation rates were low for humpback whales and high for pygmy blue whales. Non-song sounds have been associated with feeding, foraging and social interactions (Tyack 1983; Mobley et al. 1988; Dunlop et al. 2008; Parks et al. 2011; Delarue et al. 2013). In the case of humpback whales, non-song sounds are vocalised by females, males, mother-calf and groups of adults (Dunlop et al. 2008; Zoidis et al. 2008). Thus, the likelihood of recording non-song sounds will be expected to be greater if a larger number of mother-calf pairs or adult groups are present. However, these group types often do not vocalise (Silber 1986) or vocalise less (Dunlop et al. 2008) than other group types and for shorter periods of time (Dunlop et al. 2008; Zoidis et al. 2008). Therefore, large numbers of mother-calf groups do not guarantee a higher non-song vocalisation rate, but perhaps increase the likelihood of at least one vocaliser being present.

Lower non-song rates are consistent with a cryptic and cohesive strategy reported for other cetaceans (e.g. right whales and porpoises) in transit. In these strategies, groups (mother-calf pairs in particular) only vocalise when the group is separated, vocalising then ceases after the group reunites (Norris et al. 1977; Parks et al. 2011). In this study, the low humpback whale non-song vocalisation rate may indicate that non-singing cohorts may follow this communication strategy to avoid predators similar to porpoises (Sayigh 2014) or terrestrial species like nocturnal monkeys (Bearder 2007). This explanation may be logical for Geographe Bay, as predators (e.g. white sharks, *Carcharodon carcharias,* or killer whales, *Orcinus orca*), are more likely to be observed during spring and early summer (McCauley et al. 2017), which coincides with the time of baleen whales migration. However, no predatory or interaction events have been reported for the species in the region in recent decades. Alternatively, it may be that mother-calf humpback pairs travelling through Geographe Bay limit their communication to avoid unwanted attention from male humpback whales.

The following non-song vocalisation rates have been reported for humpback whales: 1.05 whale^{-1} min^{-1} in migratory areas off the east coast of Australia (Dunlop et al. 2008), 43.1 vocalisations whale^{-1} hr^{-1} (± 55.52) on breeding grounds of Hawaii (Silber 1986), and 109 (65%) vocalising groups from a sample of 165 observed in Hawaii (Zoidis et al. 2008). The results of this study are lower than those reported in the literature. However, Dunlop et al. 2008 and Silber 1986 estimated the rates considering only the groups that were vocalising instead of considering all the groups present in the area (vocalising and not vocalising), as done in this study. Therefore, the differences between the rates reported here and those of other studies may be a representation of the differences in the dataset chosen for the analysis. Variances in the behavioural context and cohorts present in the areas (breeding grounds in Hawaii and migratory corridor during the peak period off eastern Australia), may also explain the higher rates in other studies. Previous research has found that groups with multiple adults have a higher non-song rate than mother-calf groups (Silber 1986; Dunlop et al. 2008). In Geographe Bay, the number of multiple adults was lower than that of mother-calf groups, which may also contribute to the lower non-song rate in Geographe Bay than in other migratory areas.

In contrast to humpback whales, pygmy blue whales had a greater non-song than song rate. Research on blue whales in the North Pacific found that certain calls were more frequent than others and had little variability within a season (Stafford et al. 2009). Other studies have also suggested that the ‘D’ call (a non-song sound similar to the ‘downsweep’ reported in Chapter 2) is vocalised by all individuals of the population and may be used during migration and foraging (Oleson, Wiggins & Hildebrand 2007). Geographe Bay is a transit area for the eastern Indian Ocean pygmy blue whale population (Salgado Kent et al. 2014), so the dominance of non-song calls (the ‘downsweep’ in particular), supports the use of these sounds during migration. The results obtained here also support the use of non-song sounds for communication or socialising reported for other species. For example, bottlenose dolphins can be highly vocally active while socializing and fin whales increase their vocal rate while travelling to be able to communicate over longer distances (Watkins 1981; Edds-Walton 1997).

Other researchers reported that blue whales are less likely to vocalise non-song sounds when whales are low in density and individuals are isolated (Boisseau et al. 2008). This study does not support this statement because many of the tracked groups were singletons. Although the inclusion of group type in the analysis may provide clarification on which group type had a higher rate, this was not included because it was not always possible to match vocalisation with group tracked (e.g. multiple groups observed simultaneously). However, the ‘downsweep’ rate increased when two or more groups of pygmy blue whales were concurrently tracked (Recalde Salas et al. 2014). This suggests that group density influences vocalisation rates per group.

Another explanation for the high non-song rate in pygmy blue whales may be predation. Previous studies have found that fin and beaked whales increase the vocal rate as an antipredator strategy (Aguilar de Soto et al. 2012; Delarue et al. 2013). As previously mentioned, natural predators of baleen whales (white sharks and killer whales) are sighted in the area at the time of baleen whale migration. Then, pygmy blue whales may use a similar strategy as fin and beaked whales to avoid predators. Additional studies are needed to understand the associated behaviour of non-song sound vocalisation of pygmy blue whales in the area.

It is important to note that this study did not aim to determine the function of humpback and blue whale song and non-song sounds. Further research is needed to verify the hypotheses proposed here for each species, which would benefit from a combination of acoustical tracking and visual observations. Finally, regardless of the function of different sound types, the fact that song is repeated over long periods of time relative to non-song sounds means that singers will likely have a higher probability of being acoustically detected than those vocalising non-song sounds. These differences in detectability may have resulted in biases in song and non-song vocalisation rates documented in this study.

3.4.3. Temporal patterns in vocalisation rates

Other key factors influencing vocalisation rates were year, Julian day, and time of day (morning or afternoon). Rates for both species depended upon Julian day, the rates in the morning and afternoon varied only for pygmy blue whales and variation among years was only observed for humpback whales.

Inter-seasonal variation (across years) in vocalisation rates of migratory species can reflect changes in distribution of animals in a region or the variability in the timing of the peak in migration (e.g. Helweg & Herman 1994; Norris et al. 1999; Charif et al 2001; Munger et al. 2008; Oleson, Calambokidis, Burgess et al. 2008; Morano et al. 2012; Gavrilov & McCauley 2013; Monnahan et al. 2014; Bort et al. 2015). The population cohorts migrating past a location will also influence the numbers of animals acoustically detected. For humpback whales, the order of migration from breeding to feeding grounds has been reported as: first the departure of juveniles from breeding grounds, followed by males and females without calves, and lastly by females with calves (Craig et al. 2003). Consequently, male singers will become less numerous as the migratory season progresses. Instead, females and calves will become increasingly available for detection towards the end of the season. Any shifts in the timing of migration of the different cohorts will affect the vocalisation rates of different sound types measured in a restricted sampling period (e.g. less song if there are fewer singers in the area).

For pygmy blue whales, there were no significant yearly effects. However, this was most likely due to the high variability and relatively low numbers of detections for the species. Studies in Australia and specifically Cape Leeuwin in the southwestern region of Western Australia reported changes in the number of blue whale vocalisations among seasons (Gavrilov & McCauley 2013; Tripovich et al. 2015). Similarly, variability in vocalisations among years was reported in the North Pacific (Stafford et al. 2009; Samaran et al. 2013; Shabangu et al. 2017). The difference between the results presented here and those from previous studies may be explained by the type of acoustical cue used in the analysis. Some studies reporting variation in the peak of migration based the analysis only on the song (e.g. Stafford et al. 2009; Gavrilov & McCauley 2013). However, because the song is generally vocalised by males (McDonald et al. 2006) the difference in the number of singers among years reflects differences in the number of males passing through the area but it does not necessary imply changes in the population. The use of all the available cues may explain the differences compared to other studies as by including all sound types all available individuals and not a specific gender or cohort will be counted.

This timing of migration of the different cohorts described above can also influence the intraseasonal variability of vocalisation rate. In this study, Julian day was one of the most significant factors influencing vocalisation rates, indicating a decline as the season progressed towards December. The results of this study are similar to those reported for blue whales in the North Pacific (Stafford et al. 2009; Samaran et al. 2013; Shabangu et al. 2017) and match the reported trend in numbers migrating through Geographe Bay with peaks in September/October for humpback whales and November for pygmy blue whales, and a steady decline over November - December (Burton, pers. comm.; Salgado Kent, Gavrilov et al. 2012; Salgado Kent et al. 2014). However, the results of this study contrast with studies for humpback whales in eastern Australia where the number of whales detected visually and acoustically did not vary within the same season (Noad et al. 2017). The length of the field season may explain the differences between this study and the results from eastern Australia. While this study analysed data from the peak to the end of the southern migration, the study by Noad et al. (2017) sampled the peak of southern migration and short periods before and after.

Time of day (diel pattern) is another temporal factor that influences the vocalisation rates of some species including humpback and pygmy blue whales. Diel patterns for humpback whales have been reported to vary among breeding grounds. For example, a higher vocalisation rate was observed at night in Mexico (Cholewiak 2008) but no diurnal pattern was reported in Massachusetts (Clark & Clapham 2004) and some of the Hawaiian Islands (Helweg & Herman 1994). This study did not find differences between morning and afternoon. 24-hr cycles, however, were not assessed and this study did not include night-time. It is recommended that future studies include night-time samples to obtain a better understanding of the diel pattern of the species in the area.

In contrast to humpback whales, pygmy blue whales showed a higher vocalisation rate of non-song sounds in the morning, although, the effect was weak and with large confidence intervals. The results are opposite to those of other studies that found more calls from midday to early evening (Tripovich et al. 2015), more singing activity during dawn and night (Stafford et al. 2005; Wiggins et al. 2005; Gavrilov & McCauley 2013) or higher rates of ‘D’ calls during sunset and dusk (Wiggins et al. 2005; Oleson,

Oleson, Calambokidis, Barlow, et al. 2007; Calambokidis, Burgess, et al. 2007; Melcón et al. 2012). In general, these patterns have been linked to changes in environmental conditions (Shabangu et al. 2017) and food availability or distribution (Stafford et al. 2005; Wiggins et al. 2005; Oleson, Wiggins & Hildebrand. 2007). The diel pattern observed in Geographe Bay is unlikely explained by food availability. While some foraging locations are relatively close to the study area (e.g. Perth Canyon; Double et al. 2014), feeding or foraging behaviour has not been observed in Geographe Bay. In addition, it is unlikely that the species would feed in Geographe Bay due to its low productivity (Pattiaratchi 2007). The effects observed in this study are most likely due to the relatively few vocalisations detected and communication strategies previously discussed.

3.4.4. Vocalisation rates in association with anthropogenic and environmental conditions

Anthropogenic noise can mask animal sounds when frequency ranges of both sources overlap (Erbe et al. 2016). In response, animals may stop vocalising, increase their repetition rate (McKenna 2011; Picciulin et al. 2012; Helble 2013) or change their diel patterns (Fuller et al. 2007). Noise can also affect the detectability of vocalisations when they are masked by anthropogenic noise and result in false negative observations. For example, 'D' calls were reported to be masked by loud infrasounds and detections improved under low noise conditions (Simard et al. 2008). With this evidence, some variation was expected in baleen whale vocalisation rates when vessel noise was present. However, the presence of this anthropogenic noise source did not affect the vocalisation rates of humpback and pygmy blue whales.

Findings in this study differ from studies with blue whales in Southern California (Melcón et al. 2012), humpback whales in Alaska (Doyle et al. 2008), beluga whales in Canada (Lesage et al. 1999) and brown meagre in the Mediterranean (Picciulin et al. 2012) all of which found an increase in the vocalisation rates. The differences between studies may be explained by differences in the level of information collected in the study or the amount of vessel traffic. In terms of level, previous research used individual vocal rates to evaluate the impact of noise on vocalisation rate, here we used number of groups and a population approach. Whether there are changes in individual vocalisation rate needs to be further evaluated. The present study is however, comparable in level of study (e.g. group level) to the research undertaken by Sousa-Lima et al. (2008) in Brazil. They reported a contrasting result to the present study in that a decrease in the number of groups (singers) was observed with an increase in vessel activity (Sousa-Lima et al. 2008). The differences in the results may be related to variations in the vessel activity between areas or differences in the analytical methods. While the study in Brazil considered the number of vessel events, here we used presence/absence of vessels which may explain the different results obtained. It is also important to consider that in Geographe Bay, whales are exposed to few recreational vessels for a short period of time (less than a minute) while in other areas the exposure might be longer and more intense. These differences should be considered when evaluating the impact of noise and comparing sites. The inclusion of vessel events as well as presence is recommended for future studies focusing on impact of vessel noise on vocalisation rates.

It is also possible that the impact of vessel noise on whales is related to the acoustical characteristics of the vocalisations instead of changes in vocal rates. For instance, individuals may have increased source levels of sounds or changed the frequencies used to compensate for vessel noise as reported for right whales in Massachusetts (Parks et al. 2011). Alternative behavioural responses and their implications for management need to be investigated to better understand impacts of noise on baleen whales in the area.

Ambient noise can also influence the behaviour of marine species. In general, oceans are very variable in ambient noise levels and species may naturally develop strategies to adapt to changes. Environmental conditions such as wind and current patterns have been linked to whale presence (e.g. Woodley & Gaskin 1996, Etnoyer et al. 2006, Doniol-Valcroze et al. 2007), and ambient noise can affect their acoustic behaviour (Dunlop et al. 2010). In this study wind-related environmental conditions, such as Beaufort, were not associated with the number of vocalizing whale groups. These results are similar to those observed in humpback whales off the east coast of Australia where non-song vocalisation rates did not change under different levels of ambient noise (Dunlop et al. 2010). However, other studies have suggested that high levels of wind increase the vocalisation rate in birds (Propped & Finch 2017) and humpback whales switch from underwater vocalisations to surface activity behaviours such as breaches or tail slaps (Dunlop et al. 2010).

While the main effects of environmental conditions were not significant in this study, interactions between glare-year, and cloud cover-AM/PM were unexpected significant effects. These were minor, however, and only occurred for the specific combinations of variables. To the best of the author's knowledge, there is no information available on these factors influencing vocal behaviour for any species. The most likely explanation is of a statistical nature and related to data collection.

Finally, in other studies, the most common environmental predictors influencing vocalisation rates in pygmy blue whales were sea surface temperature and productivity (Stafford et al. 2009; Shabangu et al. 2017). These conditions were not included in this study because the data available for the area were not on a similar temporal scale as the data collected. Future studies that include sea surface temperature in migratory corridors are recommended as its association with these habitats is poorly understood.

3.4.5. Model considerations and additional research

The data used in this chapter was limited by the absence of an acoustical array that would allow to track vocalising groups and match them with the one tracked visually. Therefore, a set of assumptions had to be made in order to combine both datasets. In consequence, some biases may impact the results.

One of the main assumptions when counting the number of groups vocalising is that all groups will have different SNR and this difference will allow us to differentiate them. Although for the majority of the data this was the case, there is the possibility of underestimating the number of groups when more than one are in the area of influence at a particular time. This is particularly important for humpback whale groups vocalising non-song sounds. In breeding grounds, mother-calf groups can be very vocally active, particularly when travelling alone (Zoidis et al. 2008). Considering that the most common group type in Geographe Bay is mother–calf and they usually are not escorted by other adult whales, it is possible that the vocal rate for non-song sounds is higher than reported here. Propagation models for the area suggest a range of approximately 3 km^2 for a high SNR, therefore, it is possible that the number of humpback whale groups vocalising non-song sounds is underestimated as more than two groups might produce sounds with SNRs at the same time. However, considering that groups will arrive and depart the area at different times and travel at different speeds (unpublished data), it is likely that most groups may be counted at least once. The differences in time of arrival and departure as well as speed of travel of each group, will reduce the likelihood of having similar SNR values, reducing but not eliminating the likelihood of missing vocalising groups in the counts. Acoustical tracking is recommended to improve the estimation of vocal rates and to determine whether multiple mother-calf groups vocalise at the same time in the area.

This is not the case for blue whales though. Visual observations show that one group of pygmy blue whale is seen in the area at the time and in the rare occasion that more than one group is present the distance between groups is sufficiently large to yield different SNR values. Furthermore, the matching between visual and acoustical count for this species was above 90%. Therefore, the likelihood of underestimating the number of vocalising groups is low for this species. In addition, acoustic propagation models for the area (Salgado-Kent et al. 2012) suggests that the SNR of pygmy blue whale vocalisations will significantly decrease within 1 km from the logger, therefore, groups with different SNR should be in an area of 2 km^2 at the same time to have similar SNR values which is very rare for the species.

Another consideration of the study is the variation in vocal rates between different group types (i.e. mother-calf, competitive groups, singers). Previous studies have suggested an increase in the vocalisation rates for groups with multiple adults or when there is surface activity (Silber 1986). These behavioural components may influence the likelihood of identifying more vocally active groups (e.g. competitive groups) over quieter groups (e.g. mother-calf). Therefore, it is suggested to study how vocalisations rates vary between different group types and to include this variability in further modelling.

3.5. Conclusions

A combination of biological, temporal and behavioural parameters including species, sound type, year, and season explain the variability in the vocalisation rate of baleen whales. This study points to the following associated population attributes as the most important drivers: the presence of animals, the demographic cohorts of whales present, and the behavioural and social contexts of their vocalisations. These attributes will affect: (i) whether the animals are available to vocalise; (ii) whether they will vocalise (given they are available), and (iii) the sound type produced (given they are available and vocalise).

Differences in the non-song vocalisation rate between species can be related to specific communication strategies for each species, humpback whales may follow a more cryptic pattern and pygmy blue whales a more vocally active. Differences for song rate on the other hand may be more related to differences in the reproductive strategy for each species.

The findings of this study suggest that in Geographe Bay, vocalisation rate can be used for long-term monitoring of the presence and migratory timing of the proportion of the population that visit the bay. Monitoring of all sound types including song and non-song sounds is highly recommended to increase detections. The use of song and non-song acoustical cues will limit biases associated with cohort and group-level vocal behaviour. Moreover, by monitoring all sound types, a good understanding of the acoustical ecology of baleen whales is achieved.

3.6. Supplementary material

3.6.1. Summary of GEE Model 1 (M1) and P values

Table 3.5. Model 1 (M1) outputs; including parameter estimates, standard errors (Std. Err), Wald estimates (W), and P-values (PR (>|W|)). M1 = Generalized Estimating Equations (GEE) with response metric = number of groups calling, both baleen whale species included.

Term	Estimate	Std Err	Wald	PR(>|W|)
(Intercept)	21.21	4.12	26.52	2.6e-07 ***
Species (HW)	1.56	0.36	18.52	1.7e-05 ***
Sound type song	-1.28	0.40	10.13	0.0014 **
Year 2011	1.43	0.40	12.63	0.0003 ***
Year 2013	0.42	0.57	0.55	0.4580
Year 2014	0.76	0.45	2.83	0.0922 •
Julian day	-0.07	0.01	31.40	2.1e-08 ***
Species * Sound type song	2.97	0.41	50.70	1.1e-12 ***
Species * Year. 2011	-1.81	0.40	20.62	5.6e-06 ***
Species * Year.2013	-1.11	0.47	5.38	0.0203 *
Species * Year.2014	-2.97	0.53	20.15	7.2e-06 ***
Species * Num. groups visually tracked (BW)	0.57	0.13	18.41	1.8e-05 ***
Species * Num. groups visually tracked (HW)	0.08	0.02	11.39	0.0007 ***
Estimated Scale Parameters (Intercept)	0.98	0.31		
Estimated Correlation Parameters (Alpha)	-0.03	0.02		

*Significance codes: *** = < 0.001, ** = < 0.01, * = <0.05, • = <0.1*

Table 3.6. Summary of P values for the best model explaining the number of vocally active groups in Geographe Bay. P-values were estimated using likelihood methods.

Variable	P value
Species	<0.0001
Sound type	<0.0001
Year	<0.0001
Julian day	<0.0001
Species * Sound type	<0.0001
Species * Year	<0.0001
Species* Num. groups visually tracked	<0.0001

3.6.2. Summary of GEE Model 2 (M2) and Model 3 (M3) and P values

Table 3.7. Model 2 (M2) outputs; including parameter estimates, standard errors (Std Err), Wald estimates (W), and P-values (PR (>|W|)). M1 = Generalized Estimating Equations (GEE) with response metric = number of groups vocalising, humpback whales included only.

Term	Estimate	Std Err	Wald	PR(>|W|)
(Intercept)	15.520	3.50	19.62	9.5e-06 ***
Sound type song	2.862	0.32	76.10	<2 e-16 ***
Year 2011	0.388	0.34	1.24	0.265
Year 2013	0.645	0.32	3.93	0.047 *
Year 2014	1.284	0.35	13.41	<0.001 ***
Num. groups visually tracked	0.262	0.05	19.40	1.1e-05 ***
Julian day	-0.054	0.01	24.34	8.1e-07 ***
Sound type song * Year 2011	-0.769	0.36	4.41	0.035 *
Sound type song * Year 2013	-1.389	0.37	13.63	<0.001 ***
Sound type song * Year 2014	-2.670	0.51	27.21	1.8e-07 ***
Sound type song * Num. groups visually tracked	-0.219	0.06	12.15	<0.001 ***
Year 2011 * Num. groups visually tracked	-0.068	0.05	1.42	0.233
Year 2013 * Num. groups visually tracked	-0.003	0.04	0.00	0.949
Year 2014 * Num. groups visually tracked	-0.470	0.13	11.40	<0.001 ***
Morning/Afternoon (AM) * Cloud cover	-0.071	0.02	9.96	0.001 **
Morning/Afternoon (PM) * Cloud cover	-0.003	0.02	0.02	0.898
Julian day * Glare (spline – 1 knot)	0.001	0.00	12.63	<0.01 **
Julian day * Glare (spline – 2 knots)	-0.000	0.00	1.47	0.225
Julian day * Glare (spline – 3 knots)	0.000	0.00	1.07	0.229
Estimated Scale Parameters (Intercept)	0.71	0.08		
Estimated Correlation Parameters (Alpha)	-0.18	0.05		

*Significance codes: *** = < 0.001, ** = < 0.01, * = <0.05, • = <0.1*

Table 3.8. Model 3 (M3) outputs; including parameter estimates, standard errors (Std Err), Wald estimates (W), and P-values (PR (>|W|)). M1 = Generalized Estimating Equations (GEE) with response metric = number of groups vocalising, pygmy blue whales included only.

Term	Estimate	Std Err	Wald	PR(>|W|)
(Intercept)	13.12	3.82	11.74	0.0006 ***
Sound type song	-0.63	0.38	2.73	0.0984 •
(AM/PM) PM	0.12	0.17	0.48	0.4903
Num. groups visually tracked	-0.34	0.15	4.63	0.0314 *
Julian day	-0.04	0.01	11.87	0.0005 ***
Sound type song * (AM/PM) PM	-2.15	0.64	11.33	0.0007 ***
Estimated Scale Parameters (Intercept)	0.75	0.44		
Estimated Correlation Parameters (Alpha)	-0.40	0.18		

*Significance codes: *** = < 0.001, ** = < 0.01, * = <0.05, • = <0.1*

Table 3.9.Summary of P-values for the best model explaining the number of vocalising humpback and pygmy blue whales modelled using a GEE framework. P-values were estimated using likelihood methods.

Term	**P values**	
	Humpback whales	**Pygmy blue whales**
Sound type	<0.0001	<0.0001
Year	<0.0001	Not significant
AM/PM	Not significant	0.0039
Num. groups visually tracked	0.0098	0.0235
Julian day	<0.0001	0.0020
Year * Sound type	<0.0001	Not significant
Sound type * Num. Groups visually tracked	0.0004	Not included
Sound type * AM/PM	Not significant	0.0007
Year * Num. groups visually tracked	0.0045	Not included
AM/PM * Cloud cover	0.0049	Not significant
Julian day * Glare (spline)	0.0048	Not significant

Chapter 4.

Can sound power be used as an indicator of relative density of baleen whales in a migratory corridor?

The aim of this chapter was to evaluate whether there is a relationship between sound levels and the numbers of visually and acoustically detected groups of humpback (*Megaptera novaeangliae*) and pygmy blue whales (*Balaenoptera musculus brevicauda*) migrating through Geographe Bay, Western Australia. Specifically, different sound level metrics and temporal scales were analysed. Data were analysed for each species independently using a Pearson correlation analysis. Correlation ranks were established using a Rule of Thumb. Results indicate higher correlation coefficients between sound levels and number of groups vocalising than between sound levels and number of visually tracked groups for both species. Correlations were greater when temporal autocorrelation and overlapping sources were included in the analysis. Differences between species were observed, with humpback whales showing higher correlation ranks than pygmy blue whales, likely because humpback whales are more vocal and abundant than pygmy blue whales.

4.1. Introduction

Passive acoustic monitoring (PAM) is a common tool for the documentation, analysis and monitoring of underwater marine soundscapes; including sound from anthropogenic activities, ocean weather, and marine fauna. Consequently, with rapidly improving access to, affordability of, and capability of recording hardware and software, large amounts of sound recordings in the oceans are being acquired.

Because many species of marine fauna may produce loud sounds, the information collected in underwater recordings includes the occurrence of different species. This data has been used to develop methods to estimate marine fauna relative abundance and density. The most common method is to count the number of vocalisations present in a sample (also termed cue counting), and then to adjust this value by individual vocalisation rate to obtain a density estimate (McDonald and Fox 1999; Gannon 2008; Marques et al. 2009; Marques et al. 2011; Ponce et al. 2012; Širović et al. 2015). Using cue counting presents limitations in that most models assume that all individuals have similar acoustical behaviour; thus, variability in cue rates and overlapping sounds produced by different individuals in recordings may result in biases (Gannon 2008). In addition, using vocalisations for cue counting requires a good understanding of the acoustical ecology and repertoire for the species of interest, which is not always available. Other methods involve counting the number of individuals or groups acoustically tracked with acoustic arrays and estimating their abundance with spatially explicit capture-recapture models (SECR, Dawson & Efford 2009; Marques et al. 2013). Although this method may be more accurate, it can be expensive as it requires multiple underwater recorders. Because of these limitations, many studies have used acoustic power to obtain abundance indices of marine species calling in an area (Au et al. 2000; Gedamke et al. 2007; Širović et al. 2015; Rowell et al. 2017). This approach has been used for fish, invertebrate and marine mammal species (Gannon 2008; Erbe et al. 2015; Rowell et al. 2017).

Because species presence patterns obtained from acoustical detections are similar to those of visual surveys, some authors have suggested that the power spectral density may be expected to increase with increasing population density (Au et al. 2000; Gedamke et al. 2017; Širović et al. 2015; Rowell et al. 2017). Thus, power spectral density has been used in many studies as a proxy for relative abundance (Širović et al. 2004; McCauley 2012; Rowell et al. 2017). Furthermore, power spectral density has provided information on seasonality, residency and migration patterns for different species including blue whales (Širović et al. 2004; Širović et al. 2015; Erbe et al. 2015), fin whales (Mellinger et al. 2014; Širović et al. 2015), humpback whales (Au et al. 2000; Erbe et al. 2015) and for fish aggregations (Rowell et al. 2017). While this is an invaluable tool for monitoring populations, the relationship between power spectral density (PSD) and relative abundance has had limited evaluation and its use for density estimation has only recently been under development (Martin et al. 2013; Rowell et al. 2017). Only a few studies have attempted to quantify their relationship (Helweg & Herman 1994; Rowell et al. 2012; Seger et al. 2016; Rowell et al. 2017), and there is little information on how the relationship may vary in different environmental or animal behavioural conditions (Gannon 2008). For example, a location has a constant number of whales, however, some individuals vocalise simultaneously at certain times or vocalise more often than others, then, a larger relative abundance indices might result at those times despite the same number of animals being present.

Studies that have quantitatively correlated PSD metrics with detections from visual surveys have indicated that the relationship varies with species and location. For instance, for humpback whales (*Megaptera novaeangliae*) in Hawaii, a positive correlation was reported between PSD metrics and the number of singers per sample (Helweg & Herman 1994). For red hind (*Epinephelus guttatus*), which is a species of fish, a positive linear relationship was observed between densities and mean band levels (Rowell et al. 2012). A positive linear relationship was also observed for another species of fish, the Gulf corvina (*Cynoscion othonopterus*); but only during the peak of the spawning season after high tide. At other times the relationship was variable and not always linear (Rowell et al. 2017). These studies used signal-to-noise ratio, mean band levels, and sound pressure levels as metrics. By testing the relationship of a range of acoustic metrics with visual detections of different baleen whale species, performance of metrics can be tested and inform the development of more accurate abundance and density models. In addition, understanding the influence of potential biases in abundance indices resulting from different recording schedules (on-off recording cycle) used in passive acoustic monitoring and the presence of noise from other sources will help guide the development of cost-effective protocols for monitoring the species in future years.

Here, we evaluate the relationship between sound levels and the numbers of visually and acoustically detected groups of humpback and pygmy blue whales (*Balaenoptera musculus brevicauda*) migrating through an embayment called Geographe Bay, in southwestern Australia, during the years 2010-2011 and 2013-2014. Signal-to-noise ratios (SNRs) were calculated as power level differences between frequency bands used by whales and adjacent noise bands (Erbe et al. 2015). Correlations were then tested for the mean power of the signal and a range of SNR metrics including the mean, maximum, and 75th percentiles for different recording schedules (13.3 minutes every 15 minutes and 23 minutes every 30 minutes) and different temporal scales (mean hourly and mean ~3 hr AM and PM periods). Because vessels and blue whales produce signals at similar frequencies as many sounds humpback whales produce, correlations for humpback whales also included analyses of: (i) all recordings including those with vessel noise and blue whale sounds, (ii) recordings excluding those with vessels noise, and (iii) recordings excluding those with vessel noise and blue whales sounds.

4.2. Methods

4.2.1. Study site

Geographe Bay is a relatively shallow bay of approximately 931 m^2, located in the southern region of Western Australia approximately 220 km from Perth (Figure 4.1). The bay extends from Cape Naturaliste in the west to the city of Bunbury in the northeast. The bay’s seabed has a maximum depth of approximately 40 m, a bottom gradient of 2 m km^{-1} sloping away from the coast, and a coast that is protected from a south-westerly swell by Cape Naturaliste (Oldham et al. 2010). The surrounding region is used for forestry and agriculture and is an important tourism destination with water-based activities including recreational fishing and whale-watching.

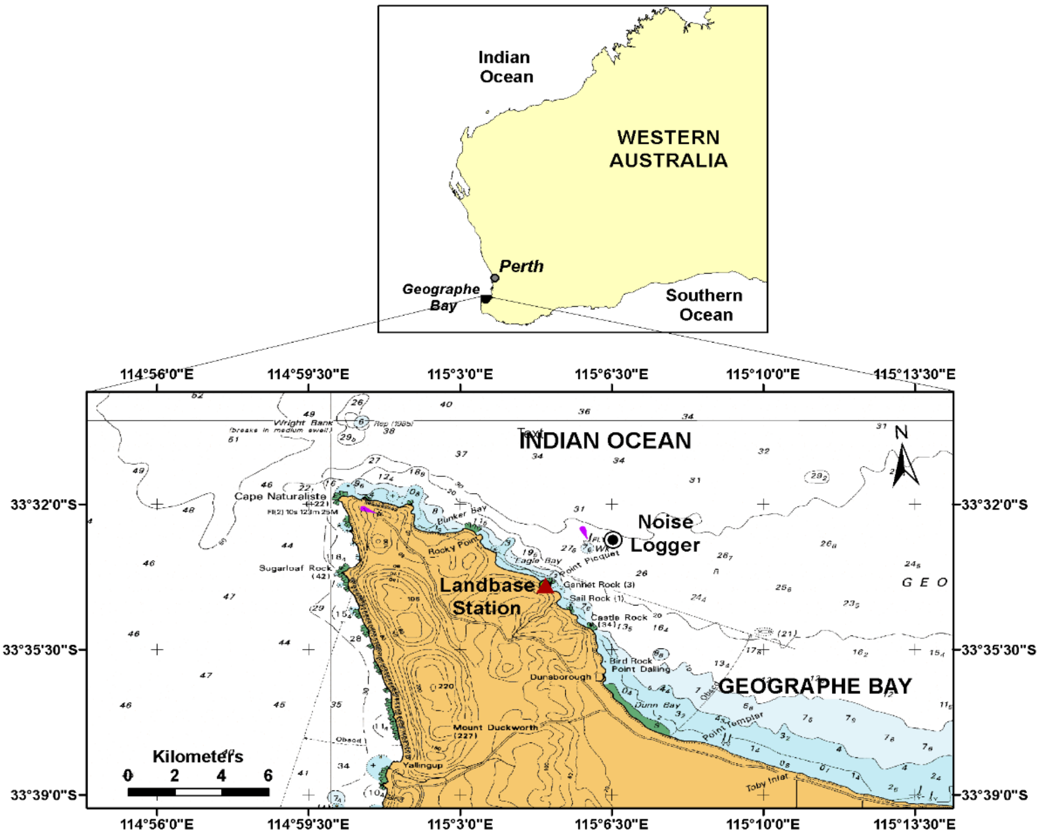


Figure 4.1. Land-based platform and acoustic recording site located in Geographe Bay, southwestern Australia.

Within this region, several baleen whale species migrate close to the coastline, including humpback and pygmy blue whales. Thus, Geographe Bay has ideal conditions to study these species. As a result, a long-term whale research program has been conducted in the area since 2010 and includes three simultaneous survey approaches: land, vessel and acoustics (Salgado Kent, Gavrilov et al. 2012; Recalde-Salas et al. 2014; Salgado Kent et al. 2014). The surveys include the collection of seasonal datasets on whale ecology, behaviour, acoustics and anthropogenic activities (vessel traffic).

Land-based visual surveys were carried out from Hill 50 in Meelup Regional Park (33° 36’ 7.48’’ S and 115° 4’ 46.55’’ E), located behind Pt. Piquet with an elevation of 50 m above Lowest Astronomical Tide (LAT). The land-based survey platform allows observations to be made of migrating whales and vessel transits through the bay. Seabed bottom-mounted acoustic recorders were deployed approximately 2 km north of Pt. Piquet. This study used land-based observations and acoustic recordings undertaken during November (just after the peak of the humpback whale and during the peak of the blue whale migration) in Geographe Bay, Western Australia, during 2010, 2011, 2013, and 2014 seasons.

4.2.2. Visual observations

Land-based visual observations were carried out using a theodolite GTS-603AF Electronic Total Station connected to a computer running the software Cyclops (2010–2011) or VADAR (2013-2014, Kniest, 2011). The theodolite set-up allowed whale groups to be tracked on a map displayed on the computer in real-time while travelling through the area. Observations were performed in shifts conducted daily between 7:30 and 17:30 with teams of three to four observers, and only during good weather conditions (wind <15 knots, Beaufort <5 and no rain). Information collected on each whale group included group size, composition (e.g. mother-calf pairs, mother-calf-escorts, groups of adults, single individuals, etc.), behavioural state (e.g. travelling, resting, or milling), and sighting cue from a comprehensive ethogram with a range of standard surface behaviours (e.g. blow, surfacing with only the back visible, fluke-up dive, fluke-down dive, breach, etc.; see Salgado Kent et al. 2014). In addition, the presence of other marine mammals (e.g. dolphins, seals) and vessels in the study area, and weather conditions were also recorded. Weather conditions included wind, rain, swell height and scales of Beaufort, glare and cloud cover (See chapters 3 and 5 for detailed methodology).

4.2.3. Acoustic recordings and processing

Acoustic recorders were deployed over the entire period in which land-based visual surveys were conducted. Recorders were built by the Centre for Marine Science and Technology (CMST; McCauley et al. 2017) and deployed at depths of 29 m (2010 and 2011), 32 m (2013) and 30 m (2014). The recorders rested on the seabed attached to a mooring with an acoustic release that allows easy retrieval (see McCauley et al. 2017 for full description and schematics of mooring configurations). These systems were programmed to record 13 minutes every 15 minutes in 2010 and 2011 and 23 minutes every 30 minutes in 2013 and 2014. The schedules varied because they were selected to fulfil the objectives of a separate study and were chosen based on battery duration and memory size of the recorders. Recorders were configured with a gain of 40 dB, sample rate of either 12,000 samples/s (2010 and 2011) and 6,000 samples/s (2013 and 2014) and anti-aliasing filter of 6 kHz for 2010 and 2011, and 2 kHz for 2013 and 2014. The frequency response of the system was calibrated before deployment and after recovery by inputting white noise of known level.

The calibrated time series were Fast-Fourier transformed in 1-s windows with 50% overlap yielding a frequency resolution of 1Hz. The resulting Power Spectral Density (PSD) matrices were used to .estimate band levels and undertake SNR calculations (see section 4.2.4). For manual counts of vocalisations, spectrograms of each sample were created using CHORUS (Gavrilov & Parsons 2014), a graphic user interface (GUI) developed in MATLAB (The MathWorks Inc.). Spectrograms were manually reviewed for sounds produced by pygmy blue and humpback whales. Only those sounds that were within an acoustical detection range of ~3 km of the recorder were documented. This range corresponded with signals that were easily distinguished from one another and could be easily attributed to different whales. Sounds produced within ~3 km range were identified based on the expected sound level of the signal based on transmission loss models previously fitted for Geographe Bay (Salgado Kent, Gavrilov et al. 2012). The ~3 km range was also used for visual observations of whales, thus detections from both sources were directly comparable (Chapter 3).

Whale vocalisations were identified using previously published non-song and song catalogues (e.g. Silber 1986; Rankin et al. 2005; Oleson, Calambokidis, Burgess et al. 2007; Dunlop et al. 2007; Gavrilov et al. 2011; Recalde-Salas et al. 2014; Chapter 2). In addition, humpback whale song was described for each season of the study (see Chapter 3 for methodology), and non-song vocalisations for both species were described for Geographe Bay (Recalde-Salas et al. 2014; Chapter 2). After identifying the type of vocalisation present within each recording, the number of groups was estimated per recording by manually counting overlapping signals (see Chapter 3 for detailed methodology). Signals from song and non-song sounds were assumed to belong to different groups as singers for both species have been reported to usually sing alone (Helweg & Herman 1994; Oleson, Calambokidis, Burgess et al. 2007). For humpback whale singers, the presence of different sound phrases in a recording combined with overlapping units was considered as an indicator of different groups producing the sounds (see Chapter 3 for details). The number of groups (including groups composed of one individual) vocalising was used as the metric in this study because it was not possible to distinguish between vocalising individuals within a group. Differences in signal-to-noise ratio between groups at different distances allow to attribute vocalisations to different groups. Counts of groups of whales vocalising within each recording were undertaken for each species (Chapter 3).

Because sounds produced by vessels and other species of marine fauna (i.e. fish, dolphins) can overlap with the frequency range of baleen whale sounds, their presence in the recording was noted. Information on presence of vessels was later used in the statistical analysis (Section 4.2.5).

Finally, the amount of time baleen whale vocalisations were present in each recording (here referred to as ‘sound duration’) was calculated for each species and then transformed into percentages. This percentage was estimated as follows: i) for recordings with few acoustical cues: by dividing the duration of all vocalisations recorded by the length of the recording and then multiplying by 100 and ii) for recordings with many acoustical cues: by subtracting the time without baleen whale vocalisations from the total length of the recording, then diving this number by the length of the recording and multiplying by 100. For example, in a 13 minutes recording we have 5 minutes without whale signals, then the percentage of the recording with baleen whale signals is 13 minutes – 5 minutes = 8 minutes, then 8 minutes / 13 minutes * 100 = 61.53%.

4.2.4. Sound level estimation

The sound level was calculated for each recording as a ratio of linear power between the frequency of interest (humpback or pygmy blue whale) and the adjacent frequency or noise band; and is referred to as the SNR here (Erbe et al. 2015). Ratios were then transformed into dB by applying $10*\log_{10}$. It is important to mention that SNR is usually calculated for the same frequency band and estimated as a ratio between the power of the signal(s) of interest recorded at a time (t) and the power of noise at adjacent times (before and/or after the signal) (Kuperman & Roux, 2014). Because the assumption for this analysis is that the number of individuals vocalising is correlated to the sound level of a specific frequency band (more individuals, higher SNR values) and the estimation is not for a specific time in the recording but rather the mean value; SNR here is defined as a ratio between adjacent bands instead of adjacent times. Given that a species can vocalise at multiple frequencies, the selection of the band of interest was as large as possible to maximise the power of the signal and the noise bands independently. Although, differences in the width of the noise and signal bands may favour one over the other (wider bands will produce higher levels as more frequencies are included), the absolute value will be normalized when estimating the mean SNR for the band.

The frequency bands corresponding to vocalisations for each species were defined by measuring the frequencies of maximum power (Max Freq, in Hz), for blue and humpback whale vocalisations using Raven Pro Software Version 1.5 (Bioacoustics

Research Program, 2014). The frequency bands corresponding to vessels were also defined in this way. For whales, vocalisations measured were those that make up song phrases and non-song (or social) sounds. A minimum of five replicates of each vocalisation type (song and non-song) was used for extracting the Max Freq so that means and variances could be calculated and variability estimated. The number of replicates measured was selected based on the minimum number of times a vocalisation was produced. Replicates were from different recordings and days to ensure that they were independent (i.e. produced by different groups).

The estimated minimum and maximum frequencies for all vocalisations were used to define the band for baleen whale sounds. The noise band was determined as those frequencies adjacent to the frequency bands defined for humpback or blue whales. However, during manual inspection some blue whale signals (downsweeps) and noise from vessels were observed to overlap with certain humpback whale sounds. In these cases, peak frequencies of these sources were included in the measured band interval for humpback whales. Consequently, three different datasets were used for comparisons between sound levels and number of humpback whale groups counted manually: i) all recordings, ii) only recordings without vessel noise, and iii) recordings without vessel noise or blue whales vocalisations. The frequency and noise band intervals used to calculate humpback and pygmy blue whale sound level metrics are summarised in Table 4.1.

Table 4.1. Summary of frequency and noise band used to calculate sound level metrics (SNRs). *Frequency bands higher than 600 Hz were not considered for noise analyses for pygmy blue whales because high frequency bands will not mask their vocalisations.

Species	**Frequency signal (*Psignal*)**	**Noise signal (*Pnoise*)**
Humpback whale	79-100 Hz 200-600 Hz 1000-1370 Hz	20-78 Hz 100-200 Hz 1371-3000 Hz
Blue whale	20-40 Hz 70-113 Hz	10-19 Hz 41-69 Hz 114-600 Hz*

Four different SNR estimates were included in this study; however, a base model was first implemented for comparative purposes. The base model consisted of the first metric (Eq. 4.1) and represented the mean power band level (BL) within the frequency band of the whale species of interest without adjusting for background noise in the recordings.

$$BL = 10 * log_{10}(mean(Psignal)) \qquad (Eq. 4.1)$$

In the equation, $Psignal$ is the power, and its mean was taken over the recording length (13 minutes in 2010, 2011 and 23 minutes in 2013, 2014).

The remainder of the metrics (Eq. 4.2 – 4.5) evaluated the SNR band level difference by adjusting for *Pnoise,* which was the power of the signal within adjacent frequency bands. The first of the SNR band level differences was SNR1, which represented the level of the mean ratio of signal power to noise power over the length of the recording (Eq. 4.2).

$$SNR1 = 10 * log_{10}(mean\left(\frac{Psignal}{Pnoise}\right)) \qquad (Eq. 4.2)$$

SNR2 was the mean of the instantaneous signal-to-noise ratio (dB) over the length of the recording (Eq. 4.3). SNR1 and SNR2 were included in this study so that results could be compared with previous studies that used SNR means in the analysis, but did not specify an equation.

$$SNR2 = mean\ (10 * log_{10}\ (Psignal) - 10 * log_{10}(Pnoise)) \qquad (Eq. 4.3)$$

Because blue whales have a low vocalisation rate and the above levels that were computed over the full duration of a recording might average out the vocalisation power, two additional SNR equations (SNR3 and SNR4) were included to concentrate on the peak times of vocalisation activity (Eq. 4.4 and Eq. 4.5). The calculation was also performed for humpback whales to reduce the influence of groups vocalising outside of the study area corresponding to manual acoustic and visual counts. SNR3 was the maximum of the level of instantaneous signal to noise power over the length of each recording.

$$SNR3 = Max\left(10 * log_{10}\left(\frac{Psignal}{Pnoise}\right)\right) \qquad (Eq. 4.4)$$

SNR4 was the 75th percentile of the level of instantaneous signal to noise power over the length of each recording. The 75th percentile corresponds to the level exceeded 25% of the time.

$$SNR4 = 75^{th}\ percentile\left(10 * log_{10}\left(\frac{Psignal}{Pnoise}\right)\right) \quad (Eq. 4.5)$$

4.2.5. Statistical analysis

Correlations between sound level metrics and manual acoustic and visual counts of whale groups were evaluated using the Pearson correlation coefficient. The correlation coefficient was used as a measure of the linear relationship between acoustic and visual counts as independent variables, and sound level metrics as dependent variables. Correlations were performed for: (i) hourly mean values and (ii) daily mean morning and afternoon values (morning and afternoon periods corresponded to continuous ~3 hour time-blocks of visual observations conducted), hereafter referred to as AM/PM. Hourly means were used for comparability with published data since this is the temporal scale that most have reported. However, because one of the main assumptions of the Pearson correlation test is independence of samples, residuals tests and autocorrelation plots were used to assess whether hourly values fit the assumptions. These tests showed that hourly means had some level of autocorrelation within 3-hour periods. Thus, data were also averaged into AM/PM blocks falling within the hours of 07.30 to 10:30 and 14:30 to 17:30, respectively. These AM/PM time block averages were also tested in correlations and compared to results from hourly means. For the purposes of this study, hourly and AM/PM blocks are referred to as the temporal scales of means of calculated metrics.

In this study, a sample size of 30 hourly or AM/PM time-block means was considered a minimum sample size to produce sufficient analytical power and reduce the likelihood of Type 1 and Type 2 errors. Pearson correlation coefficients ranging between -1 and 1 were evaluated, with values between -1 and <0 indicating a negative relationship, and between >0 and 1 a positive relationship. The degree of correlation was defined with five ranks established using the following Rule of Thumb (Hinkle et al. 1994): Negligible correlation (±0.0 - ±0.30), low correlation (±0.31 - ±0.50), moderate correlation (±0.51 – ±0.70), high correlation (±0.71 - ±0.90) and very high correlation (±0.90 - ±1.0). All analyses were undertaken using RStudio Ver. 1.0.136

(R Studio Team, 2016) and the R packages: car (Fox & Weisberg, 2011), cowplot (Wilke, 2017), doBy (Højsgaard 2006), ggplot2 (Wickham, 2009), lattice (Deepayan, 2008), lawstat (Gastwirth et al. 2017), mvtnorm (Genz et al. 2016) and reshape (Wickham, 2007).

To meet the objectives of this study for pygmy blue whales, a total of 66 Pearson correlation coefficients were calculated to test correlations between sound level metrics and visual counts, and 60 to test sound level metrics and acoustic counts of groups (Table 4.1). For humpback whales, 96 were calculated for visual and 90 for acoustic counts of groups. Analyses of humpback whales were more numerous since they included the three subsets of data (all recordings, recordings excluding vessel noise, and recordings excluding vessel noise and pygmy blue whale vocalisations). Analyses for pygmy blue whales did not have sufficient samples to conduct analyses for subsets that excluded vessels and humpback whale vocalisations. A correlation between the manually counted number of groups detected acoustically and number of groups detected visually was also undertaken for comparative purposes. Separate analyses were performed for the different recording schedules, and for all recording schedules together (Table 4.1.).

Table 4.2. Pearson correlation analyses carried out for blue whales (Recording schedule 1= 2010, 2011; Recording schedule 2 = 2013, 2014). All analyses were carried out with manual acoustic and visual counts of groups as independent variables

Survey years	Sound level metric	Variable units
2010-2011, 2013-2014	Band Level (BL; Eq. 1)	Mean hourly
		Mean daily AM/PM
	Mean Ratio SNR (SNR1; Eq 2)	Mean hourly
		Mean daily AM/PM
	Mean SNR (SNR2; Eq 3)	Mean hourly
		Mean daily AM/PM
	Max SNR (SNR3; Eq 4)	Mean hourly
		Mean daily AM/PM
	75th Percentile SNR (SNR4; Eq.5)	Mean hourly
		Mean daily AM/PM
2010-2011 (Recording schedule 1)	Band Level (BL; Eq. 1)	Mean hourly
		Mean daily AM/PM
	Mean Ratio SNR (SNR1; Eq 2)	Mean hourly
		Mean daily AM/PM
	Mean SNR (SNR2; Eq 3)	Mean hourly
		Mean daily AM/PM
	Max SNR (SNR3; Eq 4)	Mean hourly
		Mean daily AM/PM
	75th Percentile SNR (SNR4; Eq.5)	Mean hourly

		Mean daily AM/PM
2013-2014 (Recording schedule 2)	Band Level (BL; Eq. 1)	Mean hourly
		Mean daily AM/PM
	Mean Ratio SNR (SNR1; Eq 2)	Mean hourly
		Mean daily AM/PM
	Mean SNR (SNR2; Eq 3)	Mean hourly
		Mean daily AM/PM
	Max SNR (SNR3; Eq 4)	Mean hourly
		Mean daily AM/PM
	75th Percentile SNR (SNR4; Eq.5)	Mean hourly
		Mean daily AM/PM

4.3. Results

4.3.1. Effort and general means

A total of 238.58 hours of visual observations and 165.77 hours of acoustic recordings (614 recordings) were included in analyses. Of the acoustic recordings, 77.1 hours (347 recordings) were from 2010 and 2011 (schedule 1) and 88.67 hours (266 recordings were from 2013-2014 (schedule 2) (Table 4.2).

Humpback whales were detected in 81.56% of recordings (438) and pygmy blue whales in 19.62% (105). An average of 2.00 vocalising humpback whale groups (95% Confidence Interval (CI) = 1.877-2.13, Standard Deviation (SD) = 1.51, 95%) and 0.27 pygmy blue whale groups (CI = 0.22-0.31, SD = 0.57, 95%) were estimated per recording. Simultaneous visual observations resulted in an average of 1.6 humpback whale (CI = 1.48-1.73, SD = 1.46, 95%) and 0.12 blue whale (CI = 0.09-0.16, SD = 0.39, 95%) groups detected at the time of each acoustic recording.

In general, vessels were present in over 50% of the recordings; 50.14% for schedule 1 and 62.03% for schedule 2 recordings. Overall, pygmy blue and humpback whales were present in the same recording on 6.51% of occasions; with a breakdown of 5.76% in schedule 1 and 7.51% in schedule 2 recordings. Consequently, the data subset that excluded vessel noise consisted of 44% of the recordings for analyses of all years together, 49% for years having schedule 1 recordings (2010-2011), and 37% for years having schedule 2 recordings (2013-2014). The data subset that excluded vessels and pygmy blue whales consisted of 38%, 44% and 30% of the total recordings collected for analyses including all years, schedule 1 recordings (2010-2011) and schedule 2 recordings (2013-2014), respectively.

Table 4.3. Number of recordings for each data subset and temporal parameters used. Analyses with data subsets of no vessels/blue whales were only performed for humpback whales.

Variable parameters used	Data subset		
	All recordings	No vessel noise	No vessel noise or blue whale vocalisations
	All years (2010-2011, 2013-2014)		
Hourly Means	282	162	144
AM/PM Means	83	67	61
	schedule 1 (2010-2011)		
Hourly Means	130	83	80
AM/PM Means	40	31	30
	schedule 2 (2013-2014)		
Hourly Means	151	79	64
AM/PM Means	43	36	31

Based on the duration of vocalisations present in the spectrograms, humpback whale vocalisations occurred on average during 55.13% of each recording (SD = 38.73, CI = 51.85-8.41). Variability was observed between the different recording schedules used in different years. On average, humpback whale vocalisations were present for a greater percentage of time in schedule 1 recordings than in schedule 2 (schedule 1: ẋ = 70.28%, SD = 34.04, CI = 67.09-73.46; schedule 2: ẋ = 34.28%, SD = 34.94, CI= 30.43-38.11). Song occurred over a greater percentage of time than non-song (song: ẋ = 53.89%, SD = 39.38, CI = 50.55-57.23; non-song: ẋ = 1.31%, SD = 4.54, CI = 0.922-1.69), and it was present in more recordings (song only = 331 recordings; non-song only = 45 recordings; song and non-song occurring in the same recording = 119 recordings). For pygmy blue whales, vocalisations occurred on average 3.87% of the duration of recordings (SD = 15.52, CI = 2.55-5.19). No variability in the percentage of the recordings in which pygmy blue whale vocalisations occurred in were observed between recording schedules (schedule 1: ẋ = 5.27%, SD = 18.25, CI = 3.55-6.98; schedule 2: ẋ = 1.94%, SD =10.45 , CI = 0.79-3.09; Figure 4.2). Similar to humpback whales, blue whale song occurred over greater percentages of the recording duration than non-song sounds (non-song: ẋ =1.07 %, SD = 5.93, CI = 0.69-1.45; song: ẋ = 2.80%, SD = 14.46, CI = 1.57-4.025), but non-song vocalisations were present in more recordings (song = 19 recordings; non-song = 100 recordings; song and non-song in the same recording = 9 samples).

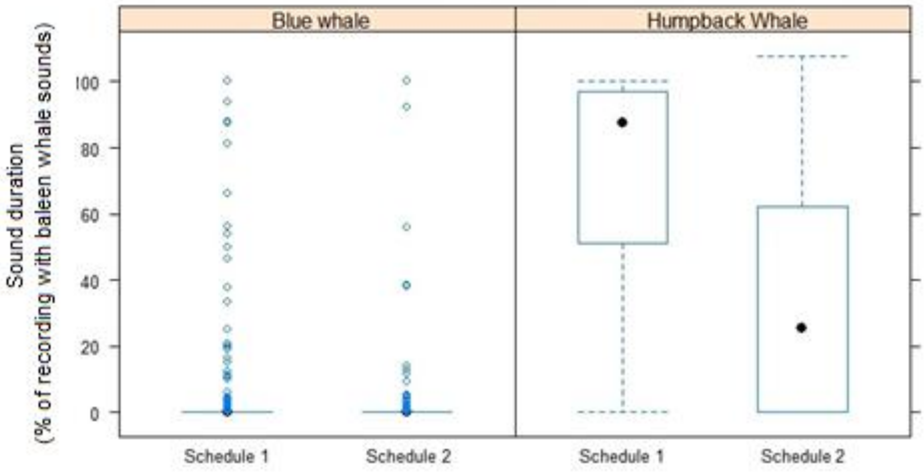


Figure 4.2. Boxplots of humpback and pygmy blue whale sound duration for recordings made using schedule 1 in 2010-2011 and schedule 2 in 2013-2014 in Geographe Bay, Western Australia.

4.3.2. Correlations between sound level metrics and counts of vocalising and visually tracked humpback whale groups

The correlation coefficients ranged between negligible to highly correlated, depending on the temporal scale used (i.e. mean over recordings per hour and mean per AM/PM), sound level metric and data subset used (Table 4.3). In general, a higher correlation was observed between sound level metrics and the number of vocalising humpback whale groups manually counted than for sound level metrics and the number of humpback whale groups visually tracked (Table 4.3, Figure 4.3).

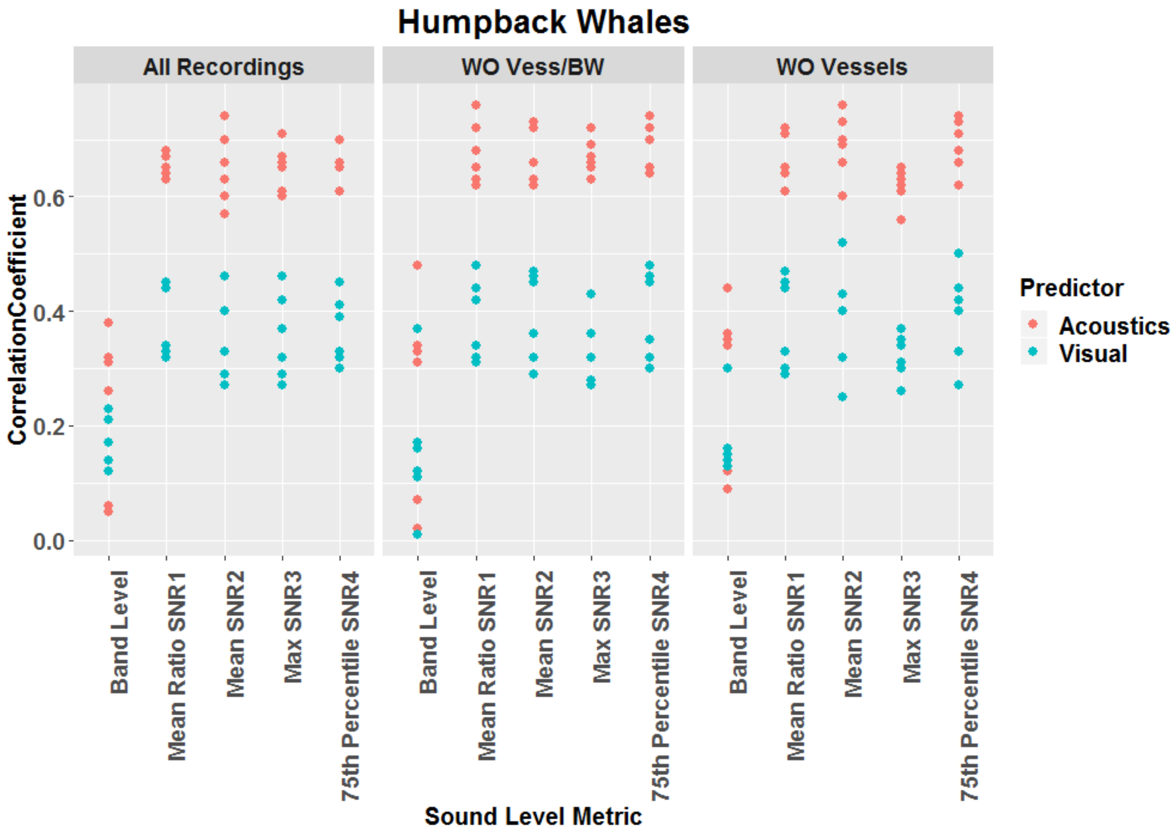


Figure 4.3. Comparison of sound level metric and correlation coefficient for visual and acoustic counts of humpback whale groups. Plots are presented for the following scenarios for comparative purposes: all recordings, recordings without vessel noise and blue whale sounds (WO vessels/BW), recordings without vessel noise (WO vessels).

Correlation coefficients for sound level metric and number of vocalising humpback whale groups ranged between 0.02 and 0.68 for mean hourly and between 0.04 and 0.76 for mean AM/PM (Table 4.3.; see supplementary material 4.6.1 for full statistical results). The highest coefficients were for SNR2 using means AM/PM and the data subset that excluded records with vessel noise (r = 0.76); and SNR1 and the number of vocalising groups per AM/PM period using the data subset that excluded records with vessel noise and pygmy blue whale vocalisations (r= 0.76). The lowest correlation ranks (negligible and low) were from relationships with BL regardless of the recording schedule and data subset used (Figure 4.4).

Table 4.4. Pearson coefficients for correlations between humpback whale sound level metrics and counts of whale groups. Sch1: schedule 1 (2010 – 2011), Sch2: schedule 2 (2013-2014). Note: Test statistic, 95% Confidence intervals and p-values are in Supplementary material 4.6.1.

Data subset	**Variable parameters used**	**Sound level metric**	**Humpback whales**					
			Level of correlation with acoustic counts			**Level of correlation with visual counts**		
			Sch1	**Sch2**	**Combined schedules**	**Sch1**	**Sch2**	**Combined schedules**
All Recordings	Hourly	Band Level	0.26	0.06	0.32	0.23	0.12	0.14
		Mean Ratio SNR1	0.63	0.64	0.65	0.33	0.34	0.32
		Mean SNR2	0.66	0.57	0.63	0.33	0.27	0.29
		Max SNR3	0.61	0.67	0.65	0.27	0.32	0.29
		75th Percentile SNR4	0.66	0.61	0.66	0.33	0.32	0.30
	AM/PM	Band Level	0.31	0.05	0.38	0.23	0.17	0.21
		Mean Ratio SNR1	0.67	0.68	0.65	0.44	0.45	0.44
		Mean SNR2	0.74	0.60	0.70	0.46	0.33	0.40
		Max SNR3	0.60	0.71	0.66	0.37	0.46	0.42
		75th Percentile SNR4	0.70	0.65	0.70	0.45	0.39	0.41
Recordings without vessel noise	Hourly	Band Level	0.34	0.09	0.35	0.15	0.15	0.13
		Mean Ratio SNR1	0.65	0.61	0.64	0.30	0.29	0.33
		Mean SNR2	0.69	0.60	0.66	0.40	0.25	0.32
		Max SNR3	0.65	0.56	0.61	0.35	0.26	0.30
		75th Percentile SNR4	0.68	0.62	0.66	0.40	0.27	0.33
	AM/PM	Band Level	0.44	0.12	0.36	0.30	0.14	0.16
		Mean Ratio SNR1	0.71	0.72	0.72	0.47	0.45	0.44
		Mean SNR2	0.76	0.70	0.73	0.52	0.40	0.43
		Max SNR3	0.64	0.62	0.63	0.31	0.37	0.34
		75th Percentile SNR4	0.74	0.71	0.73	0.50	0.42	0.44
Recordings without vessel noise & blue whale vocalisations	Hourly	Band Level	0.33	0.02	0.31	0.16	0.11	0.12
		Mean Ratio SNR1	0.62	0.65	0.63	0.34	0.31	0.32
		Mean SNR2	0.66	0.62	0.63	0.36	0.29	0.32
		Max SNR3	0.65	0.67	0.66	0.36	0.28	0.32
		75th Percentile SNR4	0.65	0.64	0.64	0.35	0.30	0.32
	AM/PM	Band Level	0.48	0.07	0.34	0.37	0.01	0.17
		Mean Ratio SNR1	0.68	0.76	0.72	0.42	0.48	0.44
		Mean SNR2	0.73	0.72	0.73	0.47	0.46	0.45
		Max SNR3	0.63	0.72	0.69	0.27	0.43	0.36
		75th Percentile SNR4	0.70	0.74	0.72	0.45	0.48	0.46

⬛	**Negligible correlation (±0.30 - ±0.30)**
⬜	**Low correlation (±0.31 - ±0.50)**
▨	**Moderately correlated (±0.51 – ±0.70)**
🟧	**Highly correlated (±0.71 - ±0.90)**
🟥	**Very highly correlated (±0.91 - ±1.0).**

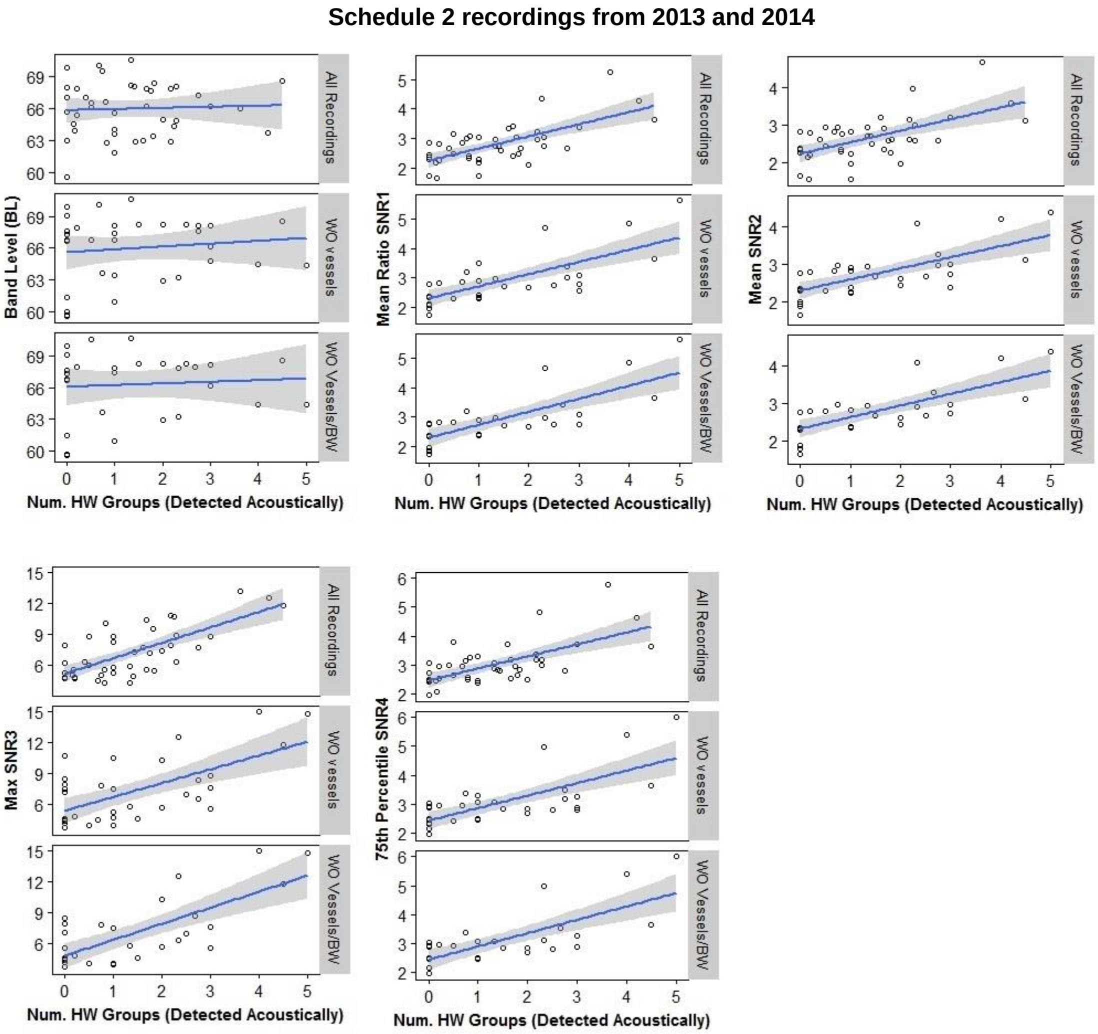


Figure 4.4. Scatterplots of mean sound level metrics vs. numbers of acoustically detected groups of humpback whales per AM/PM period in Geographe Bay for schedule 2 recordings. WO = recordings without vessel noise, WO vessels/BW = recordings without vessel noise and blue whale sounds.

Similar to the relationship between sound metric and number of vocalising groups counted per hour, higher correlation ranks resulted from the mean sound level metrics and the number of humpback whale groups visually counted per AM/PM period (Table 4.3, see supplementary material 4.6.3 for full statistical results). However, lower correlation rankings resulted regardless of the sound level metric or data subset used. A moderate correlation rank (r = 0.52) was obtained only once from the mean SNR2 per AM/PM using schedule 1 recordings and the data subset that excluded vessel noise (Figure 4.5). A low correlation rank was observed for all the other sound level metrics and recording schedules (Table 4.3).

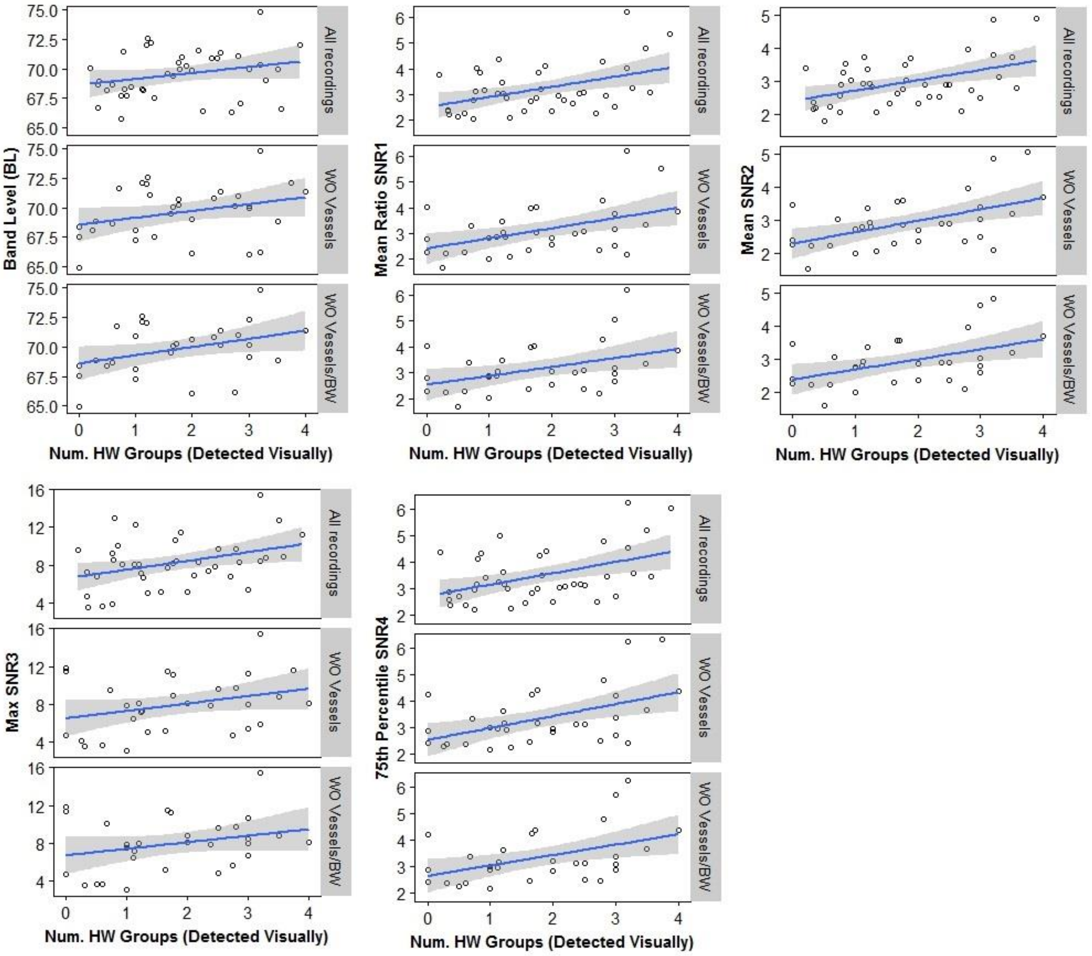


Figure 4.5. Scatterplots of mean sound level metrics vs. number of visually detected groups of humpback whales per AM/PM in Geographe Bay for schedule 1 recordings in 2011-2012. WO = recordings without vessel noise, WO vessels/BW = recordings without vessel noise and blue whale sounds.

In general, coefficients for Schedules 1 and 2 varied depending upon the metric, whether recordings had noise from boats and blue whales in them, and between schedules. The most consistent patterns between Schedules 1 and 2 were for recordings without vessel noise. Coefficients were consistently greater for Schedule 1 (2010 – 2011) than for Schedule 2 (2013 – 2014) regardless of the metric used (Table 4.3), but a clear pattern was not observed (Figure 4.6).

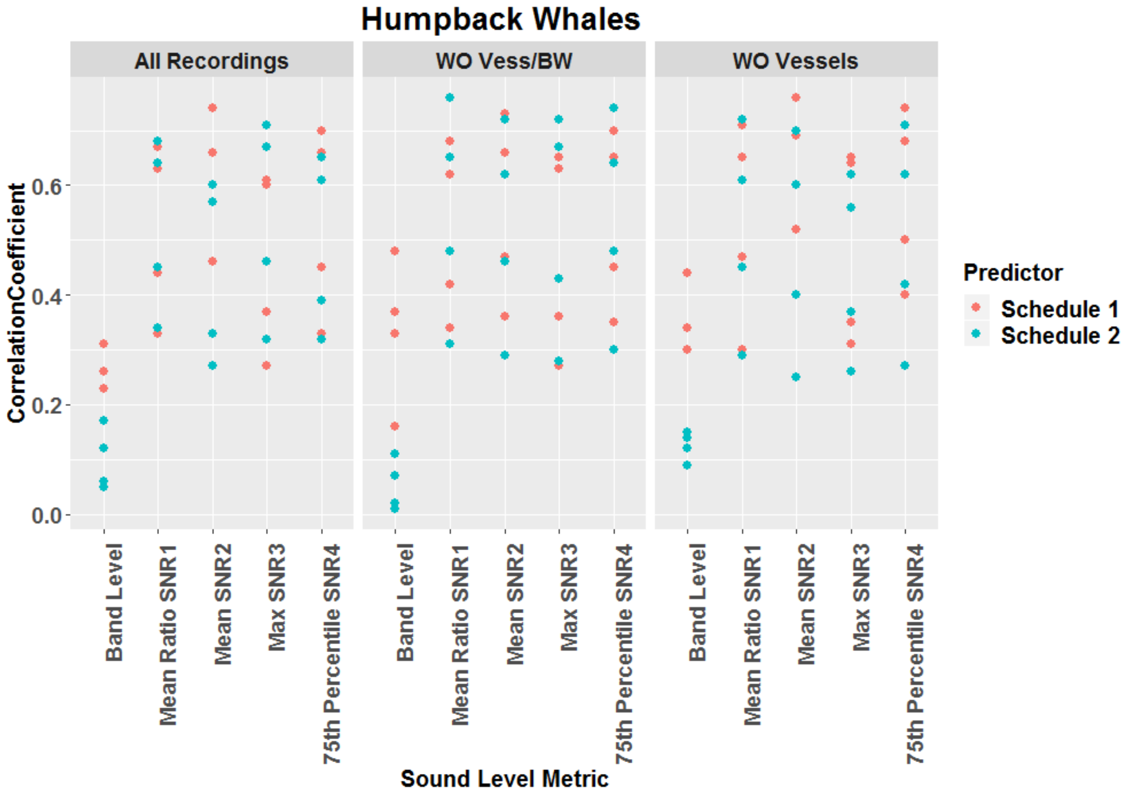


Figure 4.6. Correlation coefficients resulting from correlations between different sound level metrics and acoustic counts of humpback whales for recording Schedules 1 and 2. Plots are presented for the following scenarios for comparative purposes: All recordings, recordings without vessel noise and blue whale sounds (WO vessels/BW), recordings without vessel noise (WO Vessels).

4.3.3. Correlations between sound level metrics and counts of vocalising and visually tracked pygmy blue whale groups

Similar to humpback whales, a higher correlation was observed between sound level metrics and the number of vocalising blue whale groups manually counted than for sound level metrics and the number of blue whale groups visually tracked (Table 4.4, Figure 4.7, see supplementary material 4.6.2 and 4.6.3 for full statistical results). Most correlations for pygmy blue whales fell within the negligible correlation rank for most sound level metrics (Table 4.4).

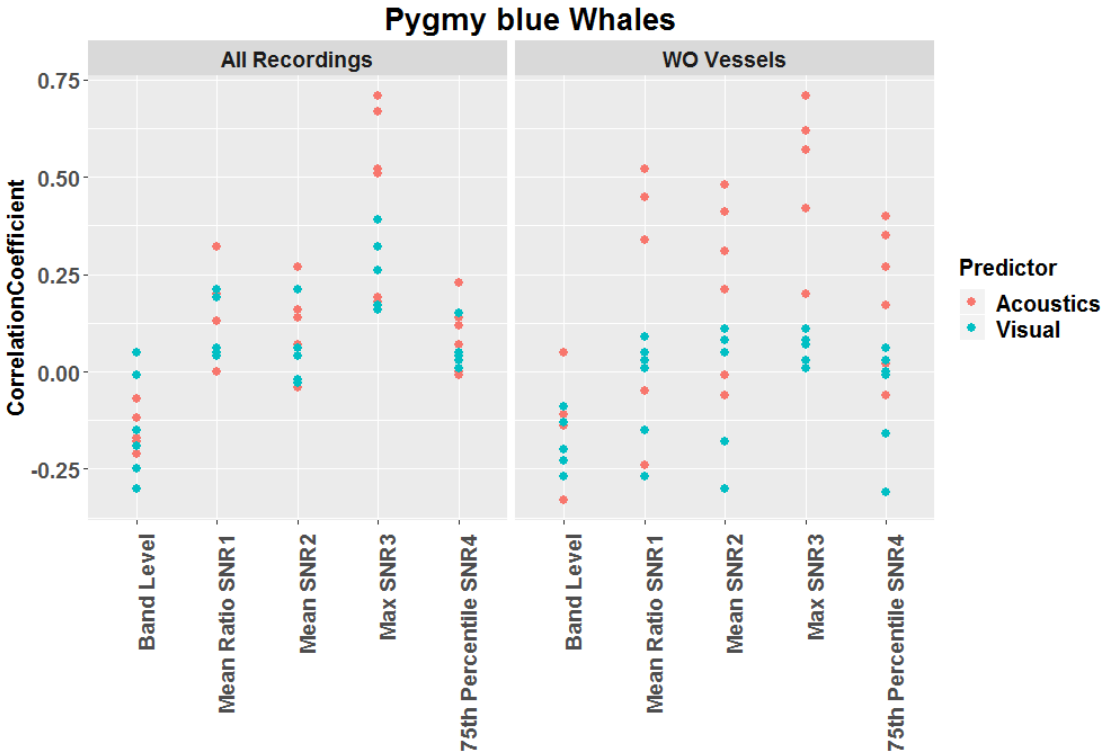


Figure 4.7. Correlation coefficients resulting from correlations between different sound level metrics and acoustics and visuals counts of pygmy blue whale groups. Plots are presented for the following scenarios for comparative purposes: all recordings, recordings without vessel noise (WO vessels).

Table 4.5. Pearson coefficients for correlations between pygmy blue whale sound level metrics and counts of whale groups. Sch1: Schedule 1 (2010 – 2011), Sch2: Schedule 2 (2013-2014). Note: Test statistic, 95% Confidence intervals and p-values are in Supplementary material 4.6.2.

Dataset attributes	**Temporal Scale of mean counts**	**SNR Metric**	**Blue whales**					
			Level of Correlation with Acoustic Counts			**Level of Correlation with Visual Counts**		
			Sch1	**Sch2**	**Combined schedules**	**Sch1**	**Sch2**	**Combined schedules**
All Recordings	Hourly	Band Level	-0.17	-0.07	-0.12	**0.05**	-0.01	**-0.15**
		Mean Ratio SNR1	0.00	0.21	0.13		0.04	0.06
		Mean SNR2	-0.04	0.14	0.07	-0.03	0.04	0.06
		Max SNR3	0.19	0.67	0.51	**0.17**	0.17	**0.16**
		75th Percentile SNR4	-0.00	0.12	0.07	0.03	0.01	0.04
	AMPM	Band Level	-0.21	-0.18	-0.18	-0.19	**-0.25**	**-0.30**
		Mean Ratio SNR1	0.05	0.32	0.20	0.05	**0.21**	**0.19**
		Mean SNR2	-0.04	0.27	0.16	-0.02	**0.21**	**0.21**
		Max SNR3	0.18	0.71	0.52	**0.26**	**0.39**	**0.32**
		75th Percentile SNR4	-0.01	0.23	0.14	0.05	**0.15**	**0.15**
Recordings without vessel noise	Hourly	Band Level	-0.20	0.05	-0.11	-0.09	**-0.09**	-0.20
		Mean Ratio SNR1	-0.05	0.45	-0.24	**-0.15**	**0.09**	**0.05**
		Mean SNR2	-0.01	0.41	0.21	**-0.18**	**0.11**	**0.08**
		Max SNR3	0.11	0.62	0.42	0.03	**0.11**	0.07
		75th Percentile SNR4	-0.06	0.35	0.17	**-0.16**	**0.06**	**0.03**
	AMPM	Band Level	-0.33	0.05	-0.14	**-0.27**	-0.13	-0.23
		Mean Ratio SNR1	-0.27	0.52	0.34	**-0.27**	0.01	0.03
		Mean SNR2	-0.06	0.48	0.31	**-0.30**	0.05	0.08
		Max SNR3	0.20	0.71	0.57	0.01	0.08	0.08
		75th Percentile SNR4	0.02	0.40	0.27	**-0.31**	-0.01	0.00

⬛ **Negligible correlation (±0.30 - ±0.30)**
⬜ **Low correlation (±0.31 - ±0.50)**
🟧 **Moderately correlated (±0.51 – ±0.70)**
🟫 **Highly correlated (±0.71 - ±0.90)**
🟥 **Very highly correlated (±0.91 - ±1.0).**

The highest correlation coefficients between sound level metrics and acoustic counts ranged from low to moderate in their ranking, and were from Schedule 2 recordings and excluding vessels. The highest of these (r = 0.71) was for Max SNR3 per AM/PM (Figure 4.8). Several correlations from Schedule 1 recordings had negative coefficients.

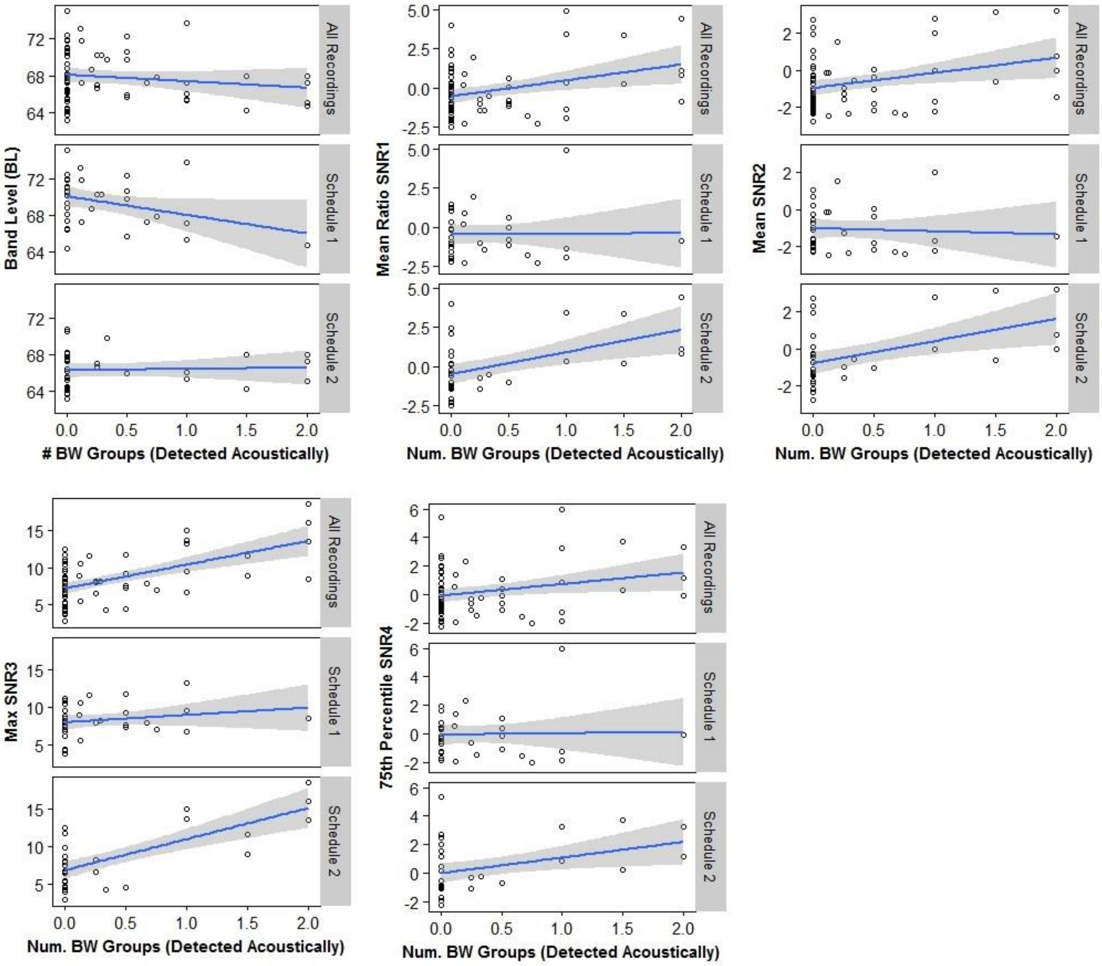


Figure 4.8. Scatterplots of sound level metrics vs. number of pygmy blue whale groups acoustically detected in Geographe Bay using data averaged daily per AM/PM and using only samples without vessels recorded. BW: pygmy blue whale.

The correlation between sound level metrics and visual counts was negligible for most cases. The highest correlation had a low correlation rank, and were for Max SNR3 per AM/PM, schedule 2 recordings (r = 0.39) with the dataset including all recordings (Table 4.4, see supplementary material Appendix 4.6.3 for full statistical results). When comparing recording schedules, higher correlation values were observed for recording schedule 2 (Figure 4.9)

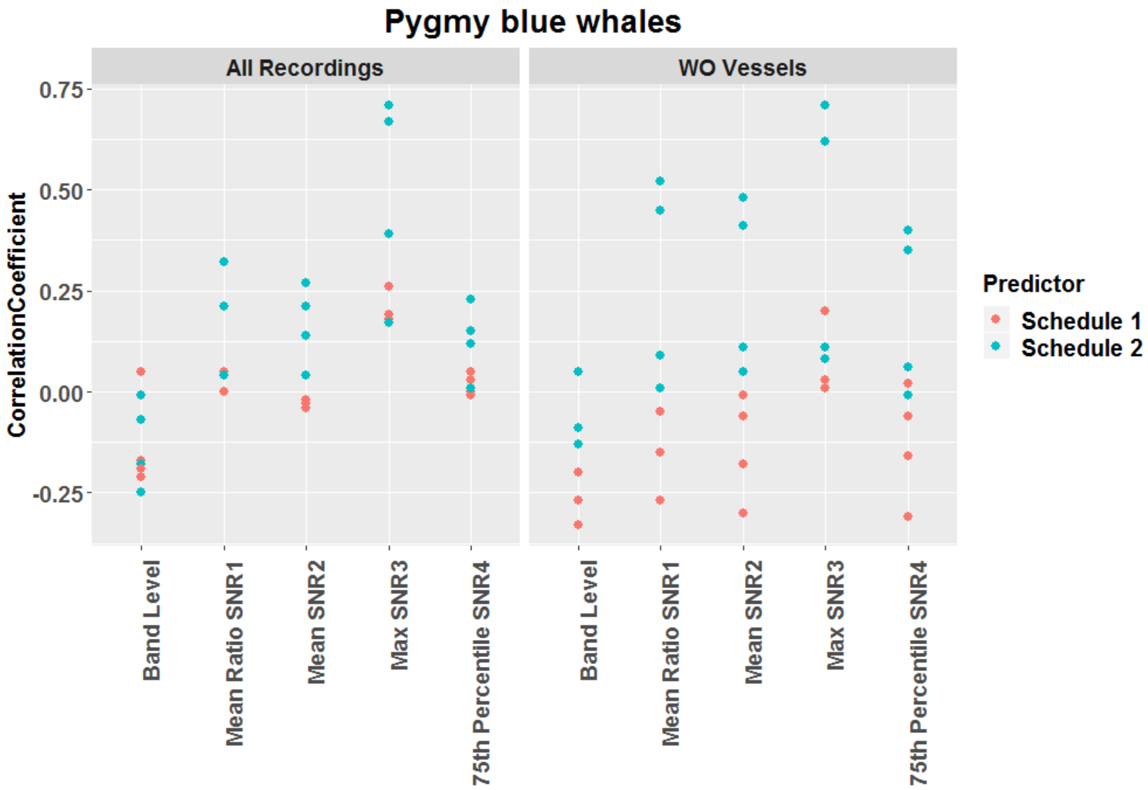


Figure 4.9. Correlation coefficients resulting from correlations between different sound level metrics and acoustic counts of pygmy blue whales for recording Schedules 1 and 2. Plots are presented for the following scenarios for comparative purposes: All recordings, recordings without vessel noise and blue whale sounds (WO vessels/BW), recordings without vessel noise (WO Vessels).

4.3.4. Correlations between the number of baleen whale groups counted acoustically and visually

The correlation between the number of acoustically and visually detected groups of pygmy blue and humpback whales in most cases resulted in higher coefficients than those obtained for correlations between sound level metrics and visual counts (Table 4.5).

Table 4.6. Pearson coefficients for correlations between manual counts of humpback and pygmy blue whale groups recorded and the number of groups visually tracked. Sch1: schedule 1 (2010 – 2011), Sch2: schedule 2 (2013-2014). Note: Test statistic, 95% Confidence intervals and p-values are in Supplementary material 4.6.3.

Data subset	**Temporal scale of mean counts**	**Level of correlation between acoustic & visual counts**					
		HW			**BW**		
		Sch1	**Sch2**	**Combined schedules**	**Sch1**	**Sch2**	**Combined schedules**
All Recordings	Hourly	**0.45**	**0.41**	**0.38**	0.54	0.27	0.35
	AM/PM	**0.53**	**0.63**	**0.55**	**0.81**	**0.53**	**0.56**
Recordings without vessel noise	Hourly	**0.52**	**0.37**	**0.42**	0.23	0.45	0.40
	AM/PM	**0.65**	**0.49**	**0.52**	0.23	0.43	0.38
Recordings without vessel noise & blue whale vocalisations	Hourly	**0.51**	**0.43**	**0.45**			
	AM/PM	**0.64**	**0.59**	**0.59**			

⬛ **Negligible correlation (±0.30 - ±0.30)**
⬜ **Low correlation (±0.31 - ±0.50)**
🟧 **Moderately correlated (±0.51 – ±0.70)**
🟫 **Highly correlated (±0.71 - ±0.90)**
🟥 **Very highly correlated (±0.91 - ±1.0).**

For humpback whales, higher correlation coefficients were observed when the data were averaged per AM/PM. The highest correlation coefficient (r = 0.65) resulted from recording schedule 1 and the data subset without vessel noise (Figure 4.10).

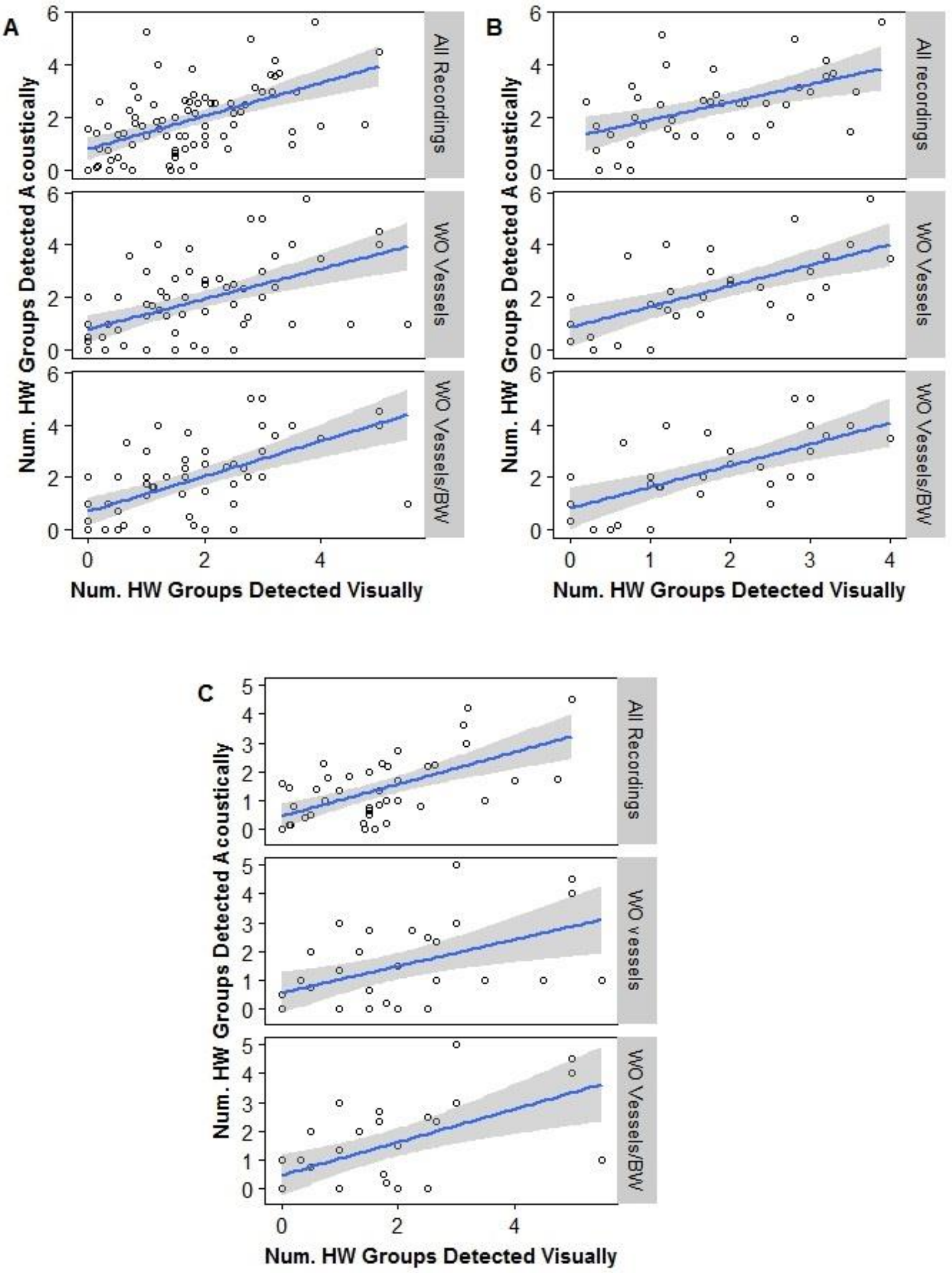


Figure 4.10. Scatterplots of mean number of humpback whale (HW) groups visually vs. acoustically detected in Geographe Bay, per AM/PM, from combined schedule recordings (A), schedule 1 recordings only (B), and schedule 2 recordings only (C). WO = recordings without vessel noise, WO vessels/BW = recordings without vessel noise and blue whale sounds.

Similar to humpback whales, for pygmy blue whales the highest correlation coefficients resulted from mean AM/PM time-blocks from schedule 1 recordings (r = 0.81; Table 4.5, Figure 4.11).

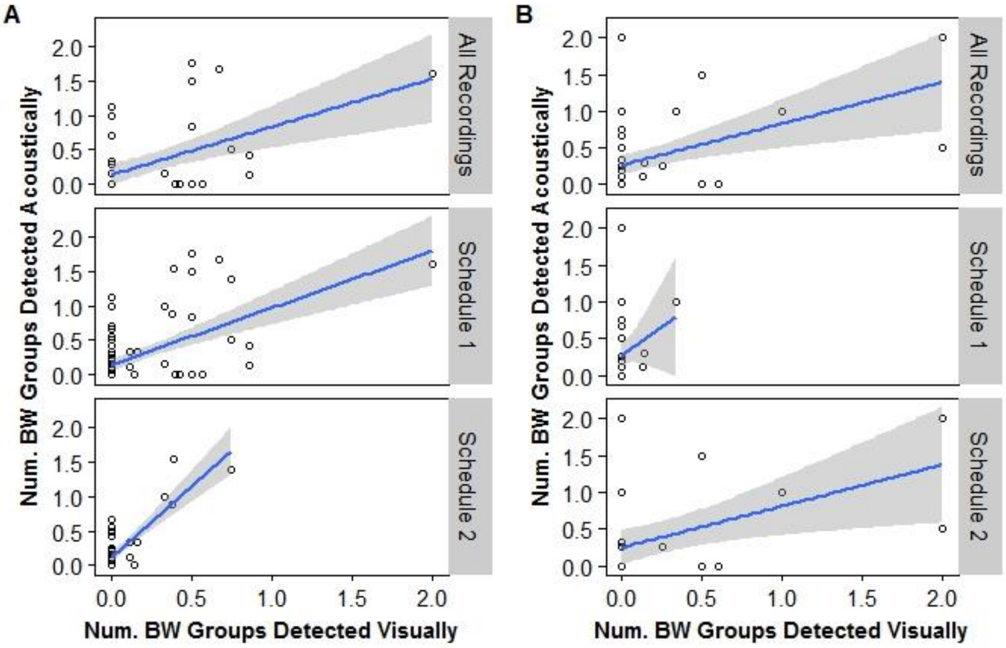


Figure 4.11. Scatterplots of mean number of pygmy blue whale (BW) groups visually vs. acoustically detected in Geographe Bay, per AM/PM, with datasets using all samples (A) and only samples without vessels (B).

4.4. Discussion

The principal aim of this chapter was to evaluate whether there were correlations between sound level metrics and numbers of vocalising and visually tracked humpback and pygmy blue whale groups. Previous studies have suggested that acoustical power and/or vocalisation rates can be highly correlated with the number of animals in an area (Au et al. 2000; McCauley et al. 2001; Oleson, Calambokidis, Barlow, et al. 2007; Gedamke et al. 2007; Gavrilov & McCauley 2013; Širović et al. 2015; Erbe et al. 2015; Seger et al. 2016; Noad et al. 2017). However, the level of correlation between these parameters has not always been evaluated.

In contrast with other studies (i.e. Au et al. 2000; Kumar 2003), the correlation between sound levels metrics and the number of visually tracked groups was low. This low correlation may be explained by differences in the area of detection of each method. While sound level metrics measure vocal power produced by vocalising groups in an area up to ~6 km and 20-30 km away for pygmy blue and humpback whales respectively (Salgado Kent, Gavrilov et al 2012), visual observations are restricted to a range in which animals could be confidently tracked (less than ~6 km from the theodolite station). However, animals at greater ranges yielded much lower received levels at the recorder, contributing much less to the overall SNR than animals close by and reducing the difference in area size.

Where differences in areas are limited or acoustic power from beyond the study area is low, differences between sound level metrics and visual observations are more likely explained by acoustical ecology and behaviour of a species in which there is differential detection of certain cohorts. For example, in *Cynoscion othonopterus (*Gulf corvina), sound levels have a linear relationship with numbers present, but only during the peak of spawning and after high tide (Rowell et al. 2017). For humpback whales specifically, differences in vocal behaviour are known to occur for different cohorts within a population; with single males singing for long periods of time and females with calves and groups of whales being less vocally active. Females with calves in particular tend to be the quietest and vocalise for shorter periods of time than singers and other adult-only groups (Dunlop et al. 2007; Zoidis et al. 2008). As song can be performed for long periods of time, singing whales can increase sound level metrics in the study area. Because singing whales spend more time under water than non-singing whales, the probability of sighting a singer at the surface of the water (and counting it during visual observations) is reduced. In contrast, less vocally active groups will have a higher probability of being detected visually, but will contribute less to sound level metrics. Therefore, the correlation between sound level metrics and visual observations will be low since each technique is targeting a different cohort.

In contrast, the correlation between sound levels metrics and numbers of vocalising groups varied from low to high; but was never very highly correlated (i.e. $r > 0.9$) for either species. In this study, manual counts of groups of vocalising whales were confined to the study area (based on SNR) since it was difficult to distinguish between vocalising groups at greater ranges. However, sound level metrics in this study were not necessarily confined to the study area. The difference in area each technique measured was likely responsible, in part, for noise introduced in correlations between the number of groups acoustically detected and SNR metrics. The level of correlation depended upon species, sound metric, temporal scale, data subset used and recording schedule. The influence of each of these is discussed below.

4.4.1. Influence of sound metrics and species on correlation coefficients

Low to high correlations resulted between most sound level metrics and numbers of vocalising groups, except for broadband level (BL, Eq. 4.1). The low correlations associated with broadband levels is indicative that adjusting for background noise levels was important for achieving indices that more accurately reflected counts of vocalising whales. Background noise levels in the ocean can vary by more than 40 dB depending upon wind and sea state conditions, although variations of up to 20 dB are common (Cato & McCauley, 2002). Consequently, without adjusting for background noise, the high variability over periods of hours and days will result in highly biased whale abundance indices.

Although for all analysis BL showed the lowest correlation coefficients, differences in the sound metric that achieved higher ranks differ between species. For humpback whales, a similar range in correlation coefficients resulted from all metrics (between 0.56 and 0.76), and for pygmy blue whales the maximum SNR3 had much higher coefficients (between 0.18 and 0.71) than all other SNR metrics (between -0.20 and 0.48).

Increases in mean and 75th percentile SNR metrics are expected in the following conditions: (1) when the duration of whale vocalisations increases in recordings (i.e., the percent of time that vocalisations occur in recordings), (2) when whale vocalisations have higher SNRs (generally when whales are closer to the receiver), and (3) when there are sufficient overlapping vocalisations to increase overall SNRs. Of these, the first two conditions are expected to be most influential. The maximum SNR would be expected to increase mainly when the intensity of vocalisations increases (generally when whales are closer). In some instances, the probability of having a whale closer to the receiver may increase with increasing numbers of whales in an area. Consequently, the density, distribution and vocal behaviour of different whale species will influence SNR metrics. For pygmy blue whales because they do not have a high vocal rate, the maximum will be achieved when a vocalisation is recorded and a single vocalisation will generate the maximum energy in the frequency range.

Overall, humpback whale SNRs had higher correlations with numbers of vocalising groups than did pygmy blue whale SNRs. Humpback whales were observed (visually) to be more abundant than pygmy blue whales. Humpback whales are also a highly vocal species, with vocalisations occurring on average over 50% of the recording length and dominating the soundscape in peak migratory periods (Seger et al. 2016). Thus, overall agreement in the range of correlations coefficients across SNR metrics for humpback whales is indicative that as more groups were vocalising, there was an increase in the proportion of vocalisations in recordings and the probability of vocalising whales being closer to the receiver (and/or vocalising with higher SNRs).

In contrast, pygmy blue whales were low in relative abundance (based on visual observations) and may be less vociferous than humpback whales and so there was high variability in the SNRs and coefficients. This variation might not be explained by changes in the population density and distribution due to the low numbers. The variability could have been due to some recordings having background noise in the same frequency band as pygmy blue whales. Wind generated noise is frequently dominant at frequencies below 200 Hz (Cato & McCauley 2002) and it may explain the variation in the SNRs and coefficients (see 4.3.7). In addition, pygmy blue whales may be less vocally active than humpback whales with their vocalisations recorded for, on average, 5 % of a recording sample. Because the low number of sounds produced by pygmy blue whales and their short duration, the received level will be low and the sounds will be averaged over the duration of the recording. Both this percentage and the received level were likely too low for the mean SNR metrics to be useful as the power of the few, short and brief pygmy blue whale signals would be "averaged out" over the duration of each recording. The SNR metric would thus have been dependent more on the variability in background noise than the variability in pygmy blue whale density.

In general, variability in vocal activity of individuals and their spatial distribution relative to the acoustic recorder over time influences how well sound metrics correlate to relative abundance. Despite the wide variability and the low correlation coefficients observed with mean sound metrics in this study, past studies on pygmy blue whales have successfully used mean sound levels to identify migration patterns (e.g. Gedamke et al. 2007; Erbe et al. 2015; Širović et al. 2015). The success of these studies would have been due to the presence of high numbers of animals and calls in the recordings, a condition that was not observed here. Consequently, a priori information on the likely number of vocalising animals (and vocalisation rates) is needed to design optimal acoustic sampling schedules and acoustic metrics.

4.4.2. Influence of temporal scale and recording schedule on correlation coefficients

The correlations between SNRs and the number of vocalising whale groups were higher when data considered temporal autocorrelation (averaged in AM/PM blocks) than when it did not (averages per hour). Previous studies on humpback and pygmy blue whales have used different time blocks to compare numbers of individuals from acoustics and visual methods (e.g. hour blocks used by Clark & Clapham 2004; Oleson Calambokidis, Barlow et al. 2007, or 4 minutes / daily blocks used by Au et al. 2000). However, on many occasions it is not clear whether temporal autocorrelation was considered or how it was included in the analysis. In areas of transit such as Geographe Bay, some groups may transit faster than others causing variability in whale abundance on short- and long-term scales. This variability implies that the numbers from one period of time are closely related to values from the following period, and so the data is positively autocorrelated. Because ecological studies should consider temporal variability to avoid temporal autocorrelation, it is recommended for future studies to include analysis of temporal scale as part of the statistical design. If this is not possible, it is recommended to analyse the data on different time scales so that temporal autocorrelation is evaluated.

Overall, recording schedule had little influence on correlations for humpback whales but it showed some influence for pygmy blue whales with higher correlations resulting from longer recordings made in 2013-2014. Considering that humpback and blue whales have different acoustical behaviour, it is possible that the differences between recording schedules are related to variability in the species vocalisation rate. It is possible that longer recordings increase the likelihood of detecting quieter species while more vocal species are less affected because they vocalise more frequently. Because recording schedule is linked to year in this study, the differences may be related to differences in the number of individuals passing by the area in a given year. According to the vocalisation rate analysis from chapter 3, this is not likely for pygmy blue whales because year was not a significant factor explaining the vocalisation rate variability. Furthermore, a greater number of pygmy blue whale groups were visually detected during the 2014 season but this did not affect the sound duration (proportion of time vocalisations occurred in recordings) for this year. On this base, it is possible that the recording schedule does influence correlation coefficients for quieter species. Studies on duty cycles have suggested that subsampling effects on acoustic metrics are more pronounced in species that are less vocally active (Thomisch et al. 2015). The results of this study support this finding but because the study of Thomisch et al. 2015 did not consider interseasonal variability and the sample size of this study was low, additional analyses are needed to better understand the influence of recording schedule on correlation coefficients.

4.4.3. Influence of masking sources on correlation coefficients

Results of this study indicated that higher correlations were obtained when overlapping noise occurring within the same frequency bands as whale signals of interest (i.e. other whale species, vessels) was removed. One method to remove the influence of overlapping noise is to select specific frequency bands of whale vocalisations that do not overlap with other sources. Širović et al. (2004) used this method to differentiate fin from blue whale signals, both in the 20-28 Hz frequency band, by using only the higher component of the fin whale calls to avoid overlap with the lower blue whale signals. In this study, a similar approach was not possible because the overlapping sources (blue whale downsweeps between 70-100 Hz, and vessel noise between 80-400 Hz) completely masked humpback whale sounds and no partial component could be used. In addition, including only non-overlapping frequencies would have excluded common non-song sounds. The inclusion of non-song sounds was considered particularly important for humpback whales because of the high number of mother-calf groups present in the area and likely producing non-song sounds only (Zoidis et al. 2008; Rekdahl et al. 2013). The subsampling approach (excluding recordings with overlapping noise from blue whales and vessels) used was successful at improving correlations from low / moderately correlated to highly correlated in humpback whales and from negligible to low / moderately correlated for pygmy blue whales. However, this can only be done when removing files with the overlapping sources does not affect the minimum sample size required for the analysis. In locations where there are high levels of overlapping noise from other sources, the use of sound level metrics may be far from optimal for obtaining abundance indices.

4.4.4. The influence of environmental conditions on correlation coefficients

Soundscape studies suggest that environmental conditions (i.e. wind, rain) contribute greatly to underwater sound (Ma et al. 2005; Erbe et al. 2015). In shallow waters, normal changes in wind speed can cause 20 dB or more noise level variation specially at low frequencies (<200 Hz) and, at wind speeds of >20 knots (~ 37 km/h) the noise level can be comparable to those observed with vessels (Cato 1997). In addition, rain has been reported in frequency bands below 1 kHz and heavy rain in bands between 2 and 10 kHz (Ma et al. 2005). These frequencies overlap with those of baleen whales and the influence of wind and rain noise should be considered for acoustics studies including sound level metrics correlations.

The analysis on the effect of environmental factors in correlation coefficients was out of the scope of this paper. Because concurrent visual survey protocols required sea states below 5, wind under 15 knots and no rain, it was assumed that the environment will have a low influence in the noise band. However, knowing that even small changes in the wind speed can somewhat affect the noise level (Cato & McCauley 2002), an analysis including changes in environmental conditions is suggested for future studies.

4.4.5. The influence of cohort and sound-type on correlation coefficients

Correlations between the number of groups vocalising and visually tracked were higher than those between visually tracked groups and sound level metrics. While previous studies suggested a non-linear relationship between the absolute number of animals present and the number of acoustical cues or vocalising individuals (Oleson, Calambokidis, Barlow et al. 2007; Ponce et al. 2012; Noad et al. 2017), this study estimated a moderate positive correlation. However, direct comparisons cannot be made because different acoustic or visual metrics were used in each study. Usually, studies using cue counts may differentiate vocal rates between cohorts or gender but assume that all visual groups are vocalising (Ponce et al. 2012). Here, the latest assumption cannot be made because the vocal rate varies according to cohorts and sound type and is not necessarily density dependent (Chapter 3). Furthermore, the use of cue counts for humpback whales is not advisable because of the high amount of sounds of which song is composed. Therefore, it is not possible to say whether the differences among studies are caused by the methodologies or due to differences in behaviour and ecology of each species.

Non-linear relationships between visual and acoustical observations are sometimes explained by differences in the detection rates for each method, presence of weak signals that auto-detectors may have missed, presence of silent animals that cannot be detected in acoustical analysis or presence of individuals vocalising underwater that are missed by visual observations. Although all these are valid reasons, an additional explanation that is not frequently considered is the type of sound used in the analysis. Previous studies with pygmy blue whales detected differences between visual and acoustical encounter rates between song and non-song sounds (Oleson, Calambokidis, Barlow et al. 2007). They found that the number of whales producing D calls (similar to the downsweeps in this study, Chapter 2; Recalde-Salas et al. 2014) was positively correlated with the number of visually observed whales, but singers were not correlated with visual counts (Oleson, Calambokidis, Barlow et al. 2007). The most common acoustical sounds detected in Geographe Bay were downsweeps and this may explain the moderate and high correlations obtained in this study.

4.5. Conclusions

Previous studies suggested a positive correlation between power levels and number of whales present in a particular area (Au et al. 2000; McCauley et al. 2001; Gedamke et al. 2007; Oleson, Calambokidis, Barlow, et al. 2007; Erbe et al. 2015; Seger et al. 2016; Noad et al. 2017). Results presented in this study indicate that this is not always the case and the accuracy of this method depends on the acoustical behaviour of the species being studied, the acoustic environment, and sound level metrics used.

A positive relationship between sound level metrics and numbers of groups vocalising or present in an area is more robust for species that are more vocally active or that vocalise more frequently such as humpback whales (Mellinger 2007). Furthermore, this study indicated that the relationship is likely to be stronger when overlapping sources in similar frequencies (e.g. vessels, other whale species, etc.) are removed. Exclusion of samples with vessels noise is recommended for humpback whale studies, if frequent vessel noise in similar frequency bands is present in the area.

For less vocal species such as blue whales occurring in an area with limited acoustic detection range or certain cohorts of humpback whales (e.g. mother-calf), the estimation of sound level metrics for ecological analysis is less robust. In these cases, the use of sound level metrics may not yield reliable abundance estimates; rather manual counts of acoustically detected groups are recommended instead. However, if a monitoring program requires the less laborious approach of using sound level metrics, Max SNR3 is recommended over other metrics as it may perform better.

Overall, the high variability in the acoustical ecology and vocalisation rates between cohorts bias relative densities using sound level metrics to those groups more acoustically active (e.g. singers). The use of manual counts of vocalising groups for both highly vocal and quieter species will likely more accurately account for the proportion of groups or individuals that are less vocally active. Because manual counts is a very laborious approach, a combination of this with sound level metrics maybe an option of a cost-effective action. For example, sound level metric methods can be used for identifying specific dates and recordings where a species of interest is present and then, subsamples of these specific recordings can be chosen to do manual counts. Ultimately, it is important that monitoring programs using acoustics use methods that best answer the management needs in question, and carefully consider the acoustical behaviour of the species or cohorts of interest. As a result, biases inherent to each method will be reduced.

4.6. Supplementary material

4.6.1 Pearson correlation analysis for humpback whales

Table 4.7. Summary of Pearson correlation test coefficients for different SNR measures vs. acoustic counts of groups of humpback whales in Geographe Bay based on hourly means. Values highlighted in bold represent the highest coefficients per each SNR and recording schedule.

SNR measures	Recordings used	Schedule 1 (2010-2011)				Schedule 2 (2013-2014)				Combined schedules (2010-2011 & 2013-2014)			
		Pearson Correlation Coefficient	**t**	**CI**	**P value**	**Pearson Correlation Coefficient**	**T**	**CI**	**P value**	**Pearson Correlation Coefficient**	**t**	**CI**	**P value**
Band level (BL - Eq. 1)	All recordings	0.25	2.84	0.07 0.41	0.005	0.05	0.65	-0.11 0.22	0.511	0.32	5.43	0.20 0.42	1.26 e-07
	Excluding recordings with vessels	**0.33**	3.05	0.11 0.52	0.003	**0.09**	0.72	-0.15 0.33	0.460	**0.35**	4.37	0.19 0.48	2.44 e-05
	Excluding recordings with vessels and blue whales	0.32	2.87	0.10 0.52	0.005	0.02	0.17	-0.25 0.29	0.864	0.31	3.59	0.14 0.46	0.0004
Mean Ratio SNR1 (Eq. 2)	All recordings	0.63	8.76	0.50 0.72	1.84 e-14	0.63	9.67	0.52 0.72	<2.2 e-16	**0.65**	13.71	0.57 0.71	< 2.2 e-16
	Excluding recordings with vessels	**0.65**	7.41	0.50 0.76	1.77 e-10	0.60	5.99	0.42 0.74	1.2 e-07	0.63	9.67	0.52 0.72	< 2.44 e-16
	Excluding recordings with vessels and blue whales	0.62	6.56	0.45 0.74	8.42 e-09	**0.65**	6.12	0.46 0.78	1.39 e-07	0.62	8.83	0.50 0.72	9.77 e-15
Mean SNR2 (Eq. 3)	All recordings	0.66	9.54	0.54 0.75	2.75 e-16	0.57	8.11	0.44 0.66	2.55 e-13	0.63	13.016	0.55 0.70	< 2.2e-16
	Excluding recordings with vessels	**0.68**	8.09	0.54 0.79	9.21 e-12	0.60	5.91	0.41 0.74	1.6 e-07	**0.65**	10.15	0.55 0.74	<2.2 e-16

	Excluding recordings with vessels and blue whales	0.65	7.18	0.49 0.77	6.45 e-10	**0.62**	5.65	0.42 0.76	7.50 e-07	0.63	8.99	0.51 0.73	4.19 e-15
Max SNR3 (Eq. 4)	All recordings	0.60	8.25	0.48 0.71	2.70 e-13	**0.67**	10.62	0.57 0.75	< 2.2e-16	0.65	13.76	0.57 0.71	< 2.2 e-16
	Excluding recordings with vessels	0.64	7.25	0.49 0.76	3.46 e-10	0.55	5.25	0.36 0.70	1.97 e-06	0.61	9.02	0.49 0.70	1.52 e-15
	Excluding recordings with vessels and blue whales	**0.65**	7.06	0.49 0.76	6.45 e-10	0.66	6.36	0.48 0.79	5.86 e-08	**0.66**	9.73	0.55 0.75	< 2.2 e-16
75th Percentile SNR4 (Eq. 5)	All recordings	0.66	9.54	0.54 0.75	2.73 e-16	0.60	8.95	0.49 0.70	2.21 e-15	0.66	14.035	0.58 0.72	< 2.2 e-16
	Excluding recordings with vessels	**0.68**	7.96	0.53 0.78	1.62 e-11	0.61	6.14	0.43 0.75	6.59 e-08	**0.66**	10.36	0.55 0.74	<2.2e-16
	Excluding recordings with vessels and blue whales	0.65	7.06	0.46 0.78	1.07 e-09	**0.64**	5.92	0.44 0.77	2.89 e-07	0.64	9.23	0.52 0.73	1.12 e-15

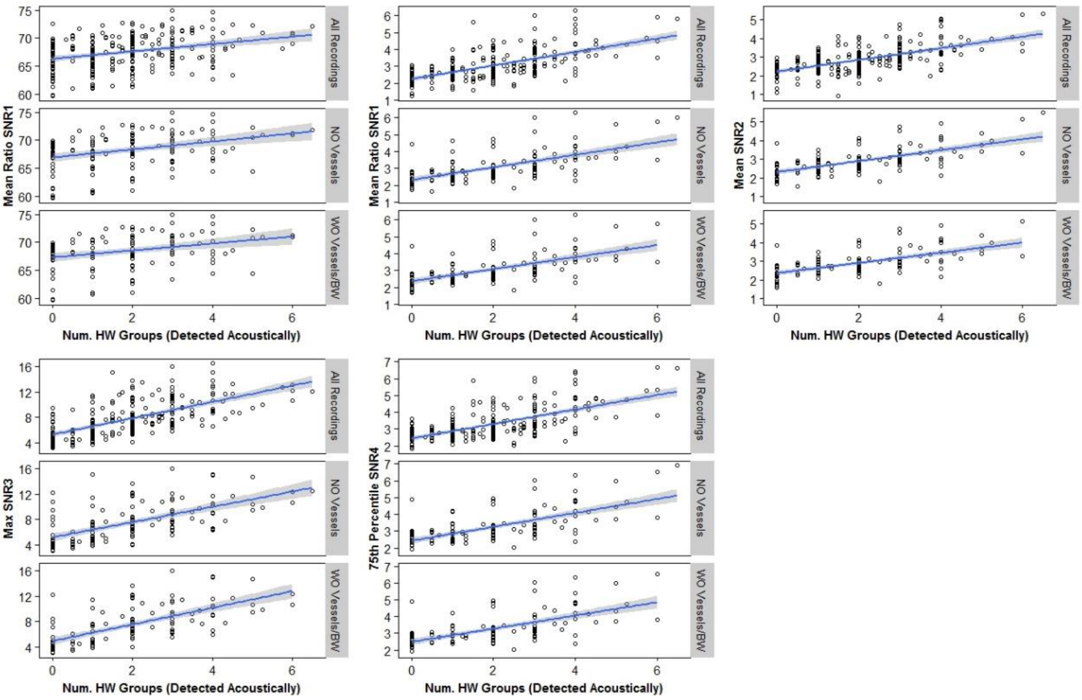


Figure 4.12. Scatterplots of mean sound level metrics vs number of acoustically detected groups of humpback whales per hour in Geographe Bay for Schedules 1 and 2 recordings. WO = recordings without vessel noise, WO vessels/BW = recordings without vessel noise and blue whale sounds.

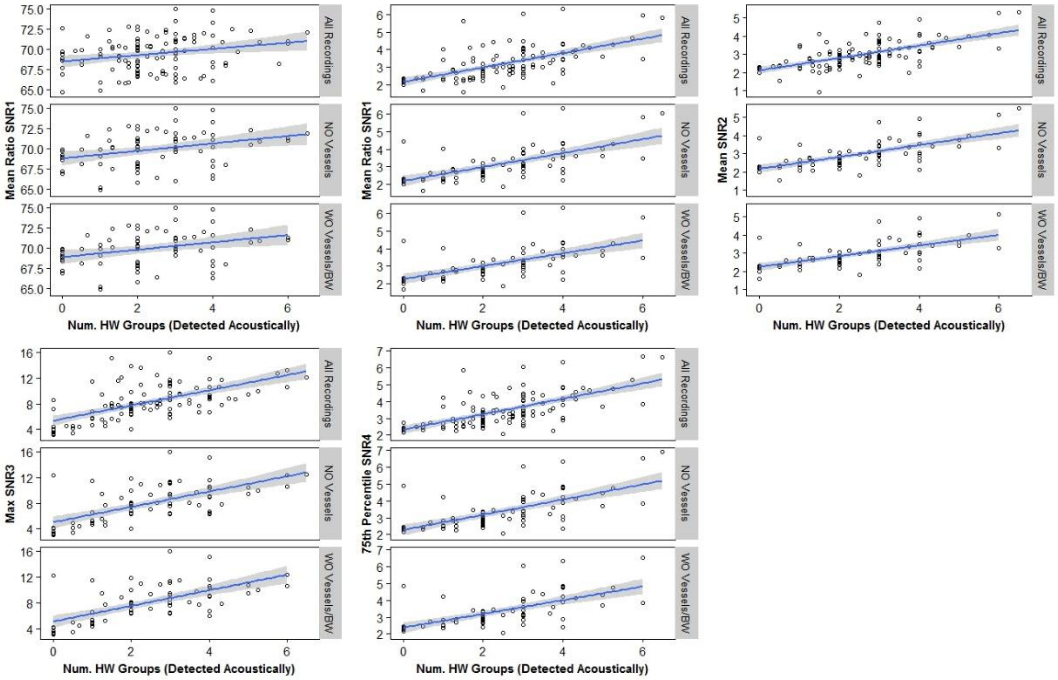


Figure 4.13. Scatterplots of mean sound level metrics vs number of acoustically detected groups of humpback whales per hour in Geographe Bay for schedule 1 recordings. WO = recordings without vessel noise, WO vessels/BW = recordings without vessel noise and blue whale sounds.

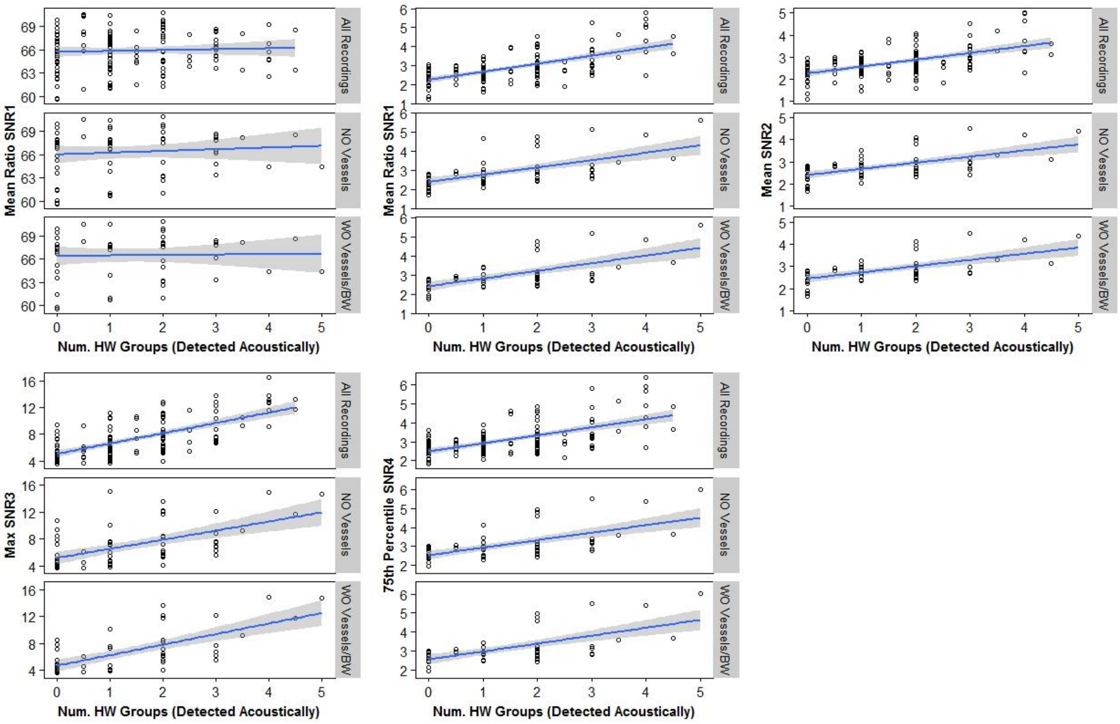


Figure 4.14. Scatterplots of mean sound level metrics vs number of acoustically detected groups of humpback whales per hour in Geographe Bay for Schedule 2 recordings. WO = recordings without vessel noise, WO vessels/BW = recordings without vessel noise and blue whale sounds.

Table 4.8. Summary of Pearson correlation test coefficients for the different sound level metrics vs acoustic counts of groups of humpback whales in Geographe Bay based on daily morning (AM) and afternoon (PM) means. Values in bold represent the highest coefficients per each SNR and recording schedule.

SNR measures	Recordings used	Schedule 1 (2010-2011)				Schedule 2 (2013-2014)				Combined schedules (2010-2011 & 2013-2014)			
		Pearson Correlation Coefficient	**t**	**CI**	**P value**	**Pearson Correlation Coefficient**	**T**	**CI**	**P value**	**Pearson Correlation Coefficient**	**t**	**CI**	**P value**
Band level (BL - Eq. 1)	All recordings	0.31	2.04	0.00 0.57	0.047	0.05	0.30	-0.25 0.34	0.761	0.38	3.67	0.17 0.54	0.0004
	Excluding recordings with vessels	0.44	2.69	0.10 0.68	0.011	**0.12**	6.99	-0.22 0.44	0.489	**0.36**	3.094	0.13 0.55	0.002
	Excluding recordings with vessels and blue whales	**0.48**	2.92	0.51 0.86	3.65 e-06	0.07	0.37	-0.30 0.43	0.711	0.34	2.73	0.09 0.55	0.0083
Mean Ratio SNR1 (Eq. 2)	All recordings	0.67	5.52	0.44 0.81	2.57 e-06	0.68	5.92	0.47 0.81	5.58 e-07	0.69	8.69	0.56 0.79	3.14 e-13
	Excluding recordings with vessels	**0.72**	5.60	0.48 0.85	4.24 e-06	0.72	5.84	0.50 0.85	1.93 e-06	**0.72**	8.19	0.57 0.81	1.61 e-11
	Excluding recordings with vessels and blue whales	0.68	4.90	0.42 0.83	3.56 e-05	**0.76**	5.99	0.54 0.88	2.48 3-06	0.72	7.69	0.56 0.82	2.47 e-10
Mean SNR2 (Eq. 3)	All recordings	0.74	6.71	0.55 0.85	5.92 e-08	0.60	4.78	0.36 0.76	2.26 e-05	0.70		0.56 0.79	2.20 e-13
	Excluding recordings with vessels	**0.76**	6.45	0.56 0.87	0.011	0.70	5.44	0.46 0.84	5.99 e-06	**0.73**	8.50	0.59 8.27	4.67 e-12
	Excluding recordings with vessels and blue whales	0.73	5.74	0.51 0.86	3.65 e-06	**0.73**	5.40	0.48 0.86	1.16 e-05	0.73	7.92	0.57 0.82	1.00 e-10
Max SNR3 (Eq. 4)	All recordings	0.60	4.63	0.35 0.76	4.17 e-05	0.71	6.55	0.52 0.83	2.47 e-06	0.67	8.02	0.52 0.77	6.63 e-12
	Excluding recordings with vessels	**0.64**	4.62	0.38 0.81	6.69 e-05	0.62	4.45	0.35 0.79	0.0001	0.63	6.47	0.45 0.75	1.63 e-08

	Excluding recordings with vessels and blue whales	0.63	4.35	0.35 0.81	0.0001	**0.73**	5.39	0.48 0.86	1.18 e-05	**0.69**	7.06	0.52 0.80	2.66 e-09
75th Percentile SNR4 (Eq. 5)	All recordings	0.70	6.08	0.50 0.83	4.35 e-07	0.65	5.46	0.43 0.79	2.47 e-06	0.70	8.97	0.57 0.79	9.05 e-14
	Excluding recordings with vessels	**0.74**	6.05	0.52 0.86	1.20 e-06	0.71	5.70	0.49 0.85	2.86 e-06	**0.73**	8.51	0.59 0.82	4.49 e-12
	Excluding recordings with vessels and blue whales	0.70	5.25	0.46 0.84	1.39 e-05	**0.74**	5.61	0.50 0.87	2.47 e-10	0.72	7.81	0.57 0.82	1.54 e-10

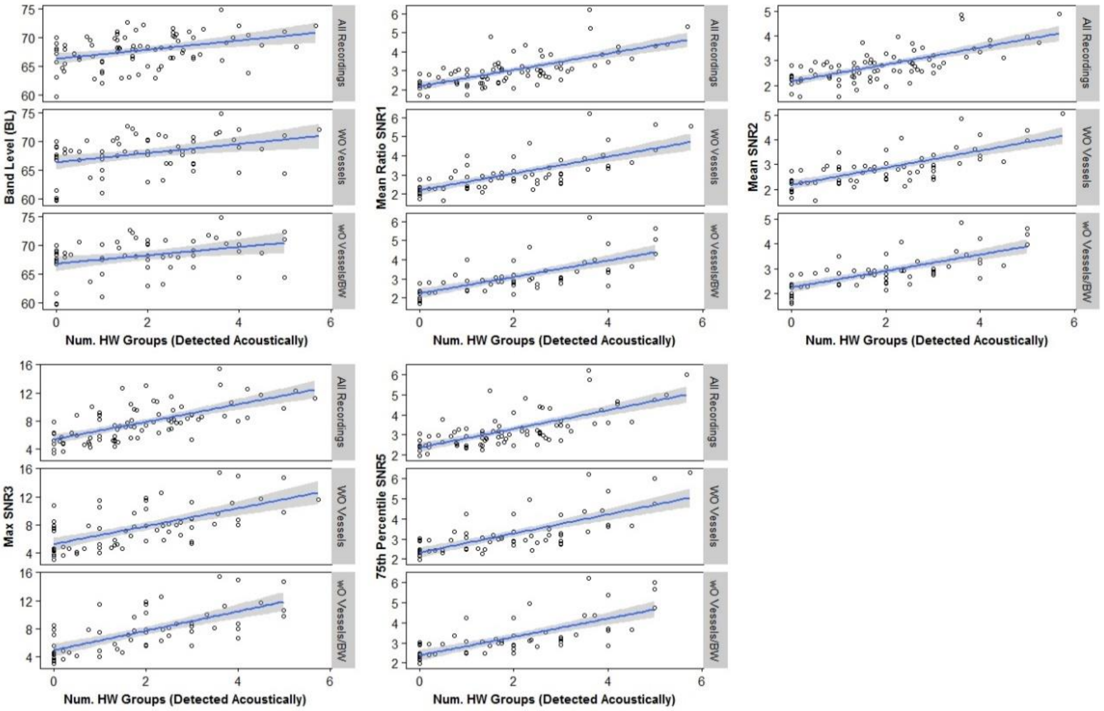


Figure 4.15. Scatterplots of mean sound level metrics vs number of acoustically detected groups of humpback whales per AM/PM in Geographe Bay for Schedules 1 and 2 recordings. WO = recordings without vessel noise, WO vessels/BW = recordings without vessel noise and blue whale sounds.

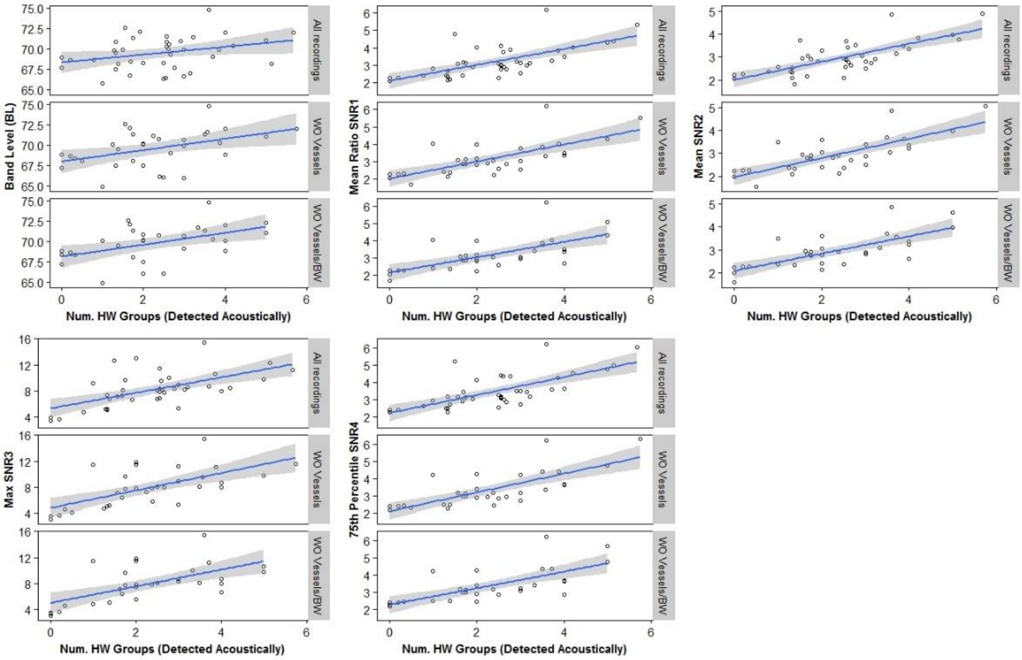


Figure 4.16. Scatterplots of mean sound level metrics vs number of acoustically detected groups of humpback whales per AM/PM in Geographe Bay for Schedule 1 recordings. WO = recordings without vessel noise, WO vessels/BW = recordings without vessel noise and blue whale sounds.

Table 4.9. Summary of Pearson test correlation test coefficients for different sound level metrics vs number of groups of humpback whales visually counted in Geographe Bay based on hourly means. Values highlighted in bold represent the highest coefficients each SNR and recording schedule.

SNR measures	Recordings used	Schedule 1 (2010-2011)				Schedule 2 (2013-2014)				Combined schedules (2010-2011 & 2013-2014)			
		Pearson Correlation Coefficient	**t**	**CI**	**P value**	**Pearson Correlation Coefficient**	**t**	**CI**	**P value**	**Pearson Correlation Coefficient**	**t**	**CI**	**P value**
Band level (BL - Eq. 1)	All recordings	**0.23**	2.50	0.04 0.39	0.013	0.12	1.47	-0.04 0.28	0.141	**0.14**	2.32	0.02 0.26	0.02
	Excluding recordings with vessels	0.15	1.34	-0.07 0.36	0.184	**0.15**	1.21	-0.09 0.38	0.22	0.13	1.51	0.17 0.47	0.13
	Excluding recordings with vessels and blue whales	0.16	1.33	-0.07 0.38	0.18	0.11	0.81	-0.16 0.37	0.02	0.12	1.37	-0.05 0.29	0.17
Mean Ratio SNR1 (Eq. 2)	All recordings	0.33	3.75	0.15 0.48	0.0002	**0.34**	4.19	0.18 0.47 0.51	4.95 e-05	0.32	5.33	0.20 0.42	2.064 e-07
	Excluding recordings with vessels	**0.39**	3.58	0.17 0.56	0.0006	0.29	2.36	0.04 0.50	0.021	**0.33**	4.10	0.17 0.47	7.03 e-05
	Excluding recordings with vessels and blue whales	0.34	3.01	0.11 0.53	0.18	0.31	2.29	0.03 0.53	0.025	0.32	3.75	0.15 0.47	0.0002
Mean SNR2 (Eq. 3)	All recordings	0.34	3.85	0.16 0.48	0.0001	0.27	3.27	0.10 0.41	0.001	0.29	4.77	0.17 0.39	0.17
	Excluding recordings with vessels	**0.40**	3.76	0.19 0.57	0.0003	0.25	2.05	0.00 0.47	0.044	**0.32**	3.99	0.16 0.46	0.0001
	Excluding recordings with vessels and blue whales	0.36	3.14	0.13 0.54	0.002	**0.29**	2.11	0.01 0.51	0.039	0.32	3.70	0.15 0.47	0.0003
Max SNR3 (Eq. 4)	All recordings	0.27	3.04	0.09 0.31	0.002	**0.32**	3.93	0.16 0.46	0.0001	0.29	4.82	0.17 0.39	2.419 e-06
	Excluding recordings with vessels	0.35	3.24	0.18 0.57	0.001	0.26	2.11	0.01 0.47	0.03	0.30	3.69	0.14 0.44	0.0003

	Excluding recordings with vessels and blue whales	**0.36**	3.16	0.13 0.54	0.002	0.28	**2.06**	0.00 0.51	0.044	0.32	3.67	0.14 0.46	0.0003
75th Percentile SNR4 (Eq. 5)	All recordings	0.33	3.72	0.15 0.47	0.0003	**0.32**	3.96	0.16 0.46	0.0001	0.30	5.07	0.18 0.40	7.511 e-07
	Excluding recordings with vessels	**0.40**	3.69	0.18 0.57	0.0004	0.27	2.20	0.02 0.48	0.031	**0.33**	4.03	0.16 0.46	8.96 e-05
	Excluding recordings with vessels and blue whales	0.35	3.07	0.12 0.54	0.003	0.31	2.27	0.03 0.53	0.027	0.32	3.77	0.15 0.47	0.0002

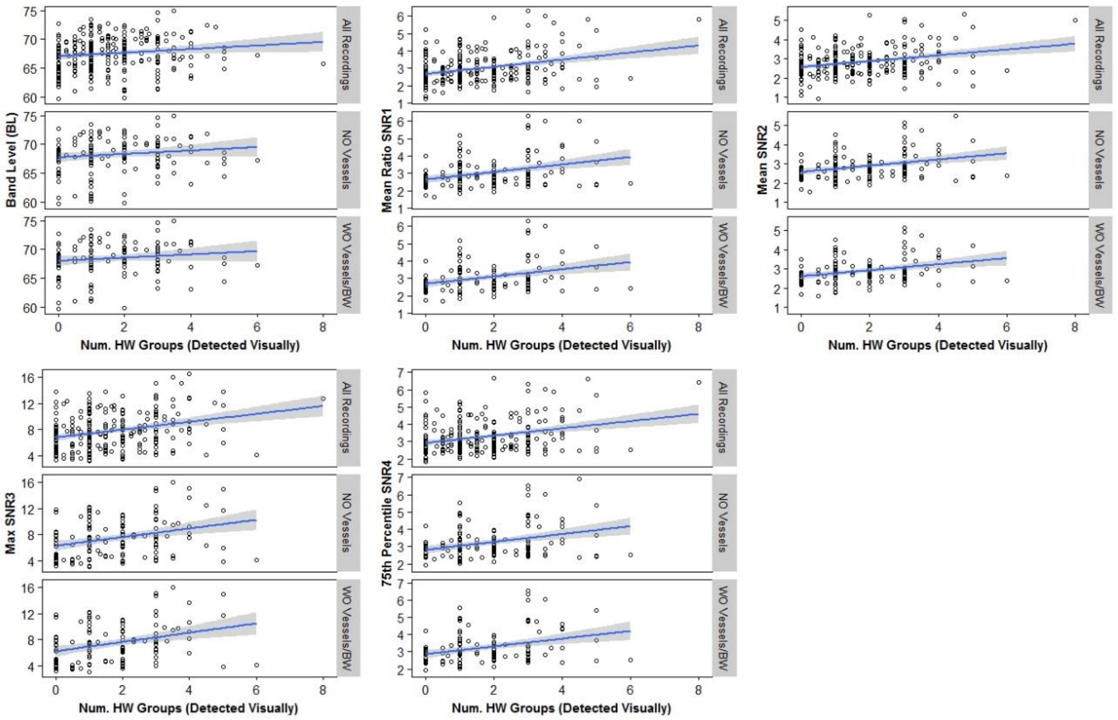


__Figure 4.17. Scatterplots of mean sound level metrics vs number of visually detected groups of humpback whales per hour in Geographe Bay for Schedules 1 and 2 recordings. WO = recordings without vessel noise, WO vessels/BW = recordings without vessel noise and blue whale sounds.__

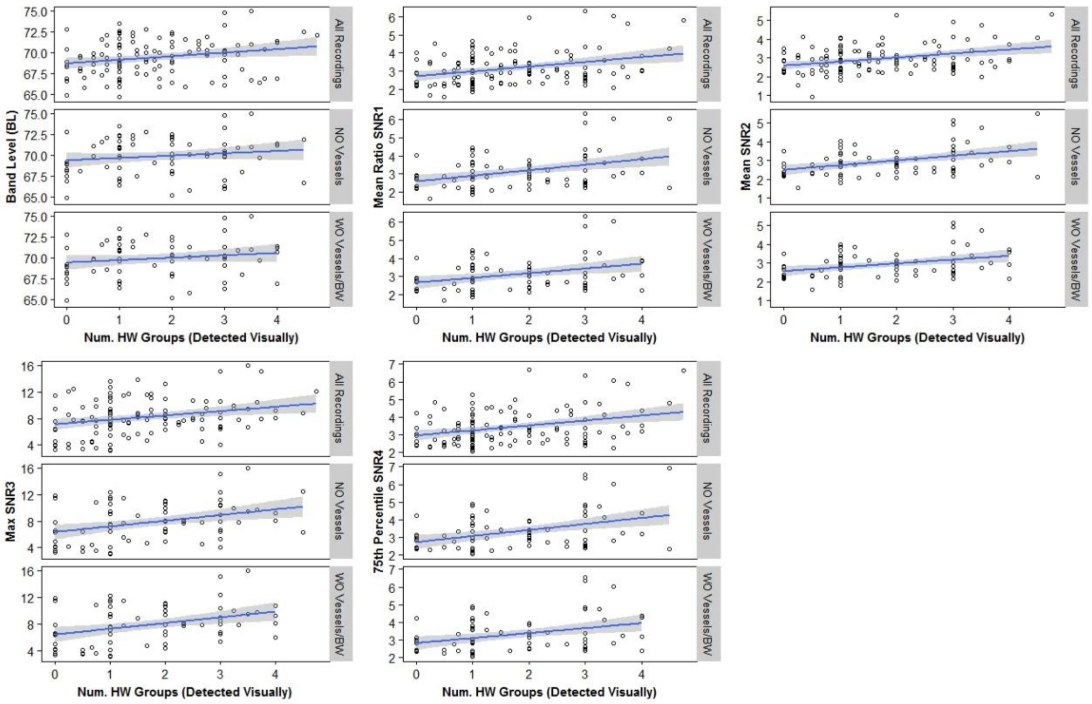


__Figure 4.18. Scatterplots of mean sound level metrics vs number of visually detected groups of humpback whales per hour in Geographe Bay for Schedule 1 recordings. WO = recordings without vessel noise, WO vessels/BW = recordings without vessel noise and blue whale sounds.__

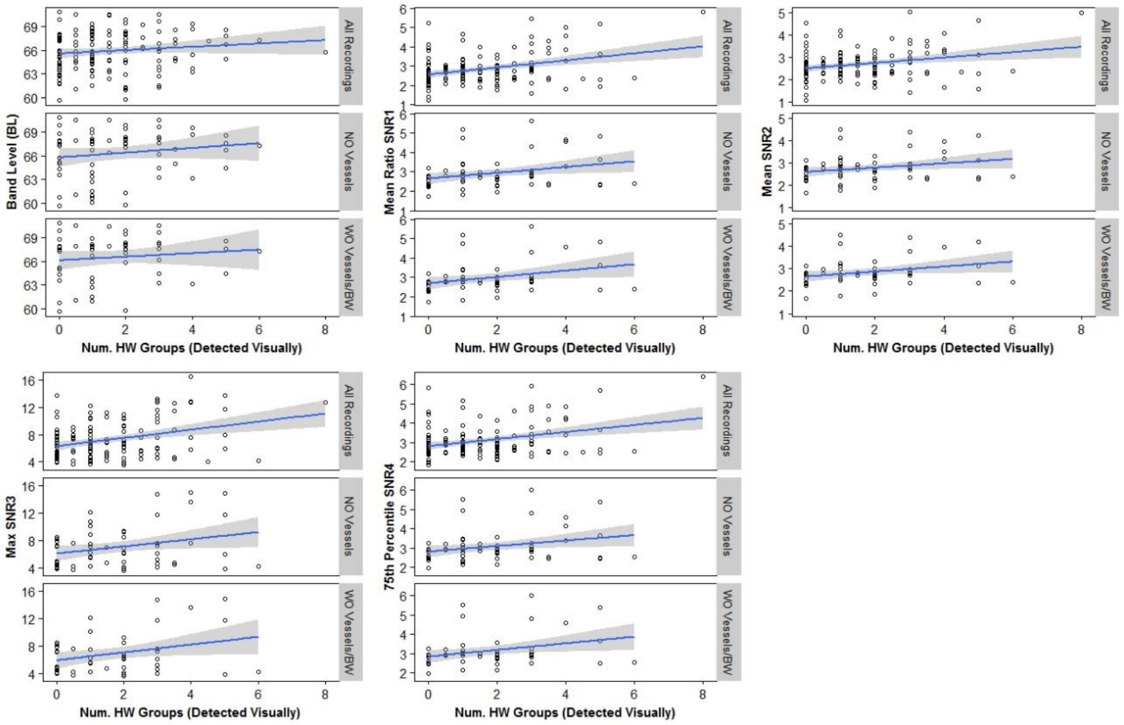


Figure 4.19.Scatterplots of mean sound level metrics vs number of visually detected groups of humpback whales per hour in Geographe Bay for Schedules 2 recordings. WO = recordings without vessel noise, WO vessels/BW = recordings without vessel noise and blue whale sounds.

Table 4.10. Summary of Pearson correlation test coefficients for the different SNR measures vs number of groups of humpback whales visually counted in Geographe Bay based on daily morning (AM) and afternoon (PM) means. Values highlighted in bold represent the highest correlation coefficients per each SNR and recording schedule

SNR measures	Recordings used	Schedule 1 (2010-2011)				Schedule 2 (2013-2014)				Combined schedules (2010-2011 & 2013-2014)			
		Pearson Correlation Coefficient	t	CI	P value	Pearson Correlation Coefficient	t	CI	P value	Pearson Correlation Coefficient	t	CI	P value
Band level (BL - Eq. 1)	All recordings	0.27	1.70	0.17 0.67	0.002	**0.17**	1.13	-0.13 0.45	0.264	**0.21**	1.96	0.00 0.40	0.053
	Excluding recordings with vessels	0.30	1.75	-0.04 0.59	0.006	0.14	0.81	-0.20 0.46	0.422	0.16	1.25	-0.09 0.38	0.213
	Excluding recordings with vessels and blue whales	**0.37**	2.08	0.00 0.64	0.008	0.10	0.49	-0.28 0.45	0.62	0.17	1.32	-0.08 0.41	0.190
Mean Ratio SNR1 (Eq. 2)	All recordings	0.44	3.06	0.15 0.66	0.003	0.45	3.24	0.17 0.66	0.002	0.48	4.38	0.24 0.59	3.47 e-05
	Excluding recordings with vessels	**0.47**	2.90	0.14 0.70	0.006	0.45	2.77	0.12 0.68	0.009	0.44	3.88	0.21 0.61	0.0002
	Excluding recordings with vessels and blue whales	0.42	2.42	0.06 0.67	0.021	**0.49**	2.82	0.13 0.72	0.009	**0.44**	3.72	0.21 0.63	0.0004
Mean SNR2 (Eq. 3)	All recordings	0.46	3.21	0.17 0.67	0.002	0.33	2.28	0.03 0.57	0.027	0.39	3.84	0.19 0.56	0.0002
	Excluding recordings with vessels	**0.52**	3.30	0.20 0.73	0.516	0.40	2.44	0.06 0.65	0.020	0.43	3.83	0.21 0.64	0.0002
	Excluding recordings with vessels and blue whales	0.47	2.81	0.13 0.71	0.008	**0.46**	2.66	0.10 0.71	0.013	**0.45**	3.82	0.22 0.63	0.0003
Max SNR3 (Eq. 4)	All recordings	**0.37**	2.43	0.06 0.60	0.019	**0.46**	3.33	0.18 0.66	0.001	**0.42**	4.13	0.22 0.58	8.58 e-05
	Excluding recordings with vessels	0.31	1.77	-0.04 0.59	0.085	0.37	2.23	0.03 0.63	0.014	0.34	2.87	0.10 0.53	0.005

	Excluding recordings with vessels and blue whales	0.27	1.51	-0.09 0.57	0.141	0.43	**2.45**	0.07 0.69	0.021	0.36	2.92	0.11 0.56	0.004
75th Percentile SNR4 (Eq. 5)	All recordings	0.45	3.09	0.15 0.66	0.003	0.39	2.71	0.10 0.61	0.009	0.41	4.02	0.21 0.57	0.0001
	Excluding recordings with vessels	**0.50**	3.16	0.18 0.72	0.003	0.42	2.59	0.09 0.66	0.0002	0.44	3.88	0.21 0.61	0.0002
	Excluding recordings with vessels and blue whales	0.45	2.67	0.10 0.69	0.012	**0.48**	2.79	0.13 0.72	0.009	**0.46**	3.87	0.22 0.64	0.0002

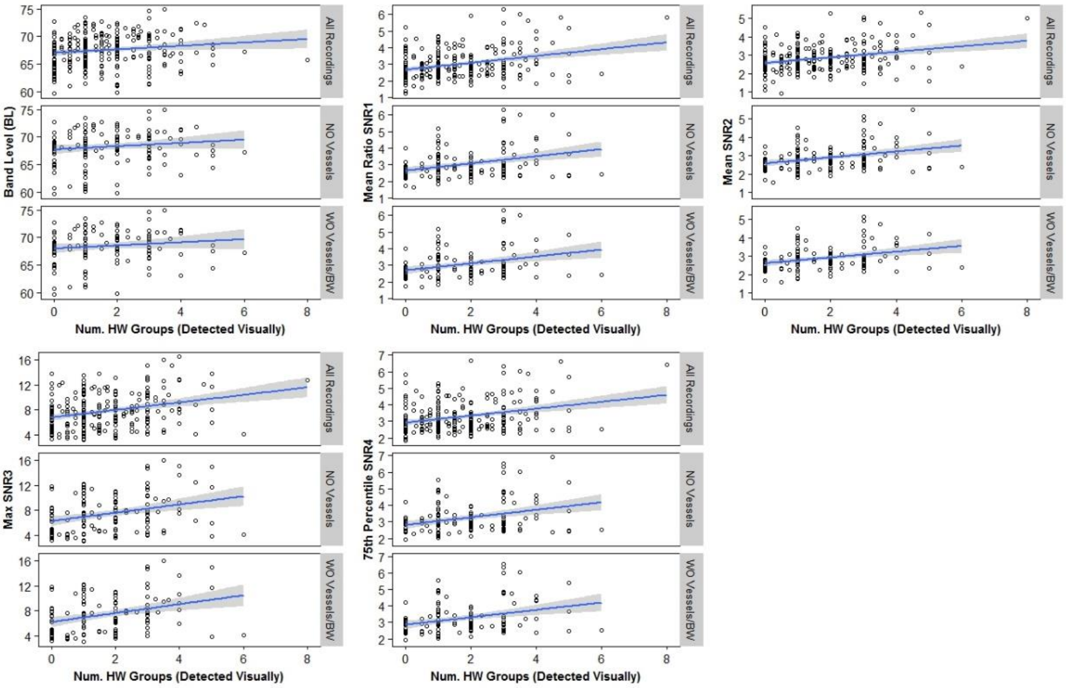


Figure 4.20. Scatterplots of mean sound level metrics vs number of visually detected groups of humpback whales per AM/PM in Geographe Bay for recording schedules 1 and 2 combined. WO = recordings without vessel noise, WO vessels/BW = recordings without vessel noise and blue whale sounds.

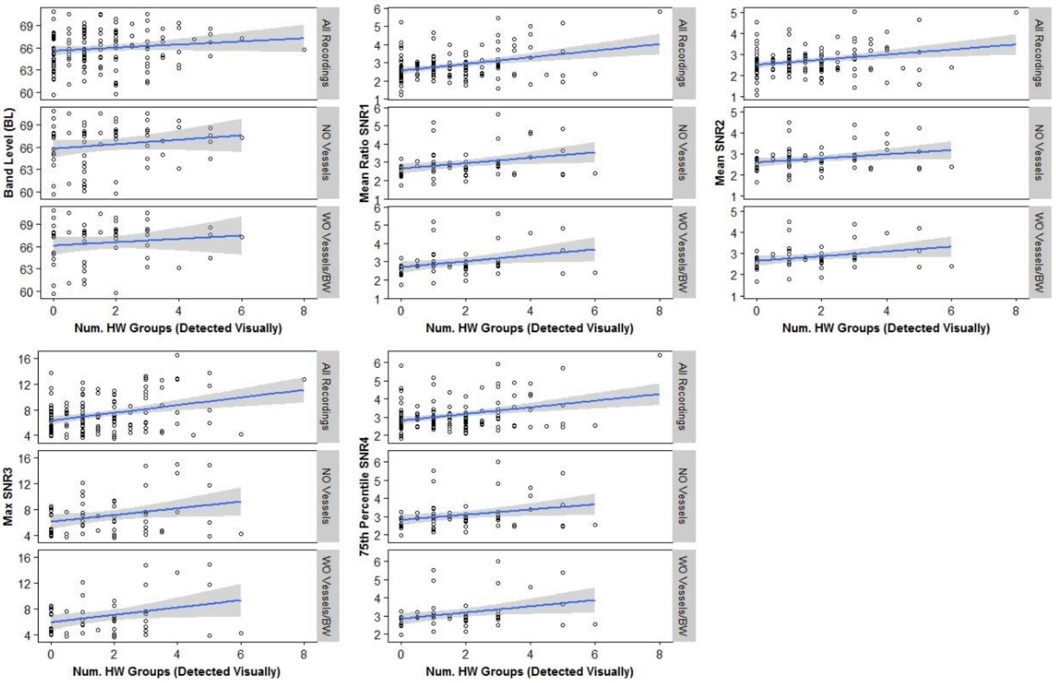


Figure 4.21. Scatterplots of mean sound level metrics vs number of visually detected groups of humpback whales per AM/PM in Geographe Bay for Schedule 2 recordings. WO = recordings without vessel noise, WO vessels/BW = recordings without vessel noise and blue whale sounds.

4.6.2. Pearson correlation analysis for blue whales

Table 4.11.Summary of Pearson correlation test coefficients for different SNR measures vs. acoustic counts of groups of blue whales in Geographe Bay based on hourly means. Values highlighted in bold represent the highest correlation coefficients per each SNR and recording schedule.

SNR measures	Recordings used	Schedule 1 (2010-2011)				Schedule 2 (2013-2014)				Combined schedules (2010-2011 & 2013-2014)			
		Pearson Correlation Coefficient	**t**	**CI**	**P value**	**Pearson Correlation Coefficient**	**t**	**CI**	**P value**	**Pearson Correlation Coefficient**	**t**	**CI**	**P value**
Band level (BL - Eq. 1)	All recordings	-0.173	-1.90	-0.34 0.00	0.059	-0.071	-0.83	-0.23 0.01	0.402	**-0.119**	-1.91	-0.23 0.00	0.056
	Excluding recordings with vessels	**-0.204**	-1.79	-0.41 0.02	0.076	**0.049**	0.38	-0.20 0.29	0.702	-0.109	-1.28	-0.27 0.05	0.200
Mean Ratio SNR1 (Eq. 2)	All recordings	0.003	0.03	-0.17 0.18	0.968	0.209	2.50	0.04 0.36	0.013	0.131	2.11	0.01 0.24	0.035
	Excluding recordings with vessels	**-0.057**	-0.49	-0.27 0.17	0.624	**0.446**	3.89	0.22 0.62	0.0002	**-0.237**	2.85	0.07 0.38	0.004
Mean SNR2 (Eq. 3)	All recordings	-0.044	-0.48	-0.22 0.13	0.629	0.141	1.66	-0.02 0.30	0.098	0.075	1.21	-0.04 0.19	0.225
	Excluding recordings with vessels	**-0.099**	-0.86	-0.31 0.12	0.391	**0.408**	3.49	0.17 0.59	0.0008	**0.206**	2.47	0.04 0.36	0.014
Max SNR3 (Eq. 4)	All recordings	**0.195**	2.15	0.01 0.36	0.033	**0.667**	10.45	0.56 0.75	<2.2 e-16	**0.507**	9.40	0.41 0.59	<2.2 e-16
	Excluding recordings with vessels	0.111	0.96	-0.11 0.32	0.339	0.616	6.11	0.43 0.74	7.60 e-08	0.422	5.45	0.27 0.54	2.27 e-07
75th Percentile SNR4 (Eq. 5)	All recordings	-0.007	-0.08	-0.18 0.17	0.934	0.122	1.44	-0.04 0.28	0.151	0.074	1.19	-0.04 0.19	0.233
	Excluding recordings with vessels	**-0.062**	-0.54	-0.28 0.16	0.59	**0.352**	2.94	0.11 0.55	0.004	**0.169**	2.01	0.00 0.32	0.045

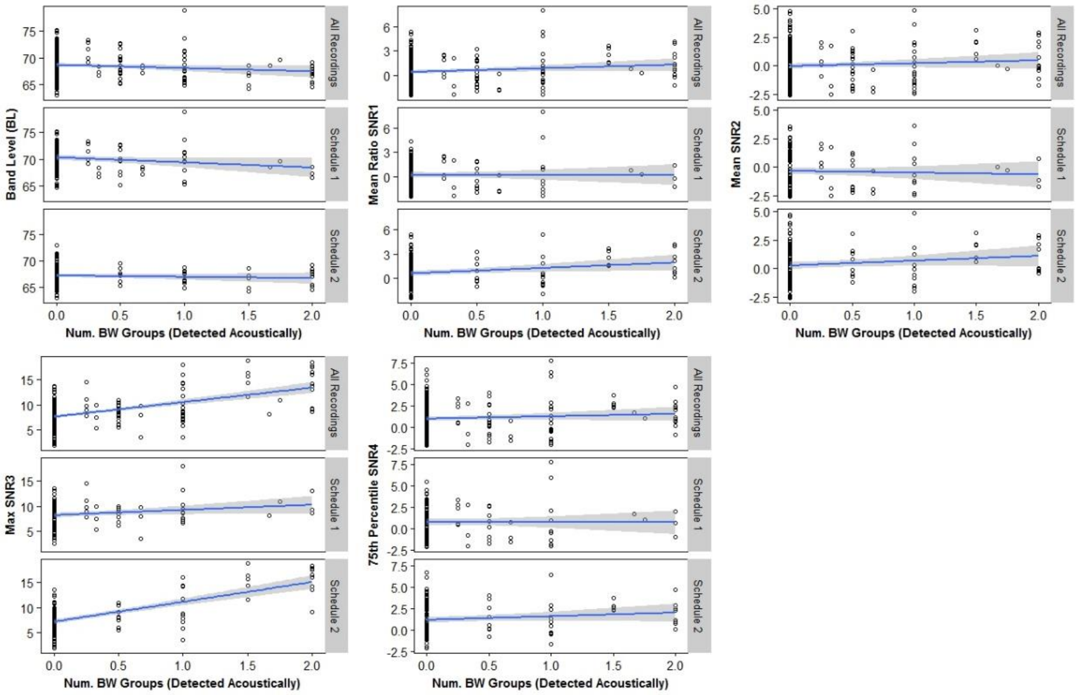


Figure 4.22. Scatterplots of sound level metrics vs number of blue whale groups acoustically detected in Geographe Bay using data averaged per hour and all samples. BW: blue whale.

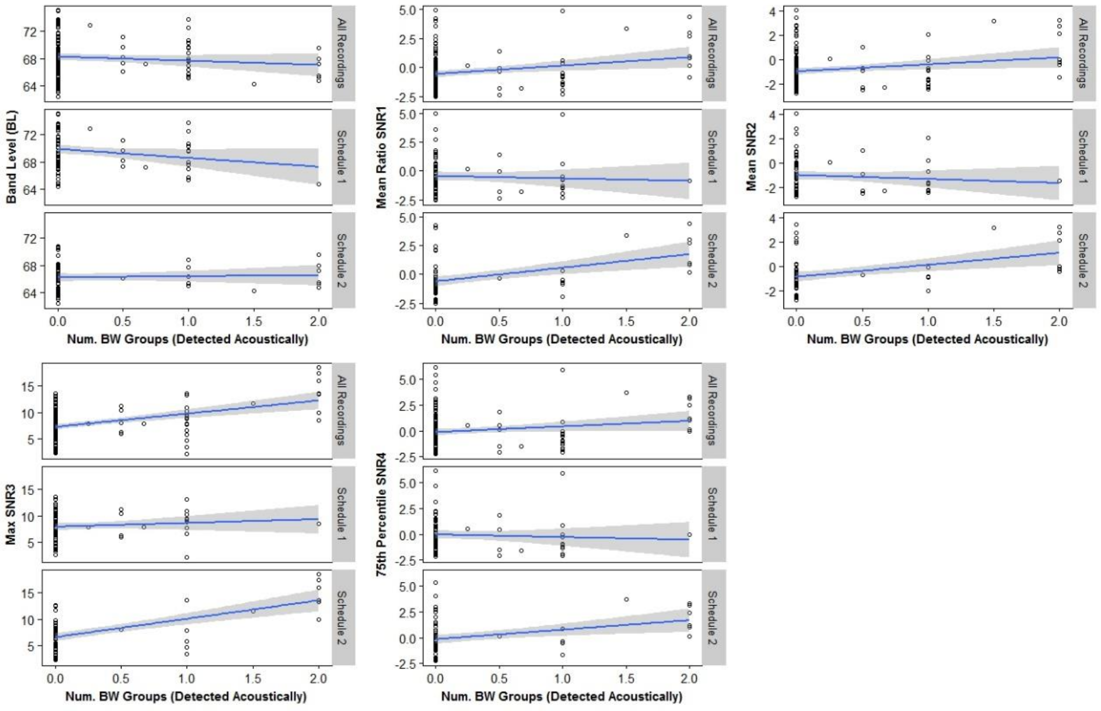


Figure 4.23. Scatterplots of sound level metrics vs number of blue whale groups acoustically detected in Geographe Bay using data averaged per hour and using samples without vessels recorded. BW: blue whale.

Table 4.12. Summary of Peterson correlation test coefficients for different SNR measures vs acoustic counts of groups of blue whales in Geographe Bay based on daily morning (AM) and afternoon (PM) means. Values highlighted represent the highest correlation coefficients per each SNR and recording schedule.

SNR measures	**Recordings used**	**Schedule 1 (2010-2011)**				**Schedule 2 (2013-2014)**				**Combined schedules (2010-2011 & 2013-2014)**			
		Pearson Correlation Coefficient	**t**	**CI**	**P value**	**Pearson Correlation Coefficient**	**t**	**CI**	**P value**	**Pearson Correlation Coefficient**	**t**	**CI**	**P value**
Band level (BL - Eq. 1)	All recordings	-0.21	-1.30	-0.48 0.11	0.199	-**0.183**	-1.19	-0.45 0.12	0.23	**-0.185**	-1.69	-0.38 0.03	0.093
	Excluding recordings with vessels	**-0.34**	-1.95	-0.61 0.01	0.059	0.049	0.27	-0.29 0.38	0.78	-0.143	-1.14	-0.37 0.10	0.255
Mean Ratio SNR1 (Eq. 2)	All recordings	0.05	0.29	-0.26 0.35	0.771	0.322	2.17	0.02 0.56	0.035	0.196	1.80	-0.01 0.39	0.074
	Excluding recordings with vessels	**-0.27**	-1.55	-0.56 0.08	0.129	**0.516**	3.36	0.21 0.73	0.002	**0.343**	2.90	0.10 0.54	0.005
Mean SNR2 (Eq.3)	All recordings	-0.037	-0.23	-0.34 0.27	0.818	0.268	1.78	-0.03 0.52	0.082	0.158	1.44	-0.05 0.36	
	Excluding recordings with vessels	**-0.062**	-0.34	-0.40 0.29	0.735	**0.480**	3.04	0.16 0.70	0.004	**0.308**	2.57	0.07 0.51	
Max SNR3 (Eq. 4)	All recordings	0.180	1.12	-0.13 0.46	0.266	**0.708**	6.43	0.51 0.83	1.03 e-07	0.524	5.54	0.34 0.66	3.53 e-07
	Excluding recordings with vessels	**0.201**	1.12	-0.15 0.51	0.269	0.706	5.56	0.47 0.84	4.30 e-06	**0.568**	5.48	0.37 0.71	7.78 e-07
75th Percentile SNR4 (Eq. 5)	All recordings	-0.007	-0.04	-0.31 0.30	0.963	0.230	1.51	-0.07 0.49	0.137	0.137	1.24	-0.80 0.34	0.215
	Excluding recordings with vessels	**0.025**	0.14	-0.32 0.37	0.889	**0.403**	2.45	0.06 0.65	0.019	**0.265**	2.18	0.02 0.47	0.032

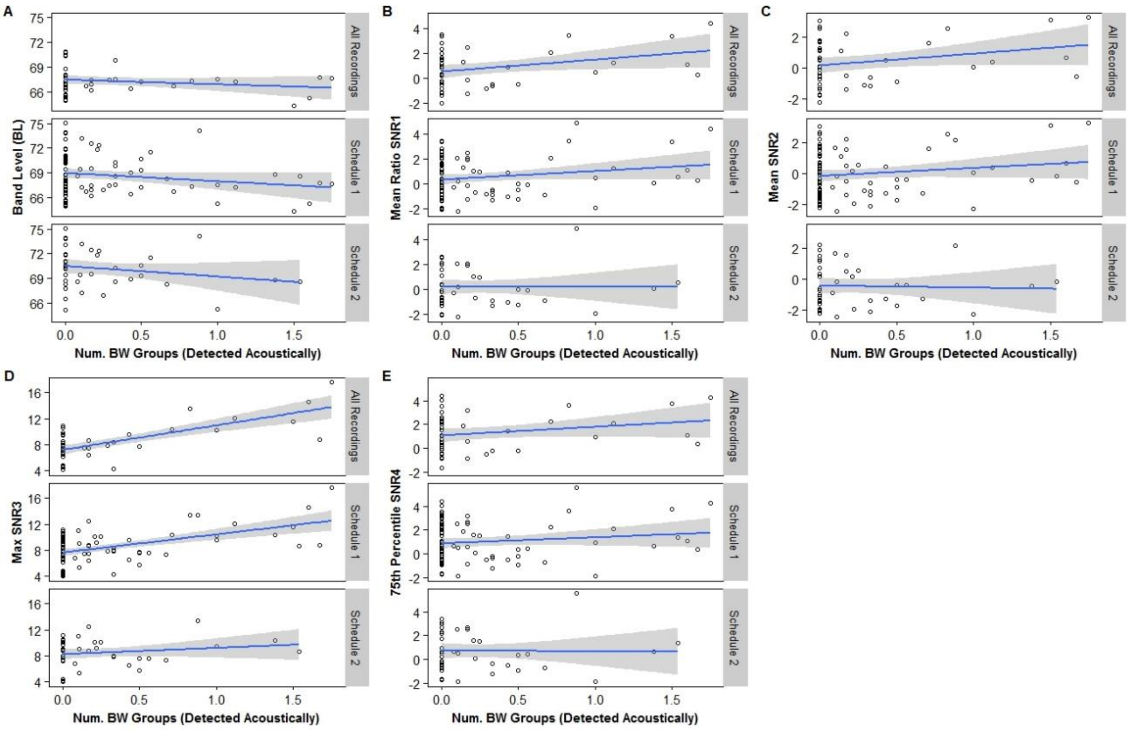


Figure 4.24. Scatterplots of sound level metrics vs number of blue whale groups acoustically detected in Geographe Bay using data averaged daily per morning (AM) and afternoon (PM). BW: blue whale.

Table 4.13. Summary of Pearson correlation test coefficient for different SNR measured vs number of blue whale groups visually counted in Geographe Bay based on hourly means. Values highlighted in bold represent the highest coefficients per each SNR and recording schedule.

SNR measures	**Recordings used**	**Schedule 1 (2010-2011)**				**Schedule 2 (2013-2014)**				**Combined schedules (2010-2011 & 2013-2014)**			
		Pearson Correlation Coefficient	**t**	**CI**	**P value**	**Pearson Correlation Coefficient**	**t**	**CI**	**P value**	**Pearson Correlation Coefficient**	**t**	**CI**	**P value**
SNR (Eq. 1) Psignal only	All recordings	**-0.05**	-0.51	-0.22 0.13	0.610	-0.09	-1.08	-0.25 0.07	0.279	**-0.15**	-2.42	-0.26 -0.02	0.016
	Excluding recordings with vessels	-0.09	-0.75	-0.30 0.14	0.454	**-0.09**	-0.73	-0.33 0.15	0.463	-0.20	-2.35	-0.35 -0.03	0.019
Mean SNR (Eq. 2)	All recordings	0.04	0.45	-0.13 0.22	0.648	0.04	0.51	-0.12 0.20	0.609	0.06	1.05	-0.05 0.18	0.293
	Excluding recordings with vessels	**-0.15**	-1.30	-0.36 0.07	0.195	**0.09**	0.72	-0.15 0.33	0.473	**0.05**	0.60	-0.11 0.21	0.543
Mean SNR (Eq. 3)	All recordings	-0.03	-0.28	-0.20 0.15	0.776	0.04	0.52	-0.12 0.21	0.602	0.06	0.93	-0.06 0.17	0.350
	Excluding recordings with vessels	**-0.18**	-1.58	-0.39 0.04	0.117	**0.11**	0.85	-0.14 0.34	0.394	**0.08**	0.95	-0.08 0.24	0.342
Max SNR (Eq. 4)	All recordings	**0.17**	1.86	-0.01 0.33	0.065	0.17	1.97	0.00 0.32	0.050	**0.16**	2.59	0.03 0.27	0.010
	Excluding recordings with vessels	0.03	0.26	-0.19 0.25	0.795	**0.11**	0.87	-0.14 0.34	0.384	0.07	0.81	-0.09 0.23	0.414
75th Percentile SNR (Eq. 5)	All recordings	0.03	0.37	-0.14 0.21	0.710	0.01	0.08	-0.16 0.17	0.080	0.04	0.59	-0.08 0.15	0.550
	Excluding recordings with vessels	**-0.16**	-1.40	-0.37 0.06	0.163	**0.06**	0.51	-0.18 0.30	0.608	**0.03**	0.30	-0.141 0.191	0.760

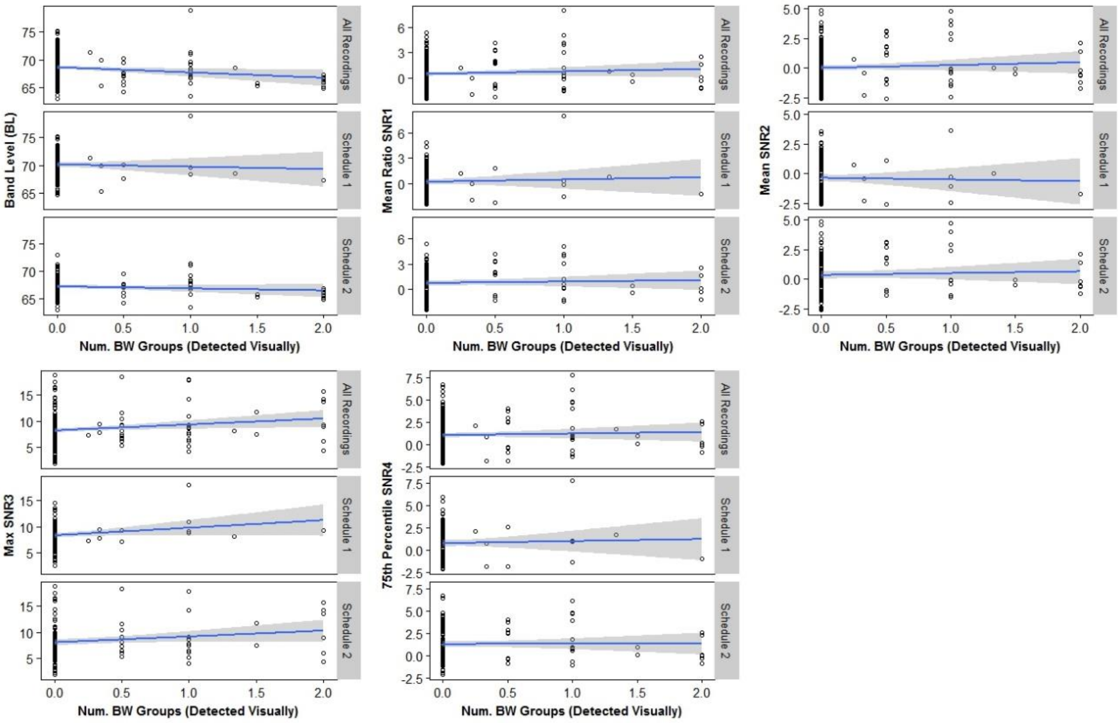


Figure 4.25. Scatterplots of sound level metrics vs groups of blue whales visually counted in Geographe Bay using data averaged per hour. BW: blue whale.

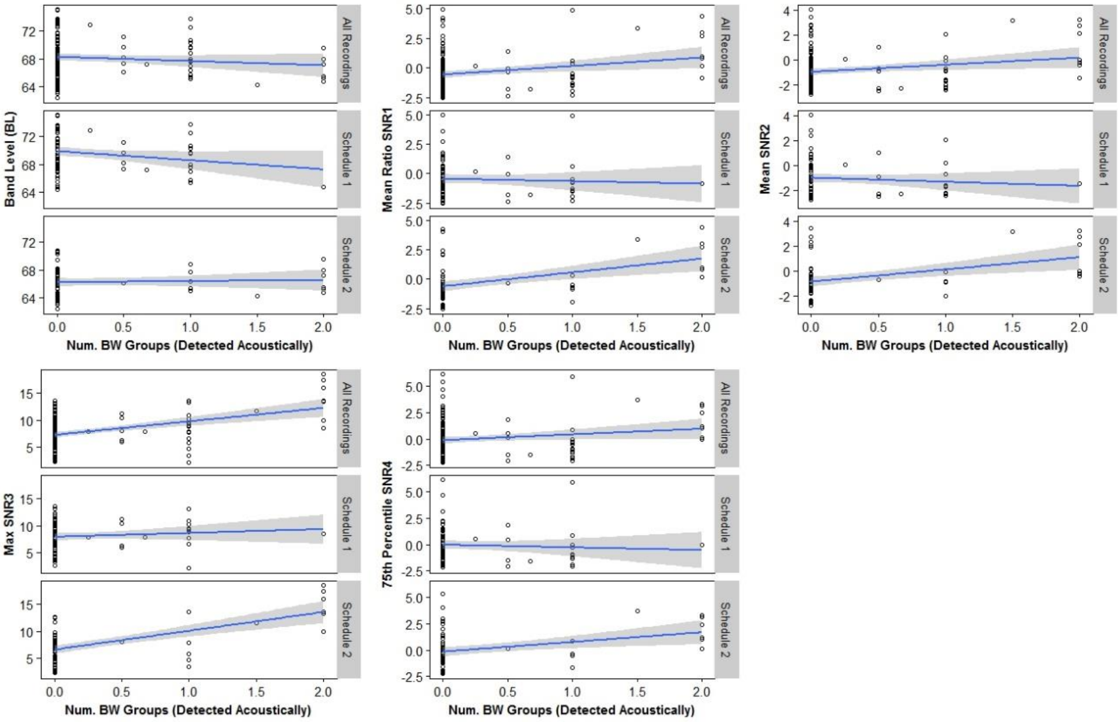


Figure 4.26. Scatterplots of SNRs vs groups of blue whales visually counted in Geographe Bay using data averaged per hour using dataset without vessels. BW: blue whale.

Table 4.14. Summary of Pearson correlation test coefficients for different SNR measures vs. number of groups of blue whales visually counted in Geographe Bay based on daily AM/PM means. Values highlighted in bold represent the highest coefficients per each SNR and recording schedule.

SNR measures	**Recordings used**	**Schedule 1 (2010-2011)**				**Schedule 2 (2013-2014)**				**Combined schedules (2010-2011 & 2013-2014)**			
		Pearson Correlation Coefficient	**t**	**CI**	**P value**	**Pearson Correlation Coefficient**	**t**	**CI**	**P value**	**Pearson Correlation Coefficient**	**t**	**CI**	**P value**
SNR (Eq. 1) Psignal only	All recordings	-0.189	-1.18	-0.47 0.13	0.242	**-0.248**	-1.64	-0.51 0.0	0.107	**-0.303**	-2.87	-0.48 -0.09	0.005
	Excluding recordings with vessels	**-0.270**	-1.54	-0.56 0.08	0.134	-0.134	-0.75	-0.45 0.21	0.454	-0.234	-1.91	-0.45 0.01	0.060
Mean SNR (Eq. 2)	All recordings	0.047	0.29	-0.26 0.35	0.77	**0.209**	1.37	-0.09 0.47	0.177	**0.195**	1.79	-0.02 0.39	0.076
	Excluding recordings with vessels	**-0.273**	-1.55	-0.56 0.08	0.129	0.015	0.088	-0.32 0.35	0.930	0.030	0.24	-0.21 0.27	0.810
Mean SNR (Eq. 3)	All recordings	-0.021	-0.13	-0.33 0.29	0.894	**0.212**	1.38	-0.09 0.48	0.172	**0.207**	1.91	-0.01 0.40	0.059
	Excluding recordings with vessels	**-0.295**	-1.69	-0.58 0.05	0.101	0.047	0.26	-0.30 0.38	0.794	0.082	0.65	-0.16 0.31	0.515
Max SNR (Eq. 4)	All recordings	**0.265**	1.69	-0.05 0.53	0.098	**0.385**	2.67	0.09 0.48	0.170	**0.325**	3.09	0.11 0.50	0.002
	Excluding recordings with vessels	0.019	0.10	-0.33 0.36	0.914	0.084	0.47	-0.26 0.41	0.638	0.078	0.62	-0.16 0.31	0.533
75th Percentile SNR (Eq. 5)	All recordings	0.050	1.37	-0.09 0.47	0.177	**0.153**	0.99	-0.15 0.43	0.325	**0.154**	1.40	-0.06 0.35	0.163
	Excluding recordings with vessels	-**0.308**	-1.77	-0.59 0.04	0.085	-0.006	-0.03	-0.34 0.33	0.969	0.004	0.03	-0.23 0.24	0.972

4.6.3. Pearson correlation analysis for number of groups acoustically detected vs number of groups visually tracked

Table 4.15. Summary of Pearson correlation test coefficients for number of humpback and blue whale groups acoustically counted vs number of groups visually counted in Geographe Bay based on hourly means. Values highlighted in bold represent the highest coefficients per each SNR and recording schedule.

SNR measures	**Recordings used**	**Schedule 1 (2010-2011)**				**Schedule 2 (2013-2014)**				**Combined schedules (2010-2011 & 2013-2014)**			
		Pearson Correlation Coefficient	**t**	**CI**	**P value**	**Pearson Correlation Coefficient**	**t**	**CI**	**P value**	**Pearson Correlation Coefficient**	**t**	**CI**	**P value**
Humpback whales	All recordings	0.45	5.39	0.29 0.58	3.62 e-07	0.41	5.252	0.26 0.54	5.66 e-07	0.38	6.56	0.27 0.48	2.85 e-10
	Excluding recordings with vessels	**0.52**	5.26	0.33 0.67	1.38 e-06	0.37	3.10	0.13 0.56	0.002	0.42	5.36	0.26 0.54	3.40 e-07
	Excluding recordings with vessels and blue whales	0.51	4.92	0.31 0.66	5.77 e-06	**0.43**	3.34	0.17 0.62	0.001	**0.45**	5.557	0.29 0.58	1.68 e-07
Blue whales	All recordings	0.54	7.03	0.40 0.66	1.47 e-10	0.27	3.34	0.11 0.42	0.001	0.35	5.951	0.23 0.45	8.76 e-09
	Excluding recordings with vessels	0.23	2.01	0.02 0.43	0.047	0.45	3.94	0.22 0.62	0.0002	0.40	5.05	0.24 0.52	1.32 e-06

Table 4.16. Summary of Pearson correlation test coefficients for number of humpback and blue whale groups acoustically counted vs number of groups visually counted in Geographe Bay based on daily AM/PM means. Values highlighted in bold represent the highest coefficients per each SNR and recording schedule.

SNR measures	Recordings used	Schedule 1 (2010-2011)				Schedule 2 (2013-2014)				Combined schedules (2010-2011 & 2013-2014)			
		Pearson Correlation Coefficient	**t**	**CI**	**P value**	**Pearson Correlation Coefficient**	**t**	**CI**	**P value**	**Pearson Correlation Coefficient**	**t**	**CI**	**P value**
Humpback whales	All recordings	0.53	3.86	0.26 0.72	0.0004	**0.63**	5.16	0.40 0.78	0.61 e-06	0.55	5.89	0.37 0.68	8.38 e-08
	Excluding recordings with vessels	**0.65**	4.68	0.38 0.81	5.62 e-05	0.49	3.12	0.17 0.71	0.003	0.52	4.87	0.32 0.68	7.62 e-06
	Excluding recordings with vessels and blue whales	0.64	4.46	0.37 0.81	0.0001	0.59	3.70	0.27 0.78	0.0009	**0.60**	5.49	0.39 0.73	9.74 e-07
Blue whales	All recordings	**0.81**	8.52	0.66 0.89	2.37 e-10	**0.53**	3.96	0.26 0.71	0.0002	**0.56**	6.09	0.39 0.69	3.53 e-08
	Excluding recordings with vessels	0.23	1.27	-0.13	0.213	0.43	2.68	0.10 0.67	0.011	0.38	3.24	0.14 0.56	0.001

Chapter 5.

Modelling detection probabilities of baleen whales: the influence of imperfect detection on acoustic monitoring of baleen whales

The aim of this chapter was to estimate acoustic detection probabilities of pygmy blue whales (*Balaenoptera musculus brevicauda*) and humpback whales (*Megaptera novaeangliae*) migrating through Geographe Bay, Western Australia, using N-mixture models. Specifically, temporal, anthropogenic, ecological and behavioural factors influencing the availability and detectability processes were evaluated for each species and different sound types (song and non-song). Detection probabilities were species specific with humpback whales having a higher detection than pygmy blue whales. Differences in the detection were observed for different humpback whale cohorts, singers had a higher detection than cohorts producing non-song sounds. Principal factors influencing the availability and detectability processes were Julian day, year and number of groups visually observed, but their significance depended upon species and sound type. The number of consecutive recordings was also significant in the detectability process particularly for humpback whales producing song. The variability in detection probabilities between and within a species, and the factors affecting it should be considered when designing acoustical surveys for monitoring, particularly when the aim of monitoring is evaluation of population trends.

5.1. Introduction

Monitoring heavily exploited species is vital in guiding regulatory and management decision making so that recovery can be achieved successfully (Milner-Gulland & Rowcliffe 2007). During the 19th and 20th centuries, a large number of baleen whale species were over-exploited, which led to severe declines of many populations and near-extinction of some (e.g., right whales, blue whales, humpback whales, etc.). Since the ban of commercial whaling in 1965, some baleen whale species such as humpback whales (*Megaptera novaeangliae*), have been recovering rapidly. Rates of recovery for other species such as blue whales (*Balaenoptera musculus*), and in particular the subspecies pygmy blue whale (*Balaenoptera musculus brevicauda*), are less certain (International Whaling Commission, 2018). While whaling effort is now much more controlled and limited through quotas imposed by the International Whaling Commission, there are other anthropogenic threats that may be affecting their recovery (e.g., noise pollution, ship strike, entanglements, etc.). Consequently, the International Whaling Commission has identified monitoring as one of the key steps in developing conservation plans that effectively manage threats to baleen whale populations (International Whaling Commission 2016a; International Whaling Commission 2016b).

Baleen whales can be surveyed in various ways including methods such as land, vessel, or aerial-based visual (aircraft or drone) observations and acoustic observations (e.g., towed acoustic arrays or remote, fixed passive acoustic monitoring). Regardless of the method, all approaches detect animals imperfectly which affects the accuracy and reliability of survey data (McCarthy et al. 2013). Even when surveys are designed to maximise consistency and are standardized by using data collection protocols, the probability of detecting a species, groups or individuals is not constant in time and/or space (Alldredge et al. 2006; Murn & Holloway 2016); and it can be influenced by species behaviour, weather conditions, and survey coverage among many other factors. Often, detection is assumed to be constant across surveys in a study, however, this assumption is usually violated and may lead to inaccurate conclusions (Thompson 2002; McCallum 2005b; Kellner & Swihart, 2014). Because of this, understanding the probability of detection of animals being surveyed and its variability is essential for determining a survey's reliability and to accurately estimate ecological parameters (Alldredge et al. 2007; Kellner & Swihart 2014).

The probability of detection can be defined as the chance that an individual or species of interest will be detected given it is present in the area being surveyed (McCarthy et al. 2013). Detection probability can be broken down into two components: (i) availability (P_a) which is the probability that a species or individual is available to be detected (i.e., it emits a detectable cue) and (ii) detectability (P_d) which is the probability that the species or individual is detected given it produces a cue (McCallum 2005b; Scott et al 2005). For visual surveys a cue can be a whale blowing or breaching, while for passive acoustic monitoring (PAM) cues are sounds produced by whales. Availability on the one hand, is affected by the behaviour of the species, and can vary with ecological conditions such as seasonality and habitat (McCallum et al. 2005b). Detectability on the other hand, is a function of conditions that affect the detection of cues (i.e., for visual observations this would be the observer's ability to see the cue, or environmental conditions such as glare on the water, etc.). While, some studies have suggested that availability is not important when detection probabilities are used for estimating population trends (Verfuss et al. 2018); other authors advise that regardless of the aim of the study, estimating detection probability without considering all components will introduce bias in the final estimates (McCallum 2005a; Riddle et al. 2010; Amundson et al. 2014; Coggins et al. 2014; Kellner & Swihart 2014). Furthermore, studies that fail to properly estimate imperfect detection will result in weakened statistical inferences upon which decision making, extinction risks and policy are based (Kellner & Swihart 2014; Kéry & Royle 2016).

The components of detection probability can be estimated using a range of modelling approaches (e.g., distance sampling, removal models, double observer methods, and many more). The relevant approach depends upon the survey design and type of data collected. The models available can estimate aspects of one or both components of detection probability (Riddle et al. 2010). For example, distance sampling (Buckland et al. 2001) estimates detectability (P_d) at range from an observer. Double observer methods (Nichols et al. 2000) estimate detectability (P_d) as a function of observer bias. Removal (Farnsworth et al. 2002) and N-mixture models (Royle et al. 2004) are designed to estimate both P_a *and* P_d for all animals producing cues in the study area and during the general period of the surveys ($P_a > 0$).

For visual-based cetacean studies that aim to estimate population trends, a common approach is to use distance sampling methods (e.g., Marques et al. 2009, Marques et al. 2013). This approach assumes that the species is present and available to be detected (i.e., at the surface of the water). Distance sampling methods estimate the probability of detection as a function of range from the observer, which generally decreases with increasing distance. Visual observations from a vessel, land or aircraft commonly measure the declination from the horizon (using clinometers, theodolites, etc.) to the observed whale and use this metric to calculate distances.

For studies that use acoustic detections to survey whales, the cues used are the sounds produced by the species of interest. Auto-detectors that search for cues are increasingly used due to their greater time efficiency than manually searching acoustic data sets (e.g., Gavrilov et al. 2013, for a review on detection algorithms see Bittle and Duncan, 2013). In acoustic studies, the detection probability as a function of cue characteristics, environmental conditions, and propagation and transmission loss at range is commonly assessed (Zimmer 2011; Helble et al. 2013). For acoustic studies, the detection range is influenced by background noise conditions; which in turn is influenced by wind, sea state conditions and anthropogenic noise (e.g., vessel and industrial noise, etc.). High ambient noise levels resulting from wind and wave activity can reduce the range at which cues can be detected. The presence of vessels may mask certain sounds when cues and vessel noise overlap in frequency bands (Hatch et al. 2008; Melcón et al. 2012; Erbe et al. 2016).

To reduce the biases in acoustic surveys caused by variability in detection, spatially explicit capture-recapture (SECR) or mark-recapture distance sampling (MRDS) methods can be used (Borchers 2012; Marques et al 2013). SECR incorporate spatial information in terms of location of the sensor or “trap” used to detect the individuals. This method can be used when distances of detected animals cannot be obtained but the same individual is detected by multiple sensors. The detection function for this method can be defined as a function of distance of the area covered by each sensor (Borchers 2012; Marques et al. 2013). MRDS can be interpreted as a type of SECR (Borchers 2012) and uses information from two observers or observation points in an overlapping area of study. In MRDS, each observer records the location of detected animals, and observations that overlap are considered recaptures. MRDS is a type of capture-recapture model that integrates a state model for animal location with the likelihood of estimated recapture (Borchers 2012). For acoustic-only surveys, SECR is preferred over MRDS (Marques et al 2013), however, only a few studies have so far used it (e.g. Marques et al. 2012; Martin et al. 2013). The main limitation of MRDS and SECR models is the need to estimate distance of the source accurately. To estimate this parameter, data should be collected using multiple acoustic sensors or acoustic arrays. The use of acoustics arrays significantly increases the cost and reduces the cost-benefit of passive acoustics methods. In addition, extensive knowledge of the acoustical ecology of the species of interest is critical but not always available (Gannon et al. 2008).

An acknowledged limitation when using these models in acoustics-only studies, is that a proportion of the population will not be available for detection since not all individuals necessarily vocalise (Riera et al. 2013). Furthermore, the availability of vocalising individuals is often considered to be constant. For instance, vocal behaviour (such as vocal rate) is generally assumed to be similar for all individuals and most studies use specific cue types which may represent some cohort of the population and not others (e.g., song in populations in which only males sing). Such assumptions do not account for variability in vocal behaviour among cohorts of a population. Some hierarchical models (e.g., hierarchical N-mixture and hierarchical distance sampling models), however, can model availability, detectability, and the influence of covariates (cohort-specific, temporal, environmental, etc.) in each process. Consequently, knowledge on sources of biases that should be considered when using acoustics-only surveys for population monitoring can be evaluated. In addition, if there are visual survey observations that have been conducted simultaneously, acoustic availability (the probability of animals vocalising during a survey) can be estimated (e.g., Akamatsu et al. 2008).

To advance the utility of acoustics-only baleen whale surveys, this study aimed to determine important sources of biases for acoustic based monitoring programs. Specifically, this study aimed to: (i) estimate detection probabilities of acoustics-based surveys of two species of baleen whales, humpback whales and pygmy blue whales in Geographe Bay (Western Australia), (ii) identify conditions (i.e., sea state, Julian day, population density, presence of vessels, % of recordings having whale sounds) influencing detection probability components (availability and detectability), and (iii) identify key survey criteria that should be considered in the development of passive acoustic optimal monitoring protocols that may influence detection probabilities of baleen whales. Because monitoring programs are fundamental for effective conservation and management, but can be expensive, well-designed programs using cost-effective methods such as acoustics are essential for future monitoring.

5.2. Methods

5.2.1. Study area

This study used data collected in November 2010-2011 and 2013-2014 in Geographe Bay, Western Australia. Geographe Bay is located in the southwest of Western Australia from approximately 33° 18’ 32’’S and 115° 38’ 6’’ E to 33° 32’ 6’’ S and 115° 0’ 29’’ E (Figure 1). Most of the bay has a depth of around 30 m, with some areas dropping to around 50 m and areas near the coast approaching depths around 20 m and less. The seafloor is mainly composed of limestone and clay (Borissova 2002). The bay is part of the Geographe Bay Commonwealth Marine Reserve, a reserve composed of 977 km^2 and part of the Leeuwin-Naturaliste bioregion (Department of the Environment and Energy, 2018b). The coastal area is part of Meelup National Park that extends over 11.5 km between Dunsborough and Bunker Bay (Meelup Regional Park, 2018). The regional park falls within the Quindalup system and has hills up to 50 m high.

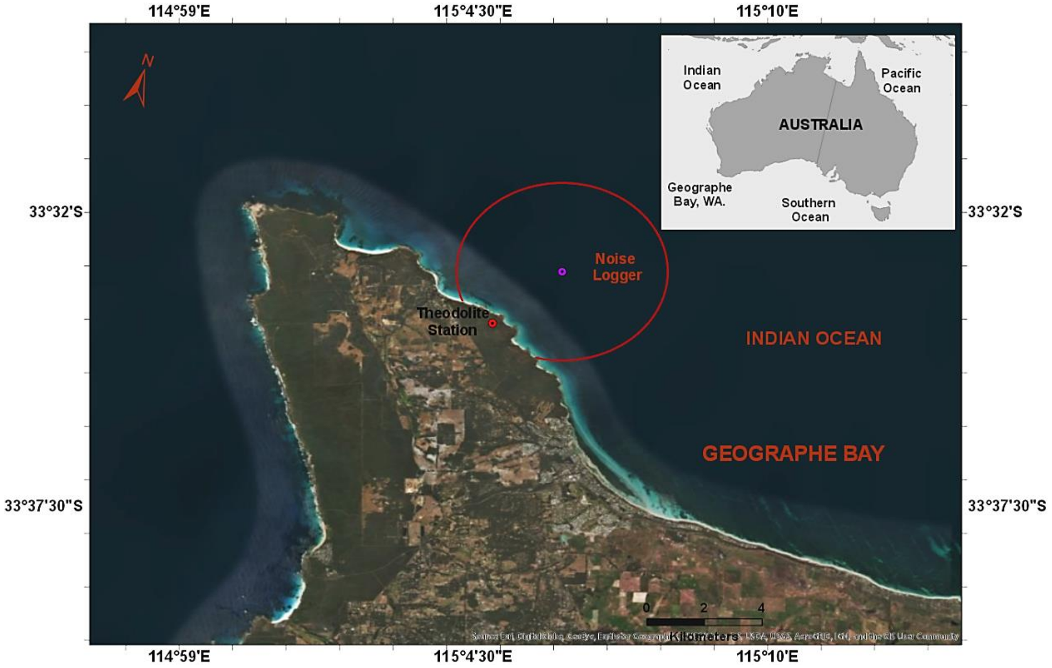


Figure 5.1. **The study area (red circle) within Geographe Bay, Western Australia.**

Humpback and pygmy blue whales pass through the inshore waters of Geographe Bay on their way to Antarctica during the southern migration. The humpback whale peak in migration can be variable among years, however it is generally in September/October. The entire migratory season, however, extends from August to early January. In comparison, pygmy blue whales migrate between October and January and have their peak in Geographe Bay in November (Salgado Kent, Gavrilov et al. 2012). Because individuals from both species pass close to land, this area is ideal for combined land and acoustic based surveys.

5.2.2. Survey design

This study used two independent platforms: land and acoustics. Data was collected simultaneously during the peak of pygmy blue whale migration and just after the peak for humpback whales.

Land-based observations were conducted from a 50-m high hill at 33° 36’ 7.48’’ S and 115° 4’ 46.55’’ E, and used a theodolite TopCon GTS-603AF Electronic Total Station connected to a computer running the real-time positioning software CYCLOPS (v.2.8.04 for 2010-2011 data - Erick Kniest, University of Newcastle) or VADAR (for 2013 – 2014 data, Erick Kniest, University of Newcastle) to track whales. At least three observers conducted observations in two shifts: (i) 7:30 to 11:30 am and (ii) 2:30 and 5:30 pm. Shift duration was weather dependent. A break in shifts at midday reduced observer fatigue and exposure to heat.

Land-based observations consisted of behaviours, local movements and geographic positions of whale groups, as well as number and composition of the groups present in the area at all times. During each survey day, each group was allocated a unique alphabetical letter between A and Z (starting with A), and double-letters (AA, BB, CC, etc.) after Z. When two or more groups joined, the name given to this group was the combination of both original names and the composition adjusted according to the confirmed structure of each of group. For example, if group A (consisting of one adult) was joined by group C (two adults), then the new group was allocated the name AC and the group composition became three adults. When a mother-calf (MC) were joined by a group of adults, these were called escorts and the group was labelled MC+n escorts. Group composition of baleen whales is unstable, particularly for humpback whales, the only exception are mothers with their calf (Clapham 1996). Therefore, it is common that groups of adults split and join, which was considered when naming the groups by labelling them with the original letter followed by a number. For example, if group C composed of 5 adults split into two groups, one of three and one of two individuals, one group was labelled C1 and the second C2. In addition to behavioural data, Information on weather and presence of vessels was also collected. Weather data included qualitative measures of wind speed (in knots) and direction (relative to magnetic north), sea state using a Beaufort scale (Barua, 2005), glare (on a scale from 0 (no glare) to 3 (intense glare)), cloud cover (in octaves), presence of haze and swell height and direction. Surveys were undertaken on days with wind speeds less than 15 knots, Beaufort conditions mostly under 4 (one occasion included Beaufort 5), and during periods without rain.

The acoustic-based surveys were conducted using acoustic loggers built at the Centre for Marine Science and Technology (see McCauley et al. 2017 for specifications). The recorders were deployed at 2.5 km northeast of the land-based station (Figure 1). The recorders were calibrated before and after deployment using white noise of known level input immediately behind the hydrophone, plus the hydrophone sensitivity. Recorders were scheduled to record for 13 minutes every 15 minutes for the 2010 and 2011 seasons, and 23 minutes every 30 minutes for the 2013 and 2014 seasons. Each individual recording of 13 or 23 minutes is called a *sample.* Recorder settings varied among years and are presented in Table 5.1.

Table 5.1. Acoustic logger settings and recording schedules for each year of study.

Year	Total Gain (dB)	Sampling frequency (kHz)	Anti-aliasing filter (kHz)	Duty cycle	Underwater recording period
2010	40	12	5	13.3 minutes every 15 minutes	14/11/2010 to 13/12/2010
2011	40	12	5	13.3 minutes every 15 minutes	10/11/2011 to 15/12/2011
2013	40	6	1.8	23 minutes every 30 minutes	14/11/2013 to 05/02/2014
2014	40	6	1.8	23 minutes every 30 minutes	31/10/2014 to 15/01/2015

The received signals were amplified using a pre-amplifier and a channel amplifier of 20 dB gain each. The amplified signals were low-pass filtered using an anti-aliasing filter and high-pass filtered with a roll-off at 8 Hz to reduce low-frequency ambient noise and increase the dynamic range of the logger. The logger position was similar for all deployments with a depth ranging from 29 to 32 m (Table 5.2).

Table 5.2.Geographic positions and depths of underwater acoustic recorders deployed in Geographe Bay, WA, in 2010-2011 and 2013-2014.

Year	Latitude (S)	Longitude (E)	Seafloor depth (m)
2010	33°32'51.66"	115° 6'29.28"	29.0
2011	33°32'52.38"	115° 6'39.18"	29.0
2013	33°32'33.00"	115° 6'39.42"	32.3
2014	33°32'45.72"	115° 7'0.90"	30.0

5.2.3. Data processing

Because visual and acoustical surveys have different limitations, some considerations were necessary to process and subsample the data so detection probabilities could be compared. First, acoustical surveys were not dependent on good weather or daylight conditions; however, land-based visual surveys were. Consequently, acoustic data were subsampled to match days and times when visual data were collected. Second, there were differences in the detection range between the methods, with the area of acoustical detection larger than the area of visual detections. Areas were standardized so detection probabilities could be estimated for the same area and population sample. To inform the selection of the sample area, the area of detection for each survey method was estimated using a) propagation models and transmission loss estimates for acoustic surveys and b) fitting a detection function to land-based surveys.

Acoustical detection mainly depends on the seafloor depth and composition, and signal characteristics (Au & Hastings 2008). The selected study area and corresponding detection range used in this study was based on propagation modelling and transmission loss estimates of blue and humpback whale vocalisations in Salgado Kent, Gavrilov et al. (2012). In Geographe Bay, the depth, flat seabed and seafloor composition resulted in estimation of sound transmission up to 20-30 km and 6-10 km for humpback and pygmy blue whales, respectively (Salgado Kent, Gavrilov et al. 2012). Considering that the maximum detection range for visual observations based on height of the station was 15 km, there was considerable overlap in observations using the two survey types in the area of study. Standardization of the study area was based on minimising the influence of range on detection. In other words, the study site included the area in which whales could be confidently detected acoustically and visually by a trained observer if (1) the whales were available to be detected, and (2) the observer was looking in the right direction (during visual surveys) and attentively listening and reviewing spectrograms (for acoustic surveys).

A radius of 3 km around the recorder was defined as the ’Study Area’, which included a 19.7 km^2 circular area off Pt Piquet (Figure 5.1). This radius in the study area corresponded to signals that had an SNR higher than 8 dB regardless of the species (Salgado-Kent, Gavrilov et al. 2012). These signals could easily be distinguished from background noise. An SNR of 8 dB corresponded to 6 km from the 50 m hill for visual surveys.

5.2.3.1. Acoustical data

Acoustical data were processed with CHORUS (Characterisation Of Recorded Underwater Sound), a Graphical User Interface running in MATLAB (The MathWorks, Inc.) and developed by CMST (Gavrilov & Parsons 2014). Signals produced by blue and humpback whales were manually searched for by plotting power spectral density (PSD) plots for each sample. Spectrograms were produced in a frequency range of 6 Hz to 4 kHz (depending on the sampling frequency) by Fourier-transforming the recorded pressure time series in a Hamming window of 1 s or 0.5 s overlapping either 50 or 90% (see Chapter 3 additional for details).

Humpback and blue whale signals were identified based on their frequencies and using catalogues and descriptions from published literature (Silber 1986; Mellinger et al. 2003; Simao et al. 2005; McDonald et al. 2006; Dunlop et al. 2007; Oleson Calambokidis, Burgess et al. 2007; Zoidis et al. 2008; Gavrilov et al. 2011; Stafford et al. 2011; Salgado-Kent, Gavrilov et al. 2012; Rekdahl et al. 2013; Recalde-Salas et al. 2014; Fournet et al. 2015; CMST unpublished call catalogues, Chapter 2).

Signals were classified into sound types including song and non-song. Song was identified as a patterned sequence of notes or units (Clark 1982; McDonald et al. 2006), while non-song vocalisations were single units that did not follow a repetitive pattern (Clark 1982; Dunlop et al. 2007; Oleson, Calambokidis, Burgess et al. 2007). Catalogues of non-song sounds for humpback and blue whales were also used to help with their identification (Silber 1986; Simao et al. 2005; Dunlop et al. 2007; Zoidis et al. 2008; Rekdahl et al. 2013; Fournet et al. 2015). Because humpback whale song changes every year, a seasonal template was developed for each year to help identify singers and non-song sounds (see Chapter 3).

After identifying and classifying the sounds, the number of groups vocalising in a sample was estimated. A group was defined as whales within less than 100 m of each other, travelling together and with coordinated behaviour (Morete et al. 2007). Groups can be singleton or composed by multiple animals. The number of groups was chosen over number of individuals vocalising because with a single stationary recorder it was not possible to identify which individual within a group was vocalising. This scale was also preferred over estimation of individuals based on cue counting as done in other studies (e.g., Marques et al. 2011; Martin et al. 2013) because it could not be assumed that all individuals had the same vocalisation rates (See Chapter 3 for additional information). Consequently, the number of groups vocalising was assessed based on behavioural attributes of the species described below.

For song, the presence of multiple songs in the sample were assumed to be vocalised by different groups. This assumption was made based on the knowledge that singers generally sing alone and tend to stop singing in the presence of other males or adults (Tyack 1981; Payne et al. 1983; McDonald 2006). Groups producing song in a sample were distinguished from one another based on a combination of conditions, including: different phrases been sung at the same time, overlap of song units in a spectrogram and differences in SNRs of sounds. Non-song sounds were assumed to be produced by different groups than those vocalising song based on the same rationale as above. When multiple non-song sounds were observed in the same sample, these were assigned to different groups when SNRs of the sounds in the spectrogram were clearly different, or the sounds were overlapping. A complete description of methods and the limitations to estimate number of groups in a sample is presented in Chapter 3.

Data was organised in a database that included date, time, number of vocalising groups, sound type, etc. Considering that temporal autocorrelation was identified in consecutive recordings made over several hours in Chapter 3, recordings were grouped per day in morning and afternoon (AM/PM) blocks. Recordings within a block were numbered in chronological order. This was undertaken as part of the statistical design to easily identify samples that likely were autocorrelated and those likely free of a correlation structure (see section 5.2.4).

5.2.3.2. Land-based data

Daily databases were directly exported from Cyclops or VADAR in CSV format and combined into a single Excel database for all years. Observations of joint and/or split groups were discarded to avoid double counting groups. Only those observations within 6 km of the land-based station were included in analysis so that the area of visual observations was standardized with that of acoustic surveys.

Each observation included the following information: Date, year, time of observation, group composition (e.g., singleton, mother-calf, etc.), behavioural state (e.g., travelling, milling, surface activity, surface passive), observation cue (e.g., dorsal fin, breach, fluke), group name (e.g., A, B, C, AA, etc.), weather information (Beaufort, wind speed, swell height, etc.), and presence of vessel. An additional column was created to indicate the acoustic sound type that might be associated with groups observed based on their group composition. For example, “possible singers” corresponded to those groups composed of a single individual and groups of mother-calf pairs with a single confirmed escort. “Possible non-singers” were groups consisting of mother-calf pairs, multiple adults and groups of mother-calf pairs with multiple escorts. This classification was only undertaken for humpback whales. For blue whales only one group was observed at a time in the study area on almost all occasions.

The visual data were organised as *samples* in the same way the acoustic data were; with visual observations beginning at 7.30 am corresponding to acoustic recordings beginning at 7:30 am, visual observations beginning at 7:45 am corresponding to recordings beginning at that time, and so on). Blocks and consecutively numbered samples within blocks were also allocated to visual observation data.

5.2.4. Probability of acoustical detection

Detection probabilities were estimated separately for humpback whales producing song, humpback whales producing non-song sounds and blue whales (song and non-song producers, together) using an extension of the generalized binomial N-mixture model for repeated count data for migratory species (Chandler et al. 2011). This model is a generalization of the N-mixture model developed by Royle (2004) and integrates emigration processes (Chandler et al. 2011).

The N-mixture model is frequently used to analyse spatiotemporal data where detections of species are made at different sites over time (e.g., Dail & Madsen 2011; Dénes et al. 2015; Tozer et al. 2016), thus the sampling design includes temporally replicated counts (Royle 2004). Here, the model was adapted from the standard multi-site sampling approach to sampling at the same site at different times of the seasonal whale migration through the area. Firstly, independent 'sites' (x) referred to in Royle (2004) are here defined as 3-hour time blocks that represented a unique sample of the population migrating through the study area. Time blocks were considered independent (see Royle 2004) based on the fact that the average travel times for humpback or blue whale groups to traverse the ~6 km monitoring area was less than the minimum 3-hour period between time blocks. The average time for whales to traverse the study area was estimated from theodolite tracking data of all groups (humpback and blue whale), and was 3.09 hours for humpback whales and 2.5 hours for blue whales. Secondly, 'visits' or repeated counts (j) as referred to in Royle (2004) corresponded to the 13.3 or 23 minutes recording samples within 3-hour time blocks (equivalent to 'site' in Royle 2004). The model here used a multi-year approach where 'visits' (which are recording samples in this study) were carried out within each time block ('sites') during 'T' years of sampling. The model further assumed that within year abundance within a time block remained constant (Fiske & Chandler 2011).

The model used in this study, as described by Chandler et al. (2011), had three hierarchical levels. The first described the total number of individuals potentially using time blocks within the migratory year. This is commonly referred to as the abundance process. The second described the proportion of the total groups present within time blocks on a particular visit (i.e., recording sample) during surveys Chandler et al. (2011), which is commonly referred to as the availability process. The third described the proportion of detected groups given they were available for detection during each visit, which is commonly described as the detectability process (Chandler et al. 2011; Tozer et al. 2016). The hierarchical structure of this model allows an evaluation of the influence each process (population, availability and detectability processes) and its variation independently to then combine their influence as a single detection probability. By modelling each process independently, different ecological, biological, environmental and technical characteristics can be added to the detection probability estimation. This also reduces uncertainty and bias in final estimations because model assumptions are reduced. For example, distance sampling methods only consider the detectability process in the estimation of the detection probability (Buckland et al. 2001). Therefore, the model assumes an availability of 1 (individuals are there and available to be detected) during the survey. This assumption may not be true for the entire duration of the survey because individuals may either not be present within the survey area at the time of sampling or may not produce a cue that makes them available to be detected. By assuming that all individuals are producing a cue at the time of the survey (i.e. available to be detected), the detection probability will be biased. Although, hierarchical models have their own set of biases (see Duarte et al. 2018 for a full review), they allow for each component of the detection process to be modelled independently and flexibility in additional input variables. Therefore, hierarchical models are considered a good option to estimate the detection probability of acoustic counts. These models assume population closure (no emigration, immigration, births, or deaths) over each visit (i.e., recording samples in this study) within a sampling year (a ‘primary occasion’). However, immigration and emigration can occur over sampling years. In addition, the models assume that no individual is double counted during a visit and detection is independent between individuals.

The first level, the abundance process, was represented by the distribution of the superpopulation of size (M_i) at each time block (‘site’) i within a year. To clarify, the superpopulation of size (M_i) was the total number of groups visually observed within each time block (‘site’) over the sampling year and that could be available and detected (if available). This level was denoted by $f(M_x | \lambda)$ as in Chandler et al. (2011). The distribution of this parameter was assumed as an outcome of a Poisson distribution for humpback whales and negative binomial distribution for blue whales, with mean λ (Royle 2004; Chandler et al. 2011).

For the second hierarchical level, the availability process (ϕ), N_{xt} was the proportion of the superpopulation (M_i) that was vocalising (available) within each time block (‘site’) during a year. In addition, for this level, the emigration model of Kendal et al. (1997) was applied; which is defined as $g(N_{xt} \mid \phi, M_x)$, where g is described as a binomial probability (N_{xt} ~ Binomial (M_x, ϕ)) and emigration is assumed at random (Kendall et al 1997, Chandler et al. 2011). Since the acoustic counts are of vocalising groups that migrate through the study area, this process is a function of both sound rate and immigration / emigration. Finally, models did not account for groups that did not vocalise at some point during the 3-hour time blocks ($\phi = 0$). Consequently, because the acoustic counts were of vocalising groups only, the availability parameter (ϕ) represented the proportion of M_i that was present and producing sound during the 3-hour time block.

For the availability process, it was assumed that all groups in the superpopulation had the same likelihood of vocalising at any time within a time block. However, because of the known difference in vocal rates (Chapter 3) between cohorts that produce song and non-song sounds, song and non-song counts were modelled separately. Since blue whales had low overall counts, separate models for song and non-song counts were only possible for humpback whales. To assess the influence of various conditions on the availability process, the following covariates were included in the models: Julian day, year and maximum number of groups visually and acoustically detected in the time block. These variables were selected because the vocal rate may vary with day, year and number of groups visually present. The latter was to consider influence of abundance where a greater number of whales in an area may increase the number of available vocalising groups. The number of humpback whale groups visually present was divided in cohorts associated with either song or non-song, respectively. Groups composed of one individual or mother-calf plus one escort were noted as being potential singers and the maximum number observed in the time block was used for the song-based model; the non-song model included the maximum number of groups of mother-calf, mother-calf plus multiple escorts and competitive groups. Even if blue whale counts were modelled separately for song and non-song sounds, this distinction could not have been made because there was insufficient behavioural information associated with sound types available. Consequently for blue whales, the maximum number of groups visually detected was estimated as the total number of pygmy blue whale groups present in the area at the time of the survey, regardless of the composition and sound likely to be produced by the group.

The third hierarchical level (detectability process (P_d)) refers to the proportion of groups that were detected given available (Chandler et al. 2011, Tozer et al 2016). The counts were derived from each 13 or 20 minutes recording within a time block. This process was modelled as a function of a range of covariates including: number of groups visually observed in each repeated count (the 13 or 23 minutes long samples), sea state, presence/absence of vessels, consecutive visit index (consecutive recordings), Julian day, year, and overall mean SNR of sound energy within whale vocal frequencies over the duration of the recording sample (estimated per methods in Chapter 4). The number of groups visually observed during each repeated count was included in the model to assess whether detection varied with overall numbers visually observed. Sea state and vessel presence/absence were included in the model because these influence the noise environment which can potentially mask and reduce the detectability of whale vocalisations. The consecutive visit index (e.g., 1, 2, …n, within a time block) allowed for an assessment of whether detectability changed as a function of sampling occasions, with some years having fewer sampling occasions of longer duration (6 occasions of 23 minutes durations) and some having more sampling occasions of shorter duration (13 of 13 minutes durations). Previous studies have suggested that detectability may increase when short and consecutive listening periods are used instead of long listening periods (Thomisch et al. 2016), the number consecutive visit index was in this study, a representation of that assumption. Year was included to account for potential changes in season-related aspects of the environment that may cause masking, such as the overall abundance and behaviour of vocalising whales, environment, and human activity. This level was represented as $h(y_{xt} \mid p, N_{xt})$, where h is a probability function and y_{xt} is a binomial outcome that represents each survey time block for each year divided into a number of samples ('visits') during which counts were made.

The probability of detection was modelled in two steps. First, availability and detectability with covariates were modelled independently using a forward stepwise approach to identify which covariates influenced each process. The models with the lowest Akaike information criterion (AIC) score were selected as the best models. Second, the overall detection probability was modelled using the best model identified for the availability and detectability processes. The final model was that with the best fit for detectability, availability and abundance processes identified by the lowest AIC (Fiske & Chandler 2011; Kéry & Royle 2016; Tozer et al. 2016). The overall fit was assessed using parametric bootstrap methods, chi-square and Freeman-Tukey tests (Kéry & Royle 2016).

The model was fitted using the R package *unmarked* (Fiske & Chandler 2011). The package uses a specific matrix format, thus the global acoustical database was divided in three independent matrices: one including the abundance process (acoustic counts), the second including the availability process covariates and the third including the detectability process covariates. Year was the "primary period" included. There were a total of 32 time blocks ("sites"), 6 or 13 repeat visits depending upon the sampling year (to standardise the matrices, the highest number of visit was included), and four migration years. A global matrix was built by combining all three databases using the function *unmarkedFrameGPC*. Models were fitted using the function *gpcount.* Probabilities for the detectability and availability processes and the combined detection probabilities were estimated using the *predict* function and plotted as a function of significant covariates using the package *ggplot2* (Wickham 2009).

5.3. Results

A total of 32 time blocks (‘sites’) per year over the period of whale migration within Geographe Bay were used for modelling. Humpback whale groups were acoustically detected 393 times over the four years of data collection. Pygmy blue whale groups were acoustically detected 103 times during the same period.

The number of humpback whale groups detected per sampling occasion varied between 0 and 7 for song and 0 and 3 for non-song (Table 5.3). In contrast, 1 to 2 groups of pygmy blue whales singing or producing non-song sounds were counted per sampling occasion (Table 5.3).

Table 5.3. Frequency distribution of the total number of humpback and blue whale groups detected producing song and non-song sounds per sampling occasion (‘visit’).

Number of detections per sampling occasion		0	1	2	3	4	5	6	7
Humpback whale	Song	153	98	125	87	24	13	4	2
	Non-song sounds	364	125	15	1	0	0	0	0
Pygmy blue whale	Song	482	20	2	0	0	0	0	0
	No-song sounds	416	68	20	0	0	0	0	0

Overall detection probabilities resulting from N-mixture models varied for humpback whale groups that produced song, humpback whale groups that produced non-song and pygmy blue whale groups that produced song and non-song combined. The highest detection probability corresponded with the cohort of humpback whale groups that produced song. Detection probabilities for both species are summarised in Table 5.4.

Table 5.4. Detection probabilities based on N-mixture models for humpback and blue whales using acoustic sampling methods.

Species and cohort	Estimated detection probability	95% CI	SE
Humpback whales that produce song	0.90	0.71 - 1.0	0.10
Humpback whales that produce non-song	0.15	0.03 - 0.29	0.03
Blue whale song and non-song combined	0.14	0.07 - 0.40	0.05

The parametric bootstrap to define whether detection probability models had or did not have a good fit was run with 100 replicates and these were sufficient for good model fit (Kéry & Royle 2016). Influences on detection probabilities are discussed in detail for each species below (Sections 5.31 and 5.3.2).

5.3.1. Humpback whale group acoustic detection probabilities

The overall estimated detection probability for the cohort of humpback whales that produced song was 0.9 (Table 5.4). The parametric bootstrap indicated a good fit for this model (see supplementary material 5.6.1.1.).

Availability and detectability processes were significantly influenced by year and Julian day; while the number of consecutive surveys only significantly influenced the detectability process. Overall, detection probability decreased with Julian day and over the years. The number of visually observed groups that were potential singers and sea state did not significant influence either the detection or availability processes (Table 5.5, Figure 5.2).

Table 5.5. Summary of N-mixture model outputs including variables influencing the detection probability of humpback whale groups that produce song.

Process	Variable in the model	Estimate	SE	Z	P(>|z|)
Availability (Φ)	Intercept	-2.82	0.15	-19.50	<0.001
	No. max. groups visually observed in a time block (potential singers)	-0.05	0.10	- 0.54	0.590
	Julian day	-0.23	0.11	- 2.94	<0.001
	Year 2011	-0.66	0.23	- 2.89	<0.001
	Year 2013	-0.66	0.26	- 2.50	0.011
	Year 2014	-2.03	0.40	- 5.03	<0.001
Detectability (P_d)	Intercept	1.02	0.14	7.27	<0.001
	Sea state	-0.03	0.10	- 0.25	0.803
	No. groups visually observed in a ´visit' (potential singers)	0.04	0.06	- 0.60	0.549
	No. consecutive recordings	0.26	0.07	3.81	<0.001
	Julian Day	-0.50	0.15	0.15	<0.001
	Year 2011	-0.33	0.21	- 1.60	0.110
	Year 2013	-1.19	0.33	- 3.63	<0.001
	Year 2014	1.82	0.41	- 4.48	<0.001
	AIC	624.16			
	No. optimum iterations	32			

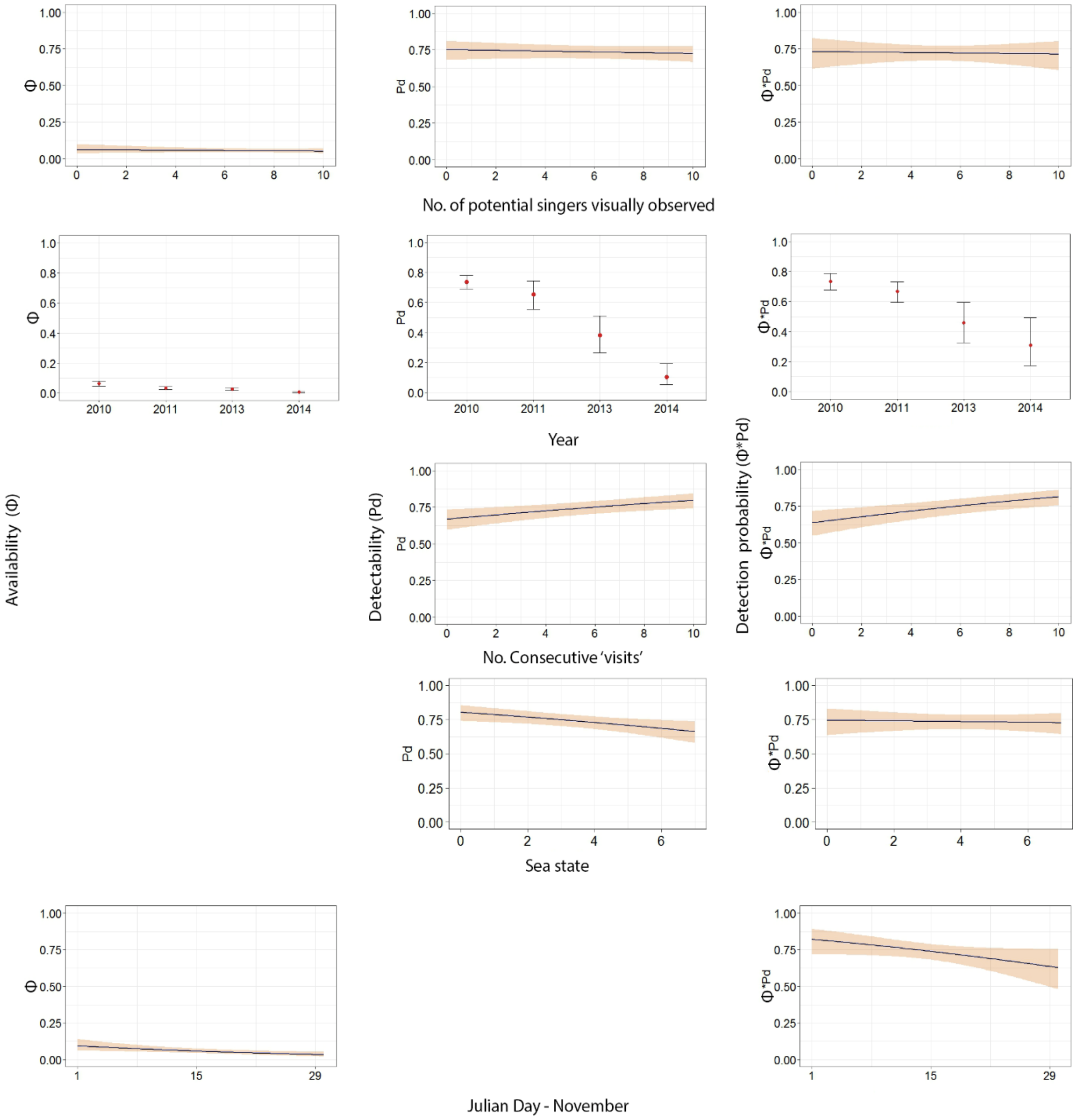


Figure 5.2. Mean availability (Φ), detectability (Pd) and detection probability for humpback whale groups that produced song as a function of year, sea state, Julian day and number of visually observed groups potentially singing. Shading represents 95% confidence intervals.

The expected detection probability for the non-song cohort was lower (0.15) than for the singing cohort (Table 5.4). The parametric bootstrap indicated a good fit for this model (see Supplementary Material 5.6.1.2.). The detectability and availability processes were significantly influenced by the number of groups visually observed that were potential non-song sound producers. Julian day, however, was only significant in the availability process. The number of visually observed groups had a positive influence on availability. Julian day in contrast had a negative influence on availability. Year and number of consecutive recordings were not significant (Table 5.6, Figure 6.3).

Table 5.6. Summary of N-mixture model outputs including variables influencing the detection probability of humpback whale groups that produce non-song sounds.

Process	**Variable in the model**	**Estimate**	**SE**	**Z**	**P(>|z|)**
Availability (*Φ*),	Intercept	-2.80	0.27	-10.31	<0.001
	No. max. groups visually observed in a time block (potential non-song sound producers)	0.36	0.11	3.14	<0.001
	Julian day	-0.55	0.15	-3.62	<0.001
Detectability (P_d)	Intercept	-2.02	0.30	-6.56	<0.001
	No. groups visually observed in a ´visit’ (potential non-song sound producers)	0.04	0.08	0.44	0.063
	No. consecutive recordings	0.13	0.08	1.52	0.127
	Year 2011	0.17	0.34	0.49	0.620
	Year 2013	0.20	0.32	0.61	0.540
	Year 2014	-0.24	0.34	-0.71	0.481
	AIC	307.34			
	No. optimum iterations	98			

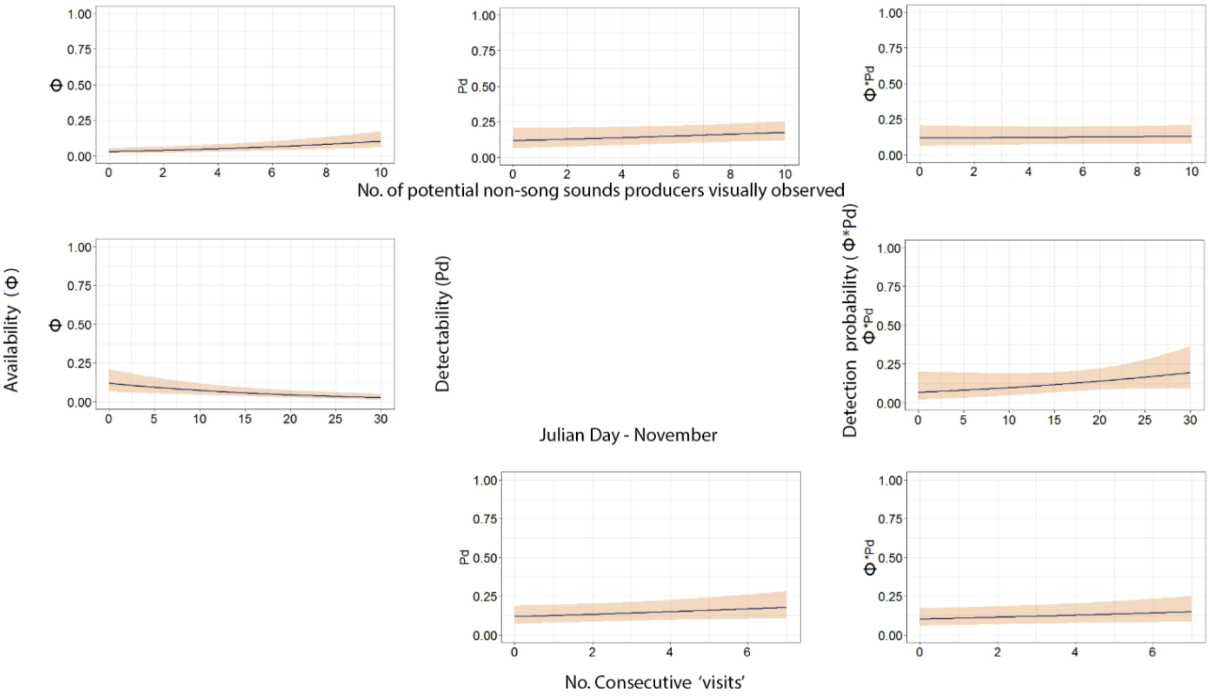


Figure 5.3. Mean availability (Φ), detectability (Pd) and detection probability for humpback whale groups that produced non-song sounds as a function of Julian day and number of visually observed groups potentially vocalising non-song sounds. Shading represents 95% confidence intervals.

5.3.2. Pygmy blue whale group acoustic detection probabilities

Detection probability of pygmy blue whale groups using acoustics was similar to that of the cohort of humpback whale groups that produced non-song sounds. Because the sample size was small, especially for song, the analysis was carried out for all the data combined. The overall detection probability for pygmy blue whales was estimated to be 0.14 (Table 5.4). The parametric bootstrap indicated a good fit for this model (see supplementary material 5.6.2.).

The detection probability, including availability and detectability processes, had a positive significant association with the number of visually observed groups. Year, sea state and the interaction between year and number of consecutive recordings also significantly influenced the detectability process, albeit to a lesser degree. Sea state was negatively associated with detection probability. Year was positively associated with detection probability; with 2011 corresponding to a year in which large numbers of groups were visually observed. Julian day and number of consecutive recordings were not significant influences in the availability and detectability processes (Table 5.7), except in 2013. A significant, albeit small, positive association was observed between the detectability process and the number of consecutive recordings in 2013.

Table 5.7.Summary of N-mixture model outputs including variables influencing the detection probability of pygmy blue whale groups detected vocalising.

Process	Variable in the model	Estimate	SE	Z	P(>|z|)
Availability (Φ),	Intercept	-3.51	0.20	-17.49	<0.001
	No. groups visually observed in a time block	0.19	0.14	1.29	0.001
	Julian day	-0.23	0.19	-1.18	0.237
Detectability (P_d)	Intercept	- 1.85	0.40	- 4.55	<0.001
	Sea state	- 0.45	0.21	- 2.13	0.003
	No. groups visually observed in a ´visit’	0.23	0.14	1.72	0.002
	Consecutive recordings	- 0.22	0.29	- 0.77	0.444
	Year 2011	1.18	0.44	2.67	<0.001
	Year 2013	0.46	0.56	0.82	0.414
	Year 2014	0.74	0.62	1.20	0.229
	Consecutive recordings*Year 2011	0.28	0.34	0.82	0.414
	Consecutive recordings *Year 2013	0.96	0.43	2.23	0.002
	Consecutive recordings *Year 2014	0.37	0.37	1.02	0.310
	Dispersion (log-scale):	11.6	23.4	0.50	0.619
	AIC	157.11			
	No. optimum iterations	112			

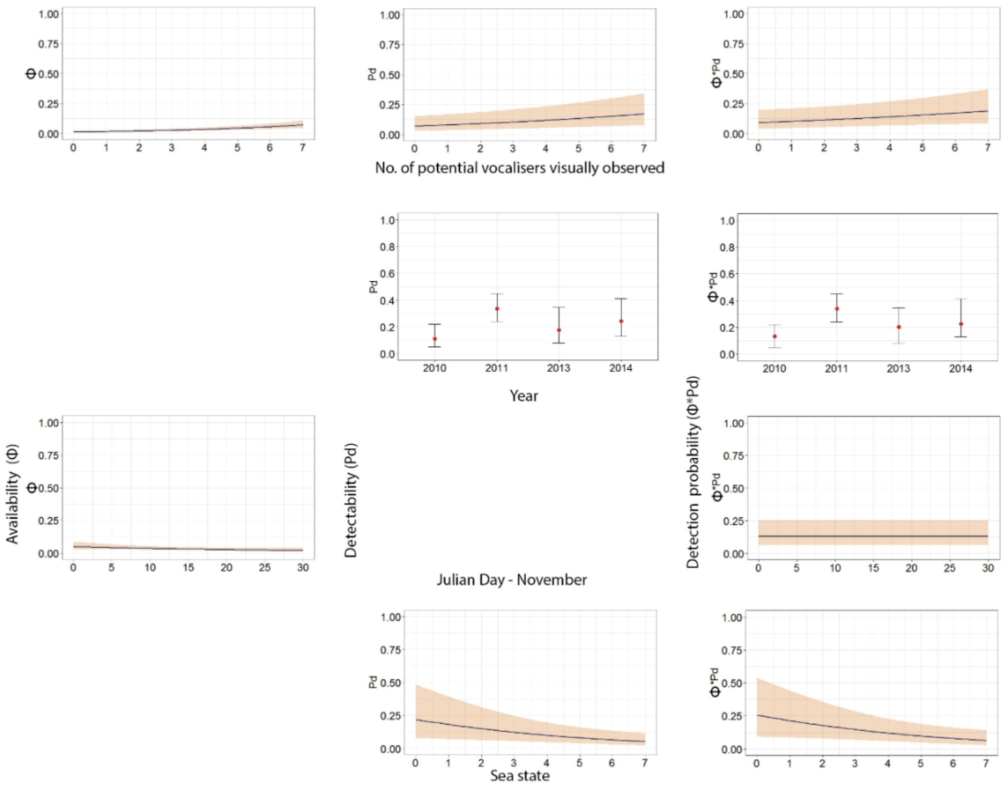


Figure 5.4. Mean availability (Φ), detectability (Pd) and detection probability of pygmy blue whales vocalising as a function of Julian day, year, sea state and number of visually observed groups potentially producing sounds. Shading represents 95% confidence intervals.

5.4. Discussion

Estimating detection probabilities of a species during its annual migration can be complicated by the variability in species' behaviour (individual and among cohorts), environment, emigration and immigration (Kwon et al. 2018). This study provides insight into temporal, behavioural and ecological conditions influencing detection probabilities of baleen whale groups producing different sound types in a migratory area. The baleen whale species included in this study were pygmy blue and humpback whales. The mean detection probability varied between species and cohorts producing different sound types (song and non-song sounds), with the highest detection probability (>0.7) associated with humpback whale groups that produced song. Detection probabilities of humpback whale groups that produced non-song sounds, however, were similarly low (<0.4) to those obtained for pygmy blue whales.

In general, detection probabilities of rare species (e.g., pygmy blue whales) are low. For some terrestrial species such as the elusive raptor, the mean detection probability was estimated to be 0.207 given availability assumed to be 1 (Murn & Holloway 2006).

In this study, detection probabilities were comparatively lower, except for the humpback whale cohort that produced song. This difference may be explained by the availability not assumed to be 1 which likely contributed to lower overall detection probability values. In addition, other studies have suggested low sound production and faint calls as reasons for low detection probabilities, resulting in the animals being acoustical "invisible" (Akamatsu et al. 2014). This explanation is not relevant to this study because SNRs of all sounds were at least 8 dB above ambient noise.

Overall, availability of baleen whales was relatively low, regardless of humpback whale cohort or baleen whale species, with values generally below 0.2. This corresponds with the relatively small proportion of the population that travels through the study area during a time block and the variability in vocal rates expected for baleen whales. Detectability, on the other hand, was high for the cohort of humpback whales that produced song (~0.75) in comparison with that producing non-song sounds (~0.12) and with pygmy blue whales (~0.10). This result was expected because of the variability in vocal rates among different group types and species. For humpback whales, these results can also be explained by differences in the visual and acoustical detection between cohorts as suggested for other species. Cohort specific differences have been reported for porpoises, in that acoustics was found to be more effective at detecting individual animals than groups of individuals which were more likely to be detected visually (Akamatsu et al. 2008). For humpback whales, females with calf and competitive groups were less likely to be detected acoustically than single singers since singers produce song over long periods of time. In contrast, these non-song sound producing cohorts had a higher likelihood of being detected visually because they spent more time at the surface and were available visually for longer periods of time. The low acoustic detections of the non-song sound cohort suggests that the recordings missed these vocalisations, either because of recording schedules being too short to capture them during visits or because their vocal rates were relatively infrequent when compared to singers (Silber 1986). Singers, in comparison, can be underwater singing for an average of 14 minutes yet be visually observed for less than 2 minutes (Chu 1988). Consequently, the likelihood of acoustical detection for singers was comparatively high, but visual detection comparatively low.

Considering both options (differences in visual vs. acoustical detection and ratio of vocalising vs. silent groups), it is possible that not all the visually observed groups were vocalising, or that some of the groups recorded vocalising were missed in the visual surveys and this was why the visual observation either did not influence the detection probability (e.g., song) or when it did, the probability was low. Whether it is one or the other cannot be determined with the current data as matching of observations is not accurate with a single logger. As this is a limitation of the method, additional measurements using an acoustical array are suggested to better understand this relationship and to accurately estimate the ratio of silent groups.

Low detection rates of non-song calls can also be caused by missed detection of a vocalising group due to masking from other sources or underestimation in the number of vocalising groups (e.g. counting two or more different groups as a single because both are at a similar distance of the recorder and produce sounds with similar SNR). For humpback whales, this sort of bias would have been more likely towards the beginning of the study period since whale numbers (and the number of vocalising groups) in the study site were greater than later in the study period. However, the chance of miss-detection is considered low because the sampling began after the peak in migration through the study area. In addition, the chance that this would have occurred in all recording samples within 3-hour blocks is highly unlikely as not all whales arrive and leave the area at the same time (unpublished data). The variation in time of arrival and departure from the study site and travel speeds would have most likely resulted in variation in ranges from the recorder (hence SNR values) among the recording samples. However, because this can cause biases in the analysis, further studies using an acoustic array are recommended to estimate the number of groups that are missed in such counts. Finally, masking and SNR-related biases discussed here are not considered to have influenced blue whale detection rates because in most occasions only one blue whale group was observed in the area at a time. For masking on non-song sounds by song, even if multiple blue whale groups had been present at the study site simultaneously, masking would not have occurred because pygmy blue whale song has a different frequency range than non-song vocalisations.

A range of conditions in the environment influenced detection probability. The greatest influence was the abundance process for humpback whales, with a decrease in singing humpback whale cohort and increase in non-song producing humpback whale cohort detection probability over Julian days. This finding was consistent with the influence of temporal parameters in the detection probability of other migratory and resident species; including the ruddy turnstone *Arenaria interpres* (Kwon et al. 2018), the killer whale *Orcinus orca* (Riera et al. 2016), the white headed vulture *Trigonoceps occipitalis* and different species of marsh birds (Tozer et al. 2016). The influence of conditions on the abundance, availability and detection processes of each species is discussed in detail below.

5.4.1. Variability in detection probabilities for humpback whales

Humpback whale detection probabilities differed between cohorts that produce different sound types, with song-producing cohorts having a higher detection probability than non-song sound-producing cohorts. This dissimilarity was expected considering the comparatively low vocal rates of non-song sounds and the predominance of singers in recordings. In exploring the components of detection probability, song and non-song sound producing cohorts had a low probability of being available; which suggests that, overall, the number of vocalising whales detected may not be representative of the number of whales that pass through the area. The detectability process, however, had a high probability for cohorts producing song and low probability for cohorts producing non-song sounds. Consequently, when groups were singing they were almost always detected; however, this was not the case for cohorts that produce non-song sounds. These, in contrast, were often not detected. This finding was expected since singers can vocalise over long periods of time, meaning that song may usually occur throughout a recording increasing the likelihood of detection. In addition, song is composed of multiple sound units produced in sequences (phrases and themes), one single unit can have a duration between 1 to 5 s (Winn et al. 1981; Chu 1988) and a complete song can have a duration of at least 5 to 7 minutes (Winn et al. 1981; Chu 1988, Guan et al. 1999). Consequently, more than one single unit can be produced in a 13 or 23 minutes recording which increased the likelihood of one singing whale to be detected. Conversely, non-song sounds are produced relatively infrequently and are not necessarily followed by a sequence of sounds (Silber 1986). This reduced the likelihood of being detected if the individual vocalises outside of the time of recording.

The detection of humpback whale groups, regardless of whether they were song or non-song producing cohorts, was influenced by Julian day. However, a negative relationship for the singing cohort and a positive one for the non-singing cohort of humpback whales was observed. A negative association of detection probability with Julian day was expected in the abundance process, because yearly surveys began just after the peak of migration and lasted until the end of the migratory period when fewer groups were expected to be present; thus fewer whales were expected to be available towards the end of the season. As a result of song only being produced by males, usually vocalising alone (Frankel et al 1995), and mostly migrating from the beginning to just after the peak of migration, detection probabilities of the singing cohort were expected to decrease over the migratory season. Although, it is likely that singers escort mother-calf groups (the last group to migrate through the study area), these group compositions (mother-calf-escort) were not regularly observed in Geographe bay (an average of 4 groups per season with a minimum of 0 and a maximum of 7; unpublished data). For the non-song sound producing cohort, it is likely that the positive association between detection and Julian day in the abundance process was a result of an increase in numbers containing mother-calf pairs in the area over the survey period. These groups, known to produce non-song sounds, are the last to arrive and migrate through Geographe Bay. Consequently, while the peak of singers may travel through earlier in the season, the peak of non-song sound producing whales may peak at the end of the migratory season. Some studies have suggested that mother-calf groups are less vocal than competitive groups (Silber 1986). However, competitive groups were not commonly observed during the study (an average of 5 groups per season with a minimum of 3 and a maximum of 9), with most groups observed at the beginning of the survey. Consequently, it is difficult to attribute the higher detection probability of non-song sounds to presence of competitive groups within the study site. Another aspect that may explain the higher detection at the end of the season is song masking. A previously discussed, the presence of singer choruses is known to mask non-song sounds or make difficult its identification. However, considering that the seasonal survey started after the peak of migration, the number of singers observed in the recordings is relatively low and masking effect is reduced when compared with the peak of the season. Although masking by song has an influence in the number of non-song groups counted, this is considered low.

Regardless of the cohort of humpback whales traveling through the study area, increasing Julian day was negatively associated with availability, which could be a result of a decrease in the immigration rate towards the end of the season, as suggested in previous studies (Kwon et al. 2018). Alternatively, a decrease in vocalising whales or vocal rates could be explained by changes in social context resulting from overall decreasing numbers of whales in the area. Some studies have suggested that a greater number of groups or individuals present in an area increases the vocal activity of individuals (Au et al. 2000). This is not necessarily true for all species and cohorts. For example, frogs often change from calling behaviour to non-calling mating strategies in response to increments in chorus density (Leary et al.

2008). Considering that in addition to singing, humpback whales have other non-vocal mating strategies including aggressive physical competitive displays and escorting mother-calf groups (Baker and Herman 1984, Clapham et al. 1992), it is possible that the density of singers influences a change in the mating strategy. This behaviour is poorly understood in humpback whales but it should be considered as a possible influence on detection probability. There was some evidence for this in non-song sound producing whales, given there was a positive relationship between availability and numbers of potential non-song producing groups sighted visually in the area. There was no such evidence, however for the cohort of humpback whales that produced song.

On a broader temporal scale, year-to-year variability in detection probability was expected for both song and non-song sound producing cohorts as a result of yearly changes in the timing of the peak of migration. Yearly variation in migratory timing has been well documented in humpback whales (e.g., Charif et al. 2001; Craig et al. 2003; Ramp et al. 2015; Erbe et al. 2015) and in other species (e.g., Oleson, Wiggins & Hildebrand 2007; Erbe et al. 2015; Kwon et al. 2018), including in Geographe Bay (Salgado Kent, Gavrilov et al. 2012; Salgado Kent et al. 2014). With the surveys in the study area beginning soon after the potential peak in migration, any yearly variations in the abundance process will affect overall detection probabilities. For example, if the peak in a particular year was in mid-October, the majority of potential singers may have already departed the area if a survey were to begin in early November. In contrast, if the peak was in late October, a greater number of singers would be expected in early November. This source of variation in detection among years may explain greater detection probabilities observed for the cohort of humpback whales that produced song in 2010 and 2011 than 2013 and 2014. Extended visual surveys have indicated earlier peaks in migration in 2013 and 2014 which may explain the yearly variation in detection (Western Whale Research, unpublished data). In this study, the number of detections of non-song sounds was much lower than that of song, and potentially contributed to an absence in variation in detection probabilities among years. Understanding annual variability in migration is important when defining the start and end of a survey because temporal variability can influence the presence of particular cohorts and potentially bias the observations.

Other covariates were significantly associated with detection probability. In particular, detection of the non-song producing cohort of whales was positively associated with the number of groups visually observed that were potential producers of non-song sounds. Consequently, as the number of these increased visually, so did their detection probability; and in particular their availability and detectability. This association may be explained by a shift in the social context associated with an increase in this cohort and decrease in the singing cohort within the study area. It is also possible that non-song sounds cohorts reduce the duration and vocal rate of some of their sounds or become quieter in the presence of singers (Dunlop 2016) which will affect their detection.

The number of consecutive ‘visits’ was positively associated with detectability and detection probability for the song producing cohort of humpback whales**.** This is similar to results by Thomisch et al. 2016, who reported that frequent and short listening periods improve the detection of highly vocal species over few and long listening periods. For non-song sounds, which are short in duration and sporadically vocalised, number or consecutive visits was not a significant factor influencing the detection probability. This contrasts with previous studies analysing occupancy of rare raptors that identified the number of visits as a key factor that positively influenced the detection probability in terms of the species presence (Murn & Holloway 2016).

5.4.2. Variability in detection probabilities for pygmy blue whales

Similar to humpback whales, the detection probability for pygmy blue whales was influenced by Julian day, the number of groups visually observed, and to a lesser degree the number of consecutive ‘visits’ in each time block. The results obtained in this study were similar to those obtained in previous studies that found Julian day influencing the detection rate of song and ‘D’ calls (Oleson, Wiggins & Hildebrand 2007). In the present study, the influence of Julian day was mainly on the availability process, which is related to immigration/emigration and vocal rates. In this study, it was not possible to distinguish between these sources nor to assess the availability of different cohorts that produce different sound types due to the overall low numbers of detections. Oleson, Wiggins & Hildebrand (2007) found that the number of acoustic encounters varied between sound cues (song units and ‘D’ calls), which differed in the timing of peak encounters. It is possible that a similar pattern in different sound types occurs in Geographe Bay; however, additional research is required to improve our current understanding of pygmy blue whale detection probabilities of different sound types in the study area.

In terms of the association between numbers of groups visually observed and detection probability, a significant positive relationship was observed in both the availability and detectability processes. Previous studies have suggested that detection rates of ‘D’ calls (the most common sound observed in this study) were associated with increasing numbers of visually observed groups (Oleson, Calambokidis, Barlow et al. 2007). Consequently, as numbers increase in the area and the social context changes, vocalisation rates may increase (availability) which may also influence to likelihood of detection given that they are vocalising (detectability).

While most years were not associated with a change in detection probability, this significantly increased from <0.3 to 0.4 in 2011. The year 2011 coincided with the greatest number of visually observed groups. It is possible that an increase in detection values may be associated with conditions amenable to detection, such as increased vocalisation rates or increased sound levels of vocalisations.

In comparison to humpback whales, the number of consecutive visits did not significantly influence the detection probability of blue whales, except in 2013. Considering that the detection probability estimated in 2013 was higher than the calculated in 2010, and both had similar numbers of visually observed groups, it is possible that the difference was caused by the longer recording schedules used in 2013 that increased the likelihood of detecting the species even in low numbers. Previous studies have indicated that longer recordings (fewer numbers of consecutive samples) perform better for ‘quieter’ species such as beaked whales, with the exception of species that are constantly vocally active (Stanistreet et al. 2016). It is likely that longer recordings perform better in the detection process of less vocally active species than shorter recordings. Additional observations and analysis are required to improve current knowledge on detection probabilities of ‘quieter’ and more vocally active species.

With regard to the influence of ambient noise on detection probabilities, previous studies identified improvements in detection probabilities of ‘D’ calls under low ambient noise associated with low sea state and wind speed (Simard et al. 2008). In this study, sea state significantly negatively influenced detectability. It is likely that as background noise increased with sea state, vocalisations with relatively low SNRs may not have been detected.

5.4.3. Influence of anthropogenic sources on detection probabilities of baleen whales

In previous studies, anthropogenic noise as produced by vessels has been reported as a significant influence on the detection and the vocal rate of baleen whales. Noise generated by vessels and seismic surveys has reportedly decreased the number of humpback whale singers (Cerchio et al. 2014), changed singing activity (Sousa-Lima & Clark, 2008), or masked the ‘D’ calls of pygmy blue whales (Simard et al. 2008). In this study, however, the presence of vessel noise did not significantly influence detection probabilities of humpback and pygmy blue whales. The differences in the results of this study may be explained by the duration and frequency range of the source of noise and the sounds produced by whales. For example, ambient noise produced by travelling recreational vessels (like those in Geographe Bay) is generally short lived and can last for less than a minute, relative to humpback whale song that can have a duration of over 20 minutes. Consequently, the overall detection of singers is generally not expected to be significantly impacted by masking, particularly if this is infrequent. This may be of concern in areas where the vessel density is high and activity is constant and the main contributor of underwater noise.

It was expected that vessel noise would have some impact on detectability of non-song sounds because of their short duration, however, this was not the case. It is possible that the impact of masking of these signals was negligible in this study, because the data were manually reviewed and groups in the study area were those with overall high SNRs. This approach likely reduced the missed detections caused by masking of vessels, thus vessels were not significant. Since manual approaches to data processing tend to be time consuming, auto-detectors are frequently used. In these cases, the influence of masking from anthropogenic sources may need to be carefully considered to avoid detection bias and false negatives. In addition, because the detection probability was not influenced by the number of vessels, it appears that vocal rate (as a function of the behaviour of whales) of either species may have not been affected by this anthropogenic source (see Chapter 3).

5.4.4. Model assumptions

The use of N-mixture models for detection probability and abundance estimation has been increasing in recent years with the extension of the basic model to handle over-dispersion, open population assumptions and variability in survey frequency. These modifications have provided some advantages over established methods such as distance sampling or capture-recapture methods (Dénes et al. 2015, Ficetola et al. 2018; Kwon et al. 2018); namely the potential to incorporate survey, species, behaviour and temporal variables in each process of the detection independently. Recent studies, however, have also raised awareness of the overfitting problems that can occur and limitations when using these models, particularly in relation to model assumptions (see Marques et al. 2013; Dénes et al. 2015; Duarte et al. 2018; Kéry 2018; Link et al. 2018). Limitations in relation to assumptions are discussed below.

The first assumption of N-mixture models is that individuals are not double counted within a visit. Double counts of groups with singers were considered highly unlikely given that song produced by a singer is generally continuous and of relatively constant energy level, thus easily tracked through a recording. Groups producing non-song sounds are also unlikely to be double counted within a visit because of their short duration and number of repetitions observed. Usually, non-song sounds were observed for a brief continuous period of time (usually less than 2 minutes).

In addition, individuals are assumed to be detected independently from each other. Because whales are social animals, their behaviours such as vocalisation rates may influence one another. Consequently, if increased vocalisation of one animal results in the increased vocalisation of another, then increased availability and detectability may occur in association with an increased availability and detectability of another. Conversely, increased vocal activity of one group could decrease the vocal activity of another. In cases where large numbers of vocalisations are present in a recording, partial masking could also have a potential effect on the detectability of certain groups. This is a particular concern for non-song sounds of humpback whales during the peak of migration because of the relatively high number of singers. Because this study occurred just after the peak of migration, the frequency at which singers may mask other groups was probably low. There may have been some inter-dependence that was unavoidable in this study, as it is likely to occur with any social species. Consequently, further research is recommended to investigate the influence of group interactions on detection probability (availability and detectability) and the implications of violations of this assumption on model outputs.

N-mixture models also assume that no movement of individuals occurs among sites (time blocks in this study) during the primary time period (within a year). In this study, careful consideration was made to define time blocks in such a way as to ensure that whales would have transited the study area completely before ‘visits’ were made during a subsequent time block. This was supported by visual observations of tracked humpback and blue whales and the estimation of speed of travel to define time blocks (‘sites’). Although it is likely that some groups travelled more slowly (i.e., singers can move more slowly than non-singing males; Noad et al. 2007), these differences were considered when defining the time blocks. Considering that slower whales can take more than three hours to cross the area of study, a three hour-gap was used between time blocks to allow for these groups to finish transiting the area. This time difference reduced the likelihood of the same whale occurring in subsequent ‘visits’. In addition, visual observations indicate that all groups, regardless of which of the two species, travel through the study area in a westerly direction. No visually tracked whale remained within the area beyond the time required to transit it (average of 2-3 hours). Once whales transiting the study area have reached the furthest westerly point on land, Cape Naturaliste, they are known to round the cape and then travel south towards the sub-Antarctic (Burton, pers. comm. and pers. obs.). In fact, studies using satellite tagging of humpback whales have indicated that there is little or no meandering, at least for females, in areas south of the northerly breeding ground in Pender Bay, northwest of Australia (Double et al. 2010). For blue whales, satellite telemetry information has shown residency times of several days in the Perth Canyon (Double et al. 2014), a foraging ground north of Geographe Bay; however, whales in Geographe Bay have only been observed transiting or resting for short periods of time (Salgado-Kent et al. 2014). Behaviours observed in the area, including relatively fast average swim speeds, constant direction of travel, absence of milling, and regular dive and interval times match those of traveling whales on migration. Consequently, it is highly unlikely any group of whales observed in the morning were the same as groups observed in the afternoon. Therefore, the assumption of no movement of individuals between ‘sites’ (time blocks in this study) was considered to be satisfied.

Another assumption of the N-mixture model is that individual survival and recruitment rates are comparable and independent among sites during the secondary period. Previous simulation studies have suggested that movement or mortality rates vary as a function of population density and bias can be expected if a model ignores density dependency (Bellier et al. 2016). Survival and recruitment rates, whether density dependent or not, were not considered as relevant in time blocks in Geographe Bay since individuals do not stay in the area for significant periods of time. Migrating groups or individuals may stay for short periods of time (a few hours) to rest but not for much longer. However, the implications of potentially violating this assumption should be considered in areas with longer residency times such as breeding or feeding grounds.

The final consideration of the model is that the variables account for all heterogeneity in the detection probability. This assumption is complicated given the amount of factors that can cause heterogeneity (e.g. individual behaviour, environmental stochasticity). Here, although many co-variates were included for both the availability and the detectability processes to fulfil this assumption, it is possible that there is still some unmodelled heterogeneity that may bias the results. For example, the effect caused by unmodelled individual / group heterogeneity could not be assessed (a larger data set is required), this is recommended for future work where possible. Furthermore, other studies have included variables of the survey design in the analysis to reduce the impact of unmodelled heterogeneity. For example, Duarte et al. (2018) and Kwon et al. (2018) used different numbers of visits in the design and included this information as explanatory variables in the analysis. In this study, the number of visits was used as a covariate in the model to reduce the impact of unmodelled heterogenity but also to analyse the effect of recording schedule.

Finally, previous studies have described poor fit when fitting models using bootstrapping methods, especially when detection probabilities are low (Duarte et al. 2018). Since bootstrap Tukey or chi-square (depending on the distribution) values in this study were all >0.3, the model was considered to be adequately fitted. However, pygmy blue whale and non-song sound humpback whale models may not have had optimal fit as a result of relatively small numbers of detections in the samples. In this study, the low number of detections was addressed through the use of a negative binomial distribution for blue whales, and it showed a good fit. The Poisson distribution for non-song sound humpback whale models was used since model fit tests indicated adequate fit. Simulations are recommended for future work to better understand the effects of low detection rates on the accuracy of parameter estimates.

In this study the potential violations in N-mixture model assumptions have been evaluated carefully. Based on the results, this new application of detection probability estimation in a whale migratory area was considered appropriate. This model has proven to give quality results for birds in staging areas that can be considered similar to baleen whale transit grounds (Kwon et al 2018). The results of this study are indicative that N-mixture models may be a powerful tool for analysing acoustic observations that do not allow individual identification, and provide valuable information that is unavailable using traditional methods. In addition, these models can be further developed and tested for abundance estimation using single logger acoustic data. This opens a new avenue for assessing population abundance of whales in migratory corridors. It is important to highlight however, that the assumptions of N-mixture models using unmarked individual observations are strict and can only be met under specific conditions and in particular areas (Duarte et al. 2018, Kéry 2018; Link 2018).

5.4.5. Implications of acoustical detection probabilities for the development of optimal monitoring protocols and abundance estimates

Past studies have highlighted the benefits of using acoustics for monitoring species presence and estimating relative abundance (Mellinger 2003; Akamatsu et al. 2014; Richman et al 2014). The results of this study indicate that while acoustics has great potential for monitoring purposes because it is relatively cost-effective and can be used independent of weather and light conditions, its application for accurate estimation and monitoring of population trends requires imperfect detection to be estimated and adjusted for. To be able to obtain the most accurate results, careful considerations on animal behaviour, their demographics and environmental conditions of the study site should be included. For species or areas not well studied or with little knowledge, it is recommended to run combined visual and acoustical surveys before using an acoustics-only approach.

For acoustic surveys of baleen whales in particular, there is the need for developing protocols that maximise information collected while reducing processing times of big datasets (Riera et al. 2013). Similar to studies on birds that used estimated detection probabilities to guide the development of monitoring protocols (e.g., Tozer et al. 2016), the results of this study were used to identify important considerations in designing quality baleen whale monitoring protocols. To begin with, the differences in detection probabilities between species indicated that standardization of acoustic surveys across species may not be appropriate. Rather, survey protocols may need to be species-specific for optimal results. Furthermore, the differences observed in detection probabilities between cohorts that produce different sound types (song and non-song) indicated that generalization of detection probabilities, even at species level, is not ideal. When possible, it is recommended that the range of sounds that animals produce is included in observations to include all cohorts of the population, and that recording schedules that maximise detection of the different cohorts are used (this is further discussed in Chapter 6).

The temporal extent of surveys should also be considered carefully, so that the beginning and end of a survey capture the population being monitored. This is particularly important at sites with populations that are not year-round residents, and where seasonal arrivals and departures can vary over years. As shown in previous studies (e.g., Oleson, Wiggins & Hildebrand 2007), the time at which a seasonal survey begins and finishes can bias the detection of certain cohorts; since depending upon the period of migration, certain cohorts may not yet be present or may be more or less vocally active. For example, if song is used to monitor humpback whales, and the survey begins during the peak and ends at the end of the seasonal migration, the likelihood of detecting the full migration may be reduced since the last cohort to migrate is mainly composed of non-singing whales. Similar results were observed with blue whales in California, where differences in acoustical and visual detection rates were associated with the time of the survey (Oleson, Calambokidis, Barlow et al. 2007). In the previous study, singers were detected more often using acoustics than visual observations, however, no differences were observed between visual and acoustic methods for the ‘D” call (non-song sound). Consequently, the inclusion of sounds that are produced by all individuals of a population regardless of sex or age, in addition to common sound types that may be used disproportionately by specific cohorts or sexes, is recommended where possible. Different sound types are often produced at different rates, thus when combining sounds, optimising the recording schedule plays a vital role in reducing bias in detection probabilities.

Most studies in the past have considered sampling schedules that allow for optimal detection. For example, optimal recording schedules have been shown to be dependent on the vocal behaviour of the species of interest (Riera et al. 2013; Thomisch et al. 2015). The behaviour of a species is dependent on how it uses the study site and the environmental conditions within it. Consequently, optimal detection can be achieved by considering achievable sampling schedules in combination with behavioural and ecological parameters of the baleen whales of interest and environmental conditions of the study area. As for detection probabilities, it may not be possible to generalise the recording schedule among species or cohorts within a species because of variability in their vocal behaviours. For instance, for humpback whales in this study, the optimal schedule for the song producing cohort of the population was not necessarily optimal for the non-song sound producing cohort.

Finally, since individuals and species are not perfectly detected, the collection of information on the variability in detection probability as part of the survey design is recommended to improve abundance estimates (Thompson et al. 2002, Tozer et al. 2016).

5.5. Conclusions

The aim of this chapter was to present a first assessment of the use of N-mixture models for estimating detection probabilities of baleen whales in a migratory corridor using acoustic observations. Although previous studies have assessed the influence of environmental conditions on detection probabilities of sounds, these have only included the detectability process (i.e. sound detection as a function of distance or influence of masking). This chapter filled some of the current gaps in knowledge on how detection probability of baleen whales, including availability and detectability processes, may be influenced by temporal, anthropogenic, ecological and behavioural conditions.

This study highlights that detection probabilities can be highly variable in different conditions and can be expected to be species specific. The results indicate that, in addition to physical factors influencing sound transmission through the water column, temporal (year, Julian day), ecological (number of groups present) and behavioural factors (type of sound, gender, etc.) also influence detection probabilities. These factors can be expected to vary with population and site under study and should be considered when designing acoustical surveys for monitoring. This considerations should also be accounted for when assessing population trends.

Finally, many baleen whale monitoring programs have focused on breeding or feeding grounds. However, there are certain benefits in monitoring transit grounds. For instance, if the breeding or feeding ground is very large, as tends to be the case for migratory baleen whales, then it may be difficult to survey and monitor the entire area seasonally. Transit grounds, particularly those that represent a corridor in which the majority of population moves through, can be surveyed over the entire migratory season, thus allowing information on a large proportion of the population to be obtained from a relatively small area.

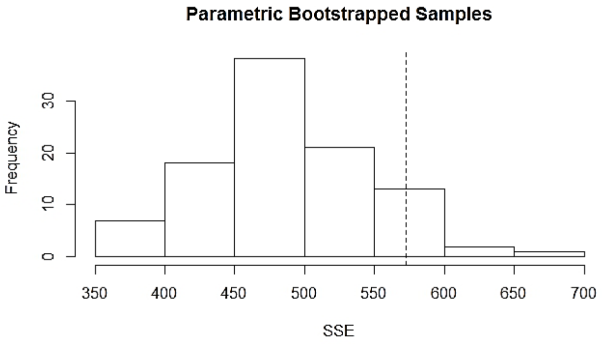
5.6. Supplementary Material

5.6.1. Model fit results for humpback whale models – parametric bootstrapping using chi-square and Freeman-Tukey tests. Simulation run with 100 replicates. Figures were plotted using chi-square test results. SSE: Sum of Squared Errors.

5.6.1.1. Cohort of humpback whales producing song

Parameter

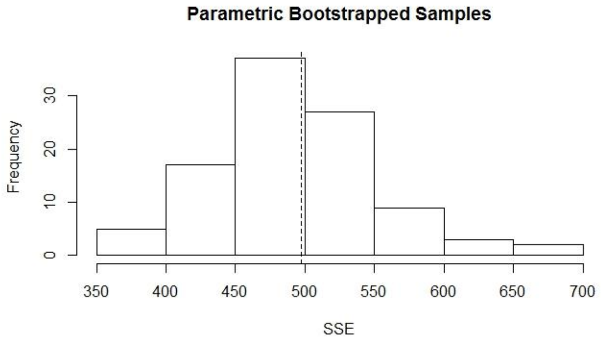
Availability (Φ)



p (chi square) = 0.1, c-hat = 1.18

p (Freeman - Tukey) = 0.3 , c-hat = 1.24

Detectability (p_d)

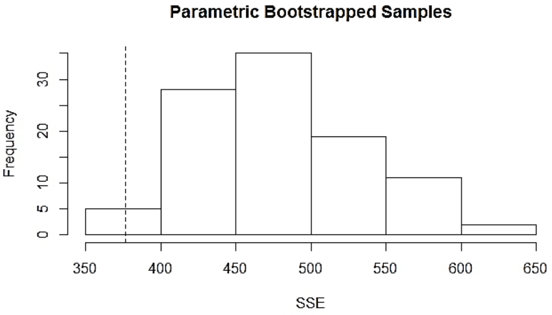


p (chi square) = 0.4, c-hat = 1.01

p (Freeman-Tukey) = 0.4, c-hat = 1.03

Detection probability

$(p_D = \Phi * p_d)$



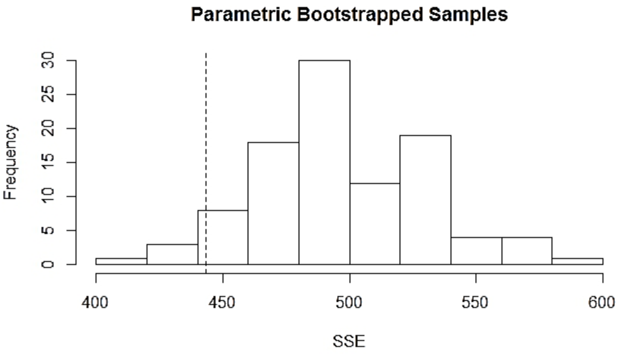
p (chi square) = 0.9, c-hat = 0.78

p (Freeman-Tukey) = 0.9, c-hat = 0.79

5.6.1.2. Cohort of humpback whales producing non-song sounds

Parameter

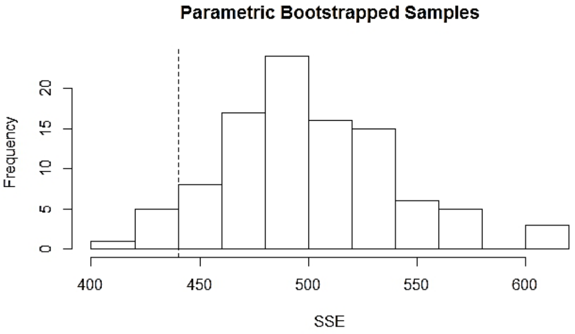
Availability (Φ)



p (chi square) = 0.94, c-hat = 0.89

p (Freeman-Tukey) = 0.71, c-hat = 0.95

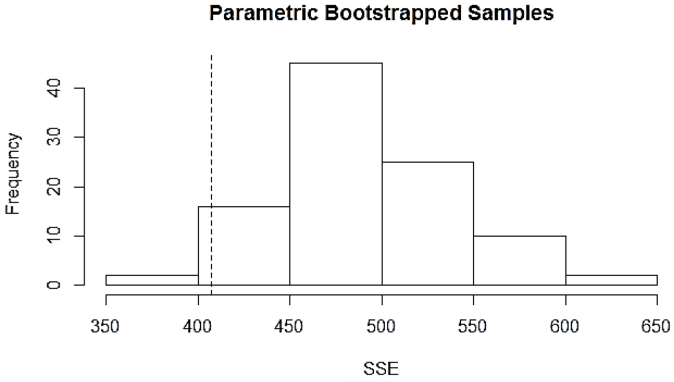
Detectability (p_d)



p (chi square) = 0.93, c-hat = 0.88

p (Freeman - Tukey) = 0.56, c-hat = 0.99

Detection probability
($p_D = \Phi * p_d$)

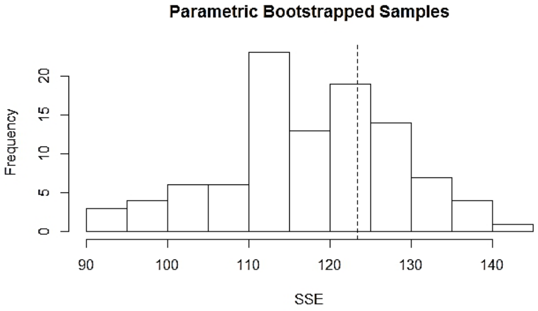


p (chi square) = 0.96, c-hat = 0.83
p (Freeman-Tukey) = 0.62, c-hat = 0.97

5.6.2. Model fit results for pygmy blue whale models – parametric bootstrapping using chi-square and Freeman-Tukey tests. Simulation run with 100 replicates. Figures were plotted using chi-square model.

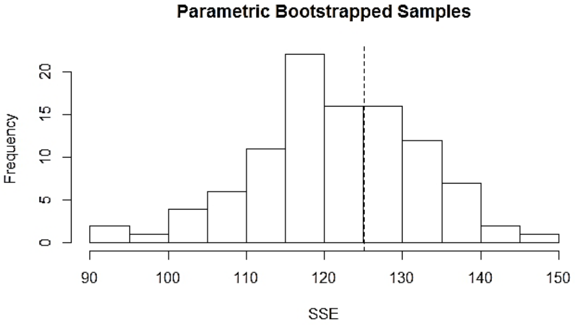
Parameter

Availability (Φ)



p (chi square) = 0.139, c-hat = 1.11
p (Freeman - Tukey) = 0.33, c-hat = 1.05

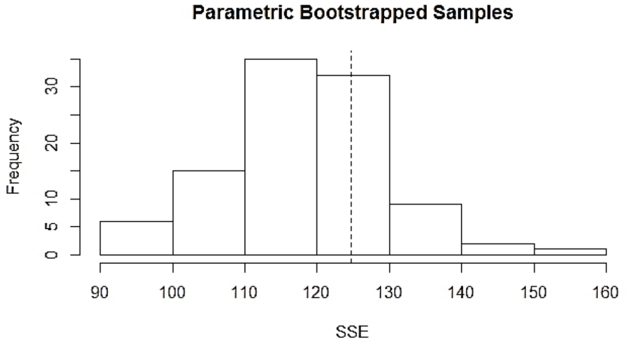
Detectability (p_d)



p (chi square) = 0.04, c-hat = 1.16
p (Freeman-Tukey) = 0.4, c-hat = 1.03

Detection probability

($p_D = \Phi * p_d$)



p (chi square) = 0.03, c-hat = 1.24

p (Freeman-Tukey) = 0.30, c-hat = 1.07

Chapter 6.

General discussion

This thesis aimed to improve current knowledge on the acoustical ecology of two species of baleen whales, pygmy blue whales (*Balaenoptera musculus brevicauda*) and humpback whales (*Megaptera novaeangliae*), in Geographe Bay, Western Australia, and consequently inform the development of optimal monitoring protocols using passive acoustics. These aims were achieved by: describing non-song sounds for each species; assessing the variability in vocalisation rates which informed acoustic monitoring methods; comparing different methods for acoustical monitoring (sound metrics *vs.* manual counts), and estimating detection probabilities for acoustical and visual methods.

This study identified 5 and 17 new non-song sounds for pygmy blue whales and humpback blue whales, respectively (Chapter 2). The identification and inclusion of these in acoustic monitoring increased the detection of both species. Despite this, differences in the most common sound types recorded were observed between species, with song most commonly recorded for humpback whales and non-song sounds types for pygmy blue whales (Chapter 3). The disparity in dominant sound types produced between species was also reflected in their species-specific influence on vocalisation rates of groups; with humpback whale groups having higher vocalisation rates of song than non-song sound types, and the inverse true for pygmy blue whale groups. These findings indicated that, despite many studies focusing on song detection for acoustic monitoring (e.g. Cato et al. 2001; Charif et al. 2001; Wiggins et al. 2005; Stafford et al. 2011; Gavrilov & McCauley 2013; Helble 2013; Balcazar et al. 2015; Noad 2017), non-song detection was important in detecting humpback and pygmy blue whales in Geographe Bay. In addition, since the evidence points to song being produced by males (Frankel et al. 1995; Darling et al. 2001; McDonald et al. 2001), female and calf cohorts would be entirely missed without the inclusion of non-song sounds. Not only were vocalisation rates of baleen whale groups significantly related to the sound detected, but also to Julian day, year (for humpback whales) and time of day (for blue whales). In contrast to other studies (e.g. Croll et al. 2001; Wiggins et al. 2005; Blackwell et al. 2013; Cerchio et al. 2014;

Shabangu et al. 2017), environmental and anthropogenic conditions were not observed to influence the vocalisation rates of groups for either species (Chapter 3).

A variety of acoustic-based methods are currently used for monitoring baleen whales; however, they vary in their applications and their inherent biases (Mellinger 2007; Van Parijs et al. 2009). For relative abundance, common approaches include using cue counts and sound energy levels as indices because they are relatively easy to measure and cost-effective to obtain (McDonald and Fox 1999; Gannon et al. 2008; Marques et al. 2009; Marques et al. 2011; Helble 2013; Marques et al. 2013; Erbe et al. 2015; Širović et al. 2015). While these indices may be indicative of relative abundance, their relationship may not necessarily be linear as sometimes presumed (Ponce et al. 2012; Seger et al. 2016). In this study, a moderate to high linear correlation between sound level metrics tested (namely signal-to-noise ratio (SNR)) and the number of vocalising groups were obtained for pygmy blue and humpback whales; but only when overlapping noise from other sources (non-target whale vocalisations and vessel noise) were removed and for a subset of recordings that were separated in time (and were not autocorrelated) (Chapter 4). In contrast, the correlation of sound level metrics and number of whale groups visually detected was significantly lower, regardless of baleen whale species. While indices of relative abundance were obtained using sound level metrics in this study, they were highly variable in how closely they reflected densities measured using counts regardless of whether they were acoustic or visual (Chapter 4). Given that manual counts of vocalising groups were much more consistent with visual counts than were indices from sound level metrics, regardless of species and whether other noise sources were present or not, counts of vocalising groups is recommended in other similar studies for monitoring to estimate population trends. Sound level metrics, however, are invaluable for confirming the presence of vocalising species, defining their migratory timing, and identifying recordings for use in manual counts which would reduce the number of recordings requiring processing. The reduction in processing would improve the method’s cost effectiveness.

Despite the improvements in accuracy using manual acoustic counts of groups, the probability of acoustic detection of groups was estimated between 0.13 and 0.9, and depended upon sea state, number of consecutive recordings and vocal sound type recorded. In general, song had a higher detection probability than non-song sounds for humpback whales, and the opposite was observed for blue whales. In addition, the number of groups likely to be producing non-song sounds was a significant factor explaining detection probability for non-song but not for song. The probability of visual detection was also influenced by sea state and Julian day. For humpback whales a higher detection probability was estimated for groups likely to be vocalising song than non-song while for pygmy blue whales non-song had a higher detection probability than song. Thus, for studies that require absolute estimates and highly accurate monitoring of trends, the incomplete detection of different vocalisation types and cohorts would need to be accounted for.

In summary, the acoustic ecology of baleen whales is species specific, and within species varies among cohorts and habitats depending upon the relative behaviour of the animals. Despite this inherent variability, passive acoustics is valuable for monitoring baleen whale populations, and has great potential beyond monitoring their presence and relative abundance indices. However, a range of considerations are required for their use in such monitoring programs.

Based on the results of this study, key considerations for the development of optimal passive acoustics monitoring protocols, particularly for monitoring design, processing and analysing resulting data, are outlined below. In addition, decision trees to help guide the optimisation of baleen whale monitoring protocols are proposed. Information from two baleen whale species was used to develop the decision trees but these can be further developed and adjusted for other marine species. Two case studies are presented as examples of how the decision tree might assist in guiding the selection of a monitoring protocol. The first case study is one prioritising humpback whales occurring in high abundance and the second prioritises rare pygmy blue whales as a focal species.

6.1. Key criteria for developing optimal passive acoustic monitoring protocols of baleen whales with emphasis on data collection, processing and analysis

The growing threat of anthropogenic impacts on species and their ecosystems is increasingly placing pressure on governments and industries to gather the scientific knowledge necessary for effective conservation, management and decision making; such as whether resource extraction and development activities should go ahead and how to manage their potential impacts (Gerber et al. 2005; Nowacek et al. 2013; Browning et al. 2017; Verfuss et al. 2018). Monitoring programs are key for generating the knowledge required to make these decisions. Effective monitoring programs, however, require experimental designs that produce valid and reproducible research with minimal bias or bias that can be accounted for (Pollock et al. 2002; Field et al. 2007; Martin et al. 2007; Conway 2011; Frick 2013; Tozer et al. 2016).

One of the principal aims of management-based monitoring is to estimate ecological parameters; including those associated with population distributions and trends (Mulder et al. 1999; Pollock et al. 2002; Cowx et al. 2009; Conway 2011). Estimation of species and population parameters allows for assessments of their status (i.e. whether they are threatened or not), whether they are increasing or declining, and how human activities may affect them. However, the challenges in designing monitoring programs that effectively assess these parameters may vary among habitats and species (Cowx et al. 2009). For instance, monitoring programs may be more easily designed and implemented for easily sighted 'distinctive' species (e.g. humpback whales) than for more cryptic, rare species (e.g. pygmy blue whales). In addition to challenges in optimal sampling designs potentially varying among species and habitats, funding is a common and ubiquitous limiting factor (Field et al. 2007). Monitoring programs can be very expensive, particularly long-term programs that allow the time required to detect changes. However, if the aim of a survey is to detect changes, surveys must be designed so that they have the power to detect a meaningful effect size. Because achieving high statistical power at a low cost is often difficult, an adequate monitoring design that improves the quality of study outcomes is frequently "forgotten" or not deeply considered when developing monitoring programs (Field et al. 2007). Thus, the ultimate goal of an optimal monitoring program is to develop a survey design that maximizes species detection (e.g. Langlois et al. 2010, Tozer et al. 2016) and is sufficiently thorough to detect the effect size of interest while minimizing field costs and effort. To achieve this, all aspects of a monitoring program must be carefully planned and considered in terms of their costs and benefits. In addition, effects of biases and limitations from survey design should be provided to managers and stakeholders so policy is developed accordingly.

Passive acoustics monitoring (PAM) as a monitoring approach has been suggested as a powerful tool for generating baseline information for management purposes. It is often preferred over other methods because it can be cost-effective, can cover large areas and can be undertaken independent of weather and environmental conditions (di Sciara & Gordon 1997; Moscrop et al. 2004; Gannon 2008; Van Parijs et al. 2009; Blumstein et al. 2011; Browning et al. 2017). In both terrestrial and aquatic species, PAM has been successfully implemented to assess species distribution, spatio-temporal patterns and impacts of noise on fauna (e.g. Moore et al. 1998; Barlow & Gisiner 2006; McDonald et al. 2006; Luczkovich et al. 2008; Van Parijs et al. 2009; Erbe et al 2015; Parsons et al. 2016; Blumstein et al. 2017). However, while acoustic-only monitoring programs for estimating ecological parameters are reasonably developed for terrestrial species (Pollock et al 2002; Vesely et al. 2006; Conway 2011; Frick 2013; Tozer et al. 2016), those for aquatic environments are still under development.

Considering that acoustics is frequently used for monitoring baleen whales in marine environments, results from this thesis were used to identify key criteria for developing acoustic monitoring protocols for these species. The criteria were based on the information available for humpback and pygmy blue whales in transit grounds from this thesis and from the available information in the literature. While the species and habitat from which the criteria have been developed are restricted, it is anticipated that monitoring protocols can be adjusted for other species and locations based on the considerations outlined under each criterion. As the criteria were based on limited information, it is suggested that the proposed criteria are used as a motivator for developing future improved versions when additional information becomes available.

The criteria considered here include: (a) the location and timing of recordings, (b) the number of acoustic recorders to be used, (c) the required sensitivity of instruments, (d) recording schedules, (e) effective identification of target species in recordings, (f) methods for processing high volumes of data, and (d) analysis of data with a focus on the considerations for estimating the probability of detection. Each criterion is discussed below.

6.1.1. Location and timing of recordings

Similar to other techniques used for monitoring (e.g. visual observation from land stations, vessels, or aircrafts), the optimal location and timing for acoustic recordings to be undertaken depends directly upon the behaviour and ecology of the target populations of a study species. This criterion can be considered the foundation for any monitoring protocol, because the extent and frequency of spatial and temporal sampling should provide the data required to accurately describe the distribution of individuals of the focal species over time for effective management (Cowx et al. 2009). While covering the spatial extent of a species' population that has a limited home range or the temporal extent of one that is resident at a particular location can be relatively straight forward, it can be more complex for migratory species.

Migratory species such as baleen whales have relatively stable departure and arrival times to feeding, breeding and transit grounds across years. When multiple migratory species share the same grounds, there may be a temporal niche separation among species (Ramp et al. 2015). This multi-species niche separation should be accounted for when defining the start and end times of surveys when multiple species occupy an area; however, survey times should allow for variability in timing of different species due to changes in environmental and behavioural conditions, which can be on the order of days or weeks. For example, in feeding grounds off Canada, humpback and fin whales share the same area, with a two-week time gap between the periods of occupancy (Ramp et al. 2015). However, Ramp et al. (2015) found that shifts in their arrivals/departures times were associated with changes in environmental conditions resulting in a temporal overlap in migratory timing of the species. Thus, if variability in timing of arrival and departure is not considered in the design, it is possible that the species is missed, part of its migration is missed, or its vocalisations are masked by the presence of another (which requires further considerations for the collection and analysis of resulting data).

Another important consideration to be made when selecting recording times, is that not all cohorts of a species migrate through, arrive or depart areas within their home range at the same time. Studies focusing on baleen whale migratory timing have reported that certain cohorts will begin migrating first or depart last depending upon the direction of travel (e.g. Dawbin 1997; Craig et al. 2003). For example, when humpback whales migrate from feeding grounds to breeding grounds, pregnant females are first to depart feeding grounds, and when accompanied by their newborn calves are the last to depart breeding grounds when migrating in the opposite direction (Dawbin 1997; Craig et al. 2003). The influence of these cohort-dependent differences in migratory timing in resulting survey data must be considered when selecting survey start and end dates. Ideally, the temporal extent of the survey design will provide representative samples of all cohorts within a population that allows for comparisons among areas and years (Cowx et al. 2009). Where possible, a conservative time allowance is recommended to account for variability in migratory timing, so the earliest and latest possible dates of all cohorts of interest can be captured. If variability in timing is not accounted for, it is possible that estimated population demographic parameters will be biased, resulting in inaccurate trend estimations. This bias was observed for certain species of fish that were monitored just after spawning or hatching. As a result, the population demographic was assumed to be dominated by juveniles when in reality it reflected the bias resulting from a narrow temporal survey extent (Cowx et al. 2009).

The timing of acoustical monitoring of certain species in relation to obtaining clear measurable cues may need greater consideration than for visual surveys. For instance, if there are co-occurring species or noise sources present at a particular time that will mask vocalisations of the target species, then surveying at that time with acoustic methods may not produce measures that can be used for population parameter estimates. Thus, underwater acoustic monitoring must consider the acoustical ecology, population demographics and behaviour of multiple species/sources occupying an area at the same time (La & Nudds 2015). For example, beginning a survey during the peak of migration of a particular baleen whale species can be the best option to sample a range of cohorts in some populations visually. For acoustics however, for some species this period may not be the best as the presence of more individuals may mean that the more vocal cohorts may mask those that vocalise less. For humpback whales in breeding grounds, for example, recordings obtained during the peak period of migration that are dominated by humpback song produced by singing males could easily mask non-song produced by all other cohorts. Thus, monitoring during the peak of singer occupancy could potentially bias the monitoring towards males. Longer surveys or surveys beginning/ending before and/or after the peak could be a better option that would capture cohorts producing song and non-song vocalisations. For less vocal or rare species, however (e.g. blue whales), the peak of migration would provide the highest likelihood of acoustical detection regardless of cohort and maximise the number of groups or individuals measured.

Similar to conspecific masking, monitoring at times and locations where other sources of noise occur in the same frequency bands as those of sound produced by target species can result in masking and/or biases in detections. For instance, placing an acoustic recorder near a constant source of mooring noise or near a shipping channel producing noise within the same frequencies as humpback whale vocalisations is likely not an optimal choice. However, if areas and times with high levels of masking (caused by ambient or anthropogenic noise) need to be monitored, information on how these factors can potentially influence population size of the species of interest is required. When soundscape information is available, an adjustment for reduced detectability can be explored.

Finally, while many acoustic monitoring programs collect continuous data covering the entire period of interest (several months or years at a time), analysis of these large datasets can be very time consuming and expensive. Consequently, subsampling designs have been proposed and are commonly implemented to reduce time spent reviewing data (Thomisch et al. 2016). In these cases, the temporal frequency of subsamples collected requires consideration. Subsample protocols should not only consider vocalisation rate, but also inter-seasonal variability and migratory timing of different cohorts over space and time. For example, if a population or cohort of interest has a high vocalisation rate and was present during the beginning of the sampling period, a low subsampling frequency may be sufficient to capture the required samples to estimate parameters of interest. However, if a second population, cohort of interest has a lower vocal rate and is present later in the season, then the subsampling protocol may require more frequently collected samples. The optimization of recording schedules is further discussed below.

6.1.2. Number of acoustic recorders to be used

The optimal number of acoustic recorders in a study depends upon (i) the spatial extent of the study relative to the detection range of the target species and (ii) the aims of the study. For instance, if the aim of the study is to monitor trends in occurrence or abundance of a species with known vocal behaviour and homogeneous distribution over time within a relatively small area, then a single recorder would likely achieve the aim of the study. If the study area is larger than the range of detection of a single recorder, however, and the distribution of the species varies over this larger area then multiple recorders will likely be needed.

For studies aimed at obtaining density estimates, a single acoustic recorder approach would require that estimates are made using acoustic transmission models developed for the range of noise conditions in the study area. For use with a non-directional single recorder, transmission loss and vocalisation intensity would need be assumed isotropic (uniform in all directions) and known in the study area. Results from the transmission models can then be used to calculate a critical SNR of recorded vocalisations below which whales are no longer considered in the area of interest. All vocalisations above the critical SNR would then be extracted as detections for data analysis. In cases where transmission loss is not isotropic in the study area and/or sound levels of vocalisations produced by whales are not constant or they are not known, density estimation would require multiple acoustic recorders set up in an array for tracking individual whales. Acoustical tracking using acoustic arrays (at least three hydrophones) has been used to identify individuals for capture-recapture based density estimation of minke whales *Balaenoptera acutorostrata,* Blainville's beaked whales *Mesoplodon densirostris* and sperm whales *Physeter macrocephalus* (Marques et al. 2009; Marques et al. 2011; Marques et al. 2012; Ward et al. 2012; Marques et al. 2013).

While acoustic arrays can improve our understanding of species distribution and density (Mellinger et al. 2007; Van Parijs et al. 2009), they are often too expensive to sustain for long-term monitoring programs and reduce the cost advantage of PAM. Consequently, a combination of different survey approaches conducted simultaneously, such as visual surveys and single or multiple acoustic recorders, may provide a relatively cost-effective option that can still provide key population parameter estimates. For instance, a survey that implements simultaneous visual and acoustic array surveys during the first stage of the program would generate the required information on individual vocalisation rates that can later be applied to a single logger scenario for the same population and location (assuming no changes in vocalisation rates occur over time). Moreover, the combination of visual and acoustic methods would be required if the aim of the study were to estimate absolute estimates of abundance or density. These surveys would provide estimates of availability bias for use in absolute abundance estimates.

6.1.3. Recording schedules

The selection of recording schedule (the duty cycle of recordings) is dictated by the capabilities of the recording equipment, the duration of the survey period, and the density, vocal rate and frequency range of the target species. Recorders vary in their range of capabilities, including their battery and memory capacities, and sample rates and frequency bandwidths (see Sousa-Lima et al. 2013 and Lucke et al. 2014 for review of underwater acoustic recorders). The longer the duration of a recording is and the higher the sample rate, the greater the memory and battery demands are. The frequency and duration of recordings (recording schedule) must allow sufficient memory and battery life to collect data for a survey, to record information for a period long enough to detect changes over time and to capture the bandwidth of interest. It should also consider the likelihood of recording sufficient detections of the focal species for the estimation of population parameters.

In some instances, short recordings (such as 5 minutes) with relatively short inter-recording periods (say every 15 minutes) over long periods of time (12 months) will allow sufficient detections to detect patterns in vocalisations over time. Previous studies have suggested that short but consecutive listening periods improve the acoustic detections over long continuous listening periods (Thomisch et al. 2015). However, for rare or less vocal species, longer and more frequent recordings will be required for adequate detection of patterns over time. In this study the resulting detection probabilities indicated that longer recordings and frequent sampling improved the likelihood of detecting less vocal or rare species. The results of this study suggest that modelling a species' detectability using different recording schedules can aid in selecting an optimal sample schedule.

6.1.4. Species identification and selection of acoustical cues

One of the main limitations in acoustic monitoring approaches is the requirement of knowledge of typical sounds and/or the acoustic repertoire of a species. To develop an acoustic repertoire catalogue, standardized methods for measurement and classification are needed so that sounds can easily be compared to those reported by different researchers. This has been proposed for describing and classifying humpback whale song (see Cholewiak et al. 2013), but has been limited for other species. In this study, standardized classification of sounds based on physical characteristics (constant waves, frequency modulated, etc.) combined with basic quantitative measures of sounds was used, and is suggested as less susceptible to biases than using onomatopoeic names that are more subjective. This method has proven to be effective for comparing sounds recorded in Australia with sounds from other areas (Erbe et al. 2017), and may aid in the identification of species in areas where simultaneous visual observations have not yet been possible.

In terms of the vocal cue (such as a sound type or song), previous studies have suggested the use of either one or multiple cues for monitoring species (e.g. Van Parijs et al. 2009). Despite this, there is still uncertainty on how cues should be selected. In general, cues that are frequently vocalised are used for monitoring because they have a greater chance of detection than those produced less frequently. However, monitoring selected cues may bias the monitoring to specific cohorts or completely miss the presence of a particular cohort when a cue different to the one(s) selected is present in the recording. For example, humpback whale monitoring has for many years considered only song produced by males (Tyack 1981; Frankel et al. 1995). As a result, in these studies females with calves, competitive groups and sub-adults that do not produce song are not considered. As indicated above, in some instances species can be entirely missed. For example, pygmy blue whales in migratory areas have commonly been monitored using song (see McCauley 2001; Gavrilov 2011), as opposed to downsweeps that have been associated with feeding-grounds for some populations (Balcazar et al. 2015). In this study in Geographe Bay, a non-feeding area, however, song was rarely recorded and the most common calls were downsweeps. Consequently, if song had been the only cue used for detection in this study, the species would have been missed in most recordings. Thus, for studies aiming to estimate and monitor population trends of an entire population (including the range of cohorts within it), it is recommended that the selected cues include the different cohorts of a species' population or as many cohorts as possible.

Selecting representative cues is of particular importance for parameter estimation of species in recovery, species with unknown recovery rates and / or those affected by severe declines such as pygmy blue whales. For instance, the estimation of birth rates and proportion of young individuals present in a population per breading season is a fundamental parameter required for population viability analyses, population growth and recovery rate estimates (Martin et al. 2007). Consequently, to execute these types of analyses for monitoring the population status of a species, the inclusion of cues produced by calves or mother-calf groups is critical. For studies using acoustic-only approaches in which knowledge of the acoustic repertoire of the focal species is unavailable, either acoustic tags or a combination of visual and acoustic-based surveys will be required to match the species to the sounds it produces across its demographic range.

When research cannot be undertaken on cohorts of interest, such as mother-calf pairs, due to funding of logistical limitations, it may be helpful to classify sounds into general types that are produced by different population cohorts; such as song and non-song as undertaken in this study. Although, this general classification will not allow the determination of whether non-song sounds were produced exclusively by mother-calf groups in the study, approximations of potential numbers of groups with calves may be able to be extracted in studies where vocalisation rates for different cohorts are known. For studies aimed specifically at understanding the acoustical ecology of mother-calf groups in breeding grounds and birth rates it will be necessary to obtain more detailed information on specific sounds produced by this cohort. However, on transit grounds such as Geographe Bay, it is possible that as long as there are cues that represent the different cohorts, modelling of population trends may be possible.

6.1.5. Processing acoustical data

Acoustic monitoring allows surveys to have greater temporal and spatial scales than using visual techniques (e.g. at night and in remote areas over extended periods). However, the quantity of data produced requires greater effort to process and analyse it, making this one of the main challenges in using this method for monitoring (Brandes 2008; Acevedo et al. 2009). Automatic detectors for specific acoustical cues or power spectrum density (PSD) plots that identify focal species based specific frequency bands have been used to reduce the number of recordings to analyse and partially solve this problem. However, the accuracy of the methods is still being evaluated, and the estimation of population parameters using data resulting from such methods is yet under development.

Although an evaluation of automated detectors was outside the scope of this study, it is worth noting that their effectiveness in producing desired population parameter estimates will depend upon cues selected (as discussed above). In general, cues used in the development of automatic detectors are based on vocalisation rates and intervals between sounds of a specific cue, among other attributes (e.g. Kumar 2003; Burtenshaw et al. 2004; Tiemann et al. 2006; Gavrilov et al. 2011; Hannay et al. 2013). In some instances, the use of vocalisation rates may bias the identification of a species in areas where vocalisation rates and intervals for specific cues vary, or they may bias detection towards particular cohorts. For example, auto-detectors developed to identify a specific unit of humpback whale song will bias the detection towards males if it is assumed to occur at specific frequencies and intervals defined by the song. However, the same unit may occur in non-song sounds, and would be missed. In addition, because humpback whale song evolves each year, an auto-detector may vary in its effectiveness from year to year.

In addition, the accuracy of auto-detectors may be compromised in the presence of overlapping units, which could potentially increase false negative error rates by not detecting the species when it is present. Searching recordings for sound events instead of specific sounds (or calls) has been suggested as a means of reducing this error (Van Parijs et al. 2009). The use of sound events is similar to the use of PSD plots. The idea is to significantly reduce the quantity of data that will be reviewed, however its effectiveness in producing accurate estimates of population trends has not been evaluated.

PSD plots, as another common approach to a common efficient means of processing high quantities of acoustical data, are often used to identify seasonal patterns of presence of species of interest and in some cases relative abundance (e.g. Au et al. 2000; Širović et al. 2004; Gedamke et al. 2007; Erbe et al. 2015). This study indicated that the correlation between the level of energy detected in a recording and the total number of groups present in an area was low. Thus, it is recommended that this approach be used to identify the presence of the species of interest in the recordings and in relative abundance of the vocal cohort of the species. To use the approach as a relative index of the population as a whole, it is suggested that the relationship between numbers in the population and acoustic detections is established at the site of interest. In addition, PSD plots can also guide subsampling efforts by identifying those recordings with the cues of interest to be selected subsampled for more detailed analysis (e.g. manual counts).

Furthermore, the use of PSD plots for analysing acoustical data should consider temporal autocorrelation (and any violations in assumptions of independence in statistical analyses), overlapping anthropogenic sources and the sound level metric that best reflects numbers of vocalising animals. First, temporal autocorrelation causes estimated sound level metrics from one period of time to be closely related to values from the following period. In these cases, it is recommended that data analysis integrate a correlation structure within models or use values sufficiently separated in time to be considered independent. Second, the sound level metric used to estimate the sound energy should consider the vocal rate of the species of interest. Results of this study suggest that for a highly vocal species (humpback whales), the mean SNR metric gave a higher correlation than other metrics; while for less vocal or rare species (blue whales), the maximum SNR was more suitable. Finally, considerations of the influence of overlapping sources (e.g. vessels) on analyses and their potential exclusion should be included as part of the post-processing procedure.

6.1.6. Analysis of data with considerations for the probability of detection

Finally, while acoustical monitoring using auto-detectors has aimed to assess detectability of vocalising animals (i.e. transmission of sound, masking etc. see Kumar 2003, Helble et al. 2013 for examples) and as a way of improving seasonal and distributional species assessments, results from these studies are limited to the cohort of animals that are vocal or must assume constant detectability and complete or known availability if inferences are to be made to the broader population. While most monitoring programs do not adjust for imperfect detection in analyses, research has shown that even for occupancy and distribution models, the probability of detection (detectability and availability) should be considered as part of the survey design (Lahoz-Monfort et al. 2014). Acoustic monitoring programs that consider imperfect detection and its potential variability in space and time at the protocol design stage are more powerful as they are statistically more successful at identifying changes in the population (Field et al 2007).

The accuracy of population parameter and species richness estimates using acoustical data are improved if sampling protocols maximize detection probabilities (La & Nudds 2016) and are designed to estimate imperfect detection. For cetaceans, population abundance and trend estimation using acoustics uses distance sampling to adjust for reduced detections with range from the receiver. These methods assume constant availability; however this assumption is not always valid, particularly for species with low vocalisation rates (Buckland et al. 2001). Consequently, when availability is not constant, population estimates that adjust for the probability of detection should include availability bias in the calculation.

A range of models have proved to be effective in a range of applications, and continue to be tested for new applications such as hierarchical and Bayesian models used in this study. These models incorporate the probability of detection for population parameter estimation by integrating both availability and detectability in addition to influencing ecological processes (see Royle 2004; Chandler et al. 2011; Dail & Madsen 2011; Amundson et al. 2014). These methods have been applied and evaluated for terrestrial species but studies on marine fauna are rare. In addition, to the best of the author´s knowledge this is the first time that hierarchical and Bayesian models have been used to model the probability of detection using underwater acoustical data. N-mixture models, such as those implemented here, have provided similar estimates to those of removal distance sampling and capture-recapture in salamander species (Ficetola et al. 2018). While this approach offers promise for marine systems, further assessment such as that undertaken for terrestrial systems (including simulations) is required.

6.2. Guide for optimising passive acoustic monitoring protocols for assessing baleen whale population parameters

Based on the criteria discussed in the previous section, decision trees have been developed here to help guide the selection of protocols that will allow the estimation of population parameters. These decision trees have been developed to provide some preliminary direction for discussion on acoustic monitoring and potential future standardisation.

Passive acoustic methods have experienced a rapid uptake by ecologists monitoring populations. However, the design of optimised monitoring protocols that allow for the estimation of population parameters are still under development. Past considerations for optimisation have focused on acoustic propagation of signals of interest (Mellinger et al 2007), technologies used (Van Parijs et al. 2009), sampling schedules (Thomisch et al. 2016), and assessment of detectability; but mostly with a focus on the influence of ambient noise on the accurate auto-detection of particular cues (Helble et al. 2013). To the best of the author’s knowledge, a decision tree to guide the development of optimal monitoring protocols for acoustical data that include features from survey design to data processing and analysis, variability in acoustical ecology, the relative likelihood of detection and the aim of the study, has not been previously developed.

The importance of developing such tools to assist in the standardisation of data collection lies with the improvement in producing comparable results among locations and times. By standardising the selection of monitoring protocols for studies with similar aims, increased comparability can be achieved while not jeopardising the overall aim of the study. Ultimately standardised protocols, data collection and analysis (Mellinger et al. 2007) will improve our ability to monitor changes in population trends over long time periods and a broad range of areas (Department of Biodiversity, Conservation and Attractions 2018).

Here, only general guidelines are proposed as there is high variability among species and locations they occupy, and the protocols introduced draw from only the two baleen whales species (rare *vs.* common) that were the focus of this study. The decision trees used to guide the selection of optimal monitoring protocols include considerations for studies aiming to: (i) identify occurrence (which is often used to asses species distribution) (Figure 6.1) and (ii) monitor ecological parameters required for abundance and population trend assessments (Figure 6.2). The protocols include a decision guide for data analyses and potential statistical models for abundance estimation using acoustical data. However, this step was simplified, and it is not comprehensive because detailed diagrams on this topic are available in Marques et al. (2013).

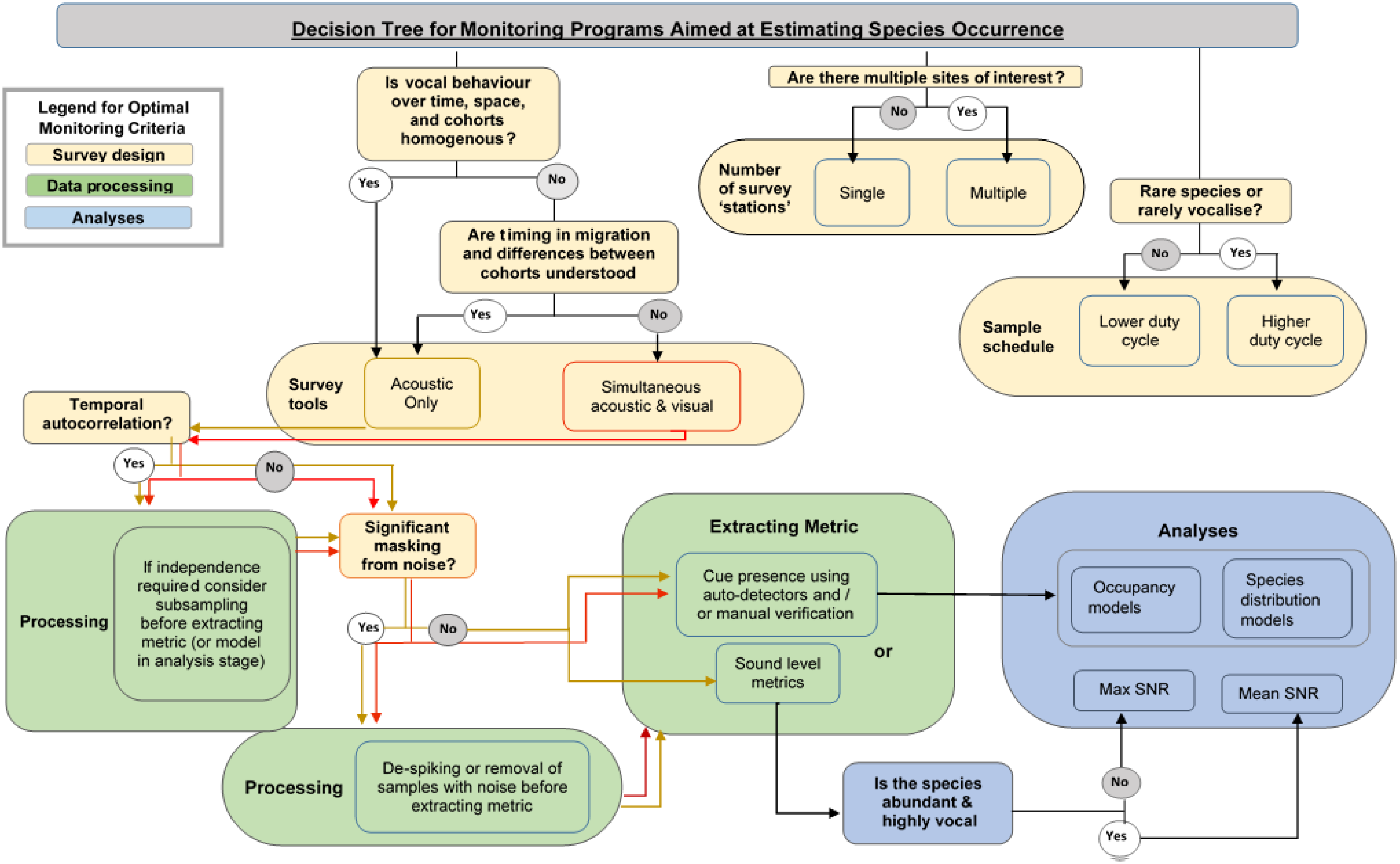


Figure 6.1. Decision tree to guide users through key criteria for undertaking optimal passive acoustic monitoring for the assessment of baleen whale population parameters based on species occurrence.

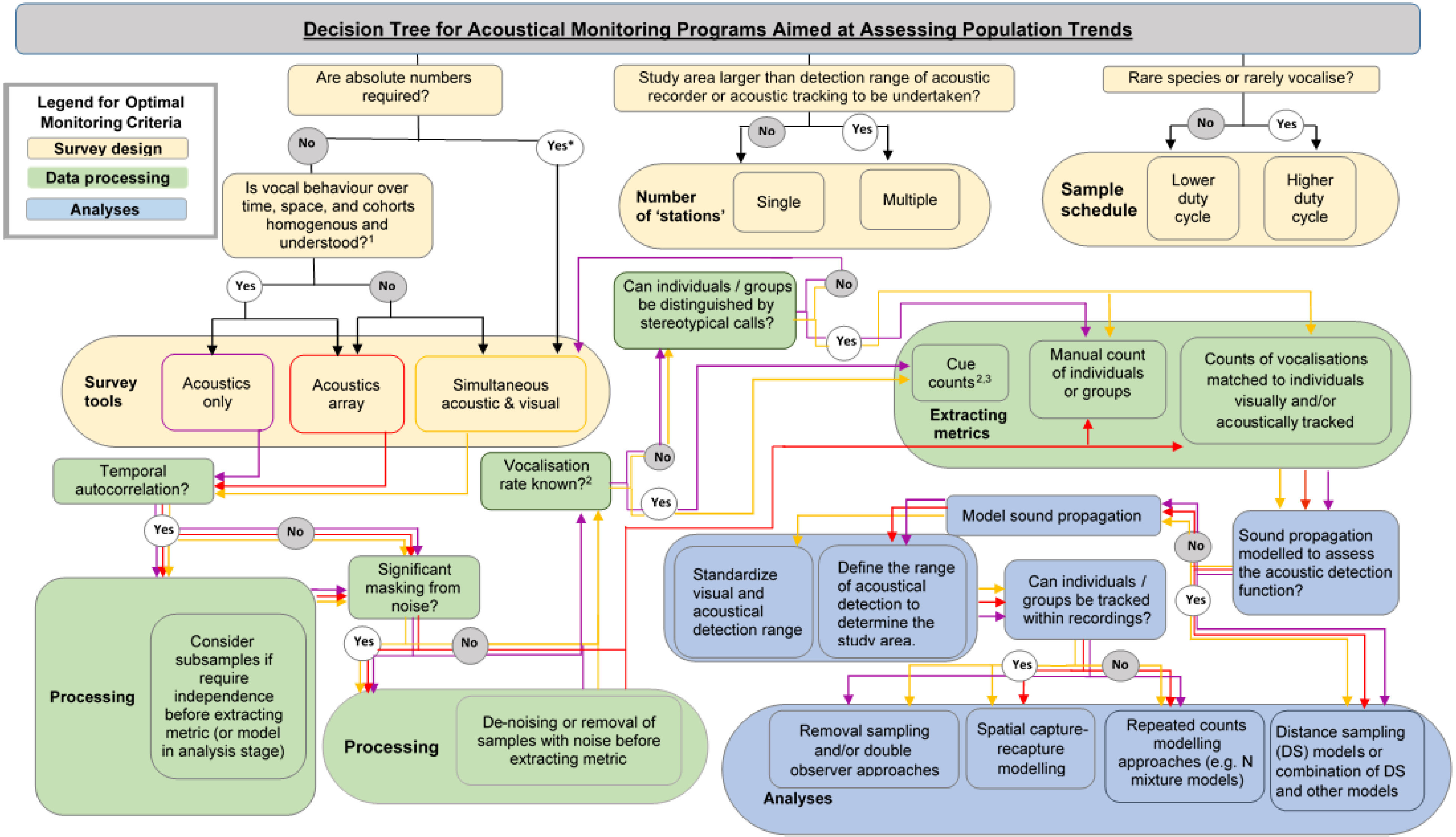


Figure 6.2. Decision tree to guide users through key criteria for undertaking optimal passive acoustic monitoring for the assessment of baleen whale population parameters. [1]Consider the timing in migration for the survey design to guarantee sampling of different species and cohorts. [2] If absolute numbers are of interest, it is necessary to use a correction factor for availability to use acoustics only. [3]If cohorts differ in the type of cues produced representative cue types per cohort should be extracted.

Based on the decision trees proposed above and the experience from this study, protocols for future monitoring of humpback and pygmy blue whales in Geographe Bay are given as case studies below. These two scenarios provide examples of monitoring trends in abundance for (i) a common and highly vocal species (humpback whale) and (ii) a rare and less vocally active species (pygmy blue whale).

For the first scenario (Study Case 1 presented in Box 6.1.) surveys using an acoustic array in combination with visual surveys undertaken over one to three years is recommended to determine vocal heterogeneity between different group types (e.g. mother-calf, competitive groups, etc.) for adjustment of detection parameters. This should be undertaken before implementing a more cost-effective approach of using a single recorder. The combined surveys are recommended to be undertaken over two time periods: one in August/September to monitor males (including singers) and newly pregnant females and juveniles that are within the first cohort to migrate, and the second in October/November to monitor competitive pods and females with calves that are the last cohorts to migrate. For processing acoustic signals, a combination of sound level metrics, auto-detectors, and manual counts is recommended. Sound level metrics will allow the identification of recordings with humpback whale signals (mainly song) that can then be subsampled, reducing the amount of data to analyse. Frequencies used for sound level metrics should cover the low (<100 Hz), mid (100 - 1000 Hz), and high frequency bands (>1000 Hz) of humpback whale vocalisations. For processing specific sounds, auto-detectors of common non-song sounds in each frequency band could be used for cue counts and to find groups vocalising non-song sounds (see Chapters 2 and 5), and to identify the presence of other sources of noise (e.g. vessels, pygmy blue whales) to be removed from sample. Sources of potential bias that should be discussed or accounted for in recordings resulting from the suggested protocol include: (i) variability in ambient noise and effects of anthropogenic noise that has not been removed, and (ii) unmodelled heterogeneity over years in which simultaneous visual and acoustic tracking are not performed (constant heterogeneity across years would need to be assumed).

Box 6.1. Study Case 1: Monitoring trends in abundance of highly vocal humpback whales in the migratory corridor within Geographe Bay.

Example Protocol for acoustically monitoring humpback whales in Geographe Bay

Survey design

- **Number of Survey stations:**
  - An array of four loggers coupled with visual surveys over one to three seasons (longer if needed) will improve detection probability models as heterogeneity in vocal production can be modelled and full availability can be estimated.
  - For long-term monitoring (>3 years duration), a single logger will offer a cost-effective method for monitoring population trends.
- **Sample schedule**:
  - Because monitoring aims to estimate population trends, it needs to maximise the likelihood to record social sounds from mother-calf groups that follow a rare species pattern. It is recommended to continue the 13 minutes every 15 minutes sampling schedule to maximise duration of the recorder's battery.
  - Time of the survey: for monitoring males, newly pregnant females without calves and juveniles it is recommended to survey between August and October. For monitoring specifically females with calves, late October to late November.

Data processing

- **Subsampling:**
  - Removing temporal autocorrelation: Use one sample every three hours, or average samples in three-hour blocks. Three samples for morning (6 to 12 pm, afternoon (12-6 pm) and night (6 to 12 am).
  - If doing manual counts of groups or individuals, use sound level estimations to identify which recordings have humpback whale sounds and use those recordings to subsample the recordings used for manual counts.
- **De-noising:**
  - Exclude samples with blue whales and vessel noise. Carry out a baseline analysis on ambient noise and its potential masking and influence on sound level metrics.
- **Extracting metrics:**
  - Cue selection: use auto-detectors for different cues and for different frequency bands. Consider sounds for different cohorts (song and non-song sounds). Samples with song can be identified using sound level metrics.

Data analysis

- **Samples selection:**
  - If using sound level estimations for identifying samples for manual review or for relative abundance, use mean sound level metric (see chapter 4).
  - If analyst is not familiar with humpback whale song, it is suggested to review additional samples so analyst can better familiarise with humpback whale song. Unfortunately, it is not possible to fully automate the counting of singers because of the complexity of humpback whale song.
- **Statistical analysis:**
  - For years with visual and tracking information it is suggested to use distance sampling combined with removal models or other double observer models. If acoustical tracking is not available, N-mixture models for open populations or other hierarchical modelling approach are advised.
  - If the monitoring program aims to analyse changes in detectability associated with sound propagation, it is recommended to use distance sampling methods.

Similar to Study Case 1, in Study Case 2 a combination of acoustical and visual surveys is recommended before an acoustics-only approach is undertaken (Study Case 2 presented in Box 6.2.). A combination of survey methods will increase the potential for identifying new pygmy blue whale sounds, and it will expand the knowledge on the behavioural context in which these sounds are vocalised. This information will enable better estimates of detection probabilities.

In terms of the duration of a survey, an extended survey between October and November is recommended for monitoring changes in time of arrival / departure and temporal differences in the migration of different cohorts. Although, previous studies have been conducted in November, the identified peak of migration for pygmy blue whales in Geographe Bay, an earlier arrival (from late September) has been observed in some seasons potentially shifting the peak of migration to late October (Mr. Burton 2018, *pers. comm*.).

For processing acoustic signals, the use of an auto-detector for song and downsweeps is recommended. An auto-detector for song signals is already available (see Gavrilov et al. 2011), however, the accuracy of a downsweep auto-detector should be validated as these signals are variable and have similarities with some humpback whale sounds. In addition, it is also possible that auto-detectors fail to identify cues due to masking by humpback whale song and vessels. Therefore, manual review of data should be undertaken to confirm the species' presence, to identify the presence of masking sources (humpback whales and vessels) and to estimate a relative number of groups or individuals present in the recordings.

Furthermore, when visual and acoustical surveys are simultaneous, manual verification of acoustical data during times of visual observations is recommended to facilitate the identification of new sound types for the species. For dates/times without visual observations, multiple recordings can be processed using sound level metrics. Power spectrum density plots can then be plotted to identify samples containing pygmy blue whales sounds. Frequencies used for sound level metrics should include frequency bands between 20-40 Hz and 70-200 Hz to cover the identified pygmy blue whale sounds.

Because the number of pygmy blue whales passing through Geographe Bay is relatively low, the proportion of vocalising groups in the area is required so adjustments for availability can be made if needed. Based on previous analysis, over 90% of the groups visually observed were vocalising. Consequently, availability is high, meaning that the number of pygmy blue whale samples on which to base the design of acoustic-only monitoring protocols is still low. This is expected for rare species and therefore data analysis and sources of potential biases should be carefully considered. Sources of potential bias that require consideration in the results of the study resulting from the survey protocol include: (i) variability in ambient noise and effects of anthropogenic noise that has not been removed, and (ii) unmodelled heterogeneity over years in which visual and acoustic tracking are not performed (constant heterogeneity across years would need to be assumed).

Box 6.2. Study Case 2: Monitoring trends in abundance of a rare species, pygmy blue whale, in the migratory corridor within Geographe Bay.

Example Protocol for acoustically monitoring pygmy blue whales in Geographe Bay

Survey design

- **Number of Survey stations:**
    - Acoustics coupled with visual surveys over one to three seasons (longer if needed). Because numbers of blue whales are very low and there is high uncertainty in terms of full repertoire and acoustical behaviour, it is necessary to continue visual observations before changing to an acoustics-only approach.
    - The use of an acoustic array is suggested when multiple groups are observed in the area at once or if identification of pygmy blue whale sounds is not possible when humpback whales groups are present in the area and vocalising sounds in a similar frequency.
- **Sample schedule**:
    - Because monitoring aims to population trends, it needs to maximise the likelihood to record pygmy blue whale sounds. A sampling schedule of at least 15 - 20 minutes every 20 - 25 minutes is recommended.
    - Time of the survey: It is recommended to monitor the area between October and late November to account for changes in timing in migration.

Data processing

- **Subsampling:**
    - Removing temporal autocorrelation: Use one sample every three hours or average samples in three-hour blocks. Three samples for morning (6 to 12 pm), afternoon (12-6 pm) and night (6 to 12 am).
    - Use sound level estimations to identify recordings with pygmy blue whale sounds. Use PSD plots to identify peaks in sound levels, manually review these samples.
    - Review presence of humpback whales and vessel noise in the recordings. Exclude samples with vessel noise. Exclude samples with humpback whale sounds when overall sample size is not affected.
- **De-noising:**
    - Carry out a baseline analysis on ambient noise and its potential masking and influence on sound levels.
- **Extracting metrics:**
    - Cue selection: use auto-detectors for downsweeps and song. It is recommended to extract samples for frequencies between 20 – 40 Hz and between 70 - 200 Hz.

Data analysis

- **Samples selection:**
    - If using sound level estimations for identifying samples for manual review or for relative abundance, use max sound level metric (see chapter 4).
    - When a pygmy blue whale is visually detected, it is recommended to review the acoustical data manually. This will help to identify new sounds for the species.
- **Statistical analysis:**
    - For years with visual and tracking information it is suggested to use distance sampling combined with removal models or other double observer models. If acoustical tracking is not available, N-mixture models for open populations or other hierarchical modelling approach is advised.
    - Because is a rare species, evaluate the use of models that consider a zero inflated distribution.
    - If the monitoring program aims to analyse changes in detectability associated with sound propagation, it is recommended to use distance sampling methods.

6.3. Conclusions

The use of passive acoustics for monitoring has increased in recent decades facilitating the development of new technologies and methods to analyse acoustical data. However, for acoustics to be successfully used for monitoring purposes there are research gaps that need to be considered. Overall, this thesis contributes to filling some of these gaps by considering the acoustical ecology of two species of baleen whales, and integrating the available information into the development of general optimal monitoring protocols.

The species used in this study represent two acoustically distinctive species: humpback whales are abundant, highly vocal and have a complex and well-studied repertoire, while pygmy blue whales are rare and their acoustical ecology is comparatively poorly known. For both species, vocalisation rates of song and non-song differed, with song having a higher probability of detection than non-song sounds for humpback whales and the opposite for blue whales, but these differed among years and Julian days. Because of these differences, considerations identified as important to optimise monitoring protocols included: the behavioural ecology of the species such as timing in migration and distribution; technical aspects of surveys such as the sampling schedules and sample size; data processing by subsampling recordings that may be temporally autocorrelated or have noise that may mask the species' cues; and options for data analysis based on the type of data collected, including sound level metrics, statistical modelling and adjustments for imperfect detection including availability and detectability components.

Finally, the work presented in this thesis represents a foundation on which to develop optimal passive acoustic monitoring protocols. The suitability of the protocol presented here can be assessed for other species and scenarios in the future; and with each iteration the protocol can be more broadly applicable. Programs using passive acoustics for monitoring population parameters are complex and considerations beyond the location, timing, and schedule for recorder deployments are required. In addition, although some species may share certain acoustical characteristics and ecological attributes, the same protocol may not necessarily be an optimal approach across species. Consequently, guidelines that reduce biases in data collected for each species and still allow temporal and geographical comparisons are required. As a final point, it is important to acknowledge that combining acoustics with visual observation is a vital step before an acoustics-only approach is undertaken. This is particularly important when the acoustical ecology of an area or a species of interest is poorly known. In conclusion, this thesis has contributed to laying a foundation for continued work in developing optimal passive acoustic monitoring protocols that can be used globally for baleen whales or other marine species.

Appendix A

Co-Author Contribution Statements

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

Chapter 2.

Publication title: Non-song vocalisations of pygmy blue whales in Geographe Bay, Western Australia.

Author	Conceived and designed the study	Collected the data	Analysed the data	Wrote the manuscript	Contributions to drafting and critical review of manuscript	Total % contribution	Signature
Angela Recalde Salas	X	X	X	X	X	70	
Dr. Chandra Salgado Kent	X	X	X		X	10	
Dr. Sarah Marley		X			X	5	
Dr. Miles Parsons	X		X		X	10	
Dr. Robert McCauley					X	5	

Publication title: Non-song vocalisations of humpback whales migrating off the coast of Western Australia

Author	Conceived and designed the study	Collected the data	Analysed the data	Wrote the manuscript	Contributions to drafting and critical review of manuscript	Total % contribution	Signature
Angela Recalde Salas	X	X	X	X	X	70	
Dr. Christine Erbe	X		X		X	15	
Dr. Chandra Salgado Kent	X	X	X		X	10	
Dr. Miles Parsons	X	X			X	5	

Appendix B

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Chapter 2.

2.1. "Reproduced from **Recalde-Salas A, Salgado Kent CP, Parsons MJG, Marley SA, McCauley RD (2014). Non-song vocalizations of pygmy blue whales in Geographe Bay, Western Australia.** ***The Journal of the Acoustical Society of America*****, 135(5): EL213-218**, with the permission of the Acoustical Society of America."

2.2. "Reproduced from **Recalde-Salas A, Salgado Kent CP, Erbe C, Parsons MJG (2020). Vocalizations of Humpback Whales in Western Australia.** ***Frontiers in marine science,*** **7. doi:** https://doi.org/10.3389/fmars.2020.00141."

References

Acevedo MA, Corrada-Bravo CJ, Corrada-Bravo H, Villanueva-Rivera LJ, Aide TM (2009). Automated classification of bird and amphibian calls using machine learning: a comparison of methods. *Ecological Informatics,* 4: 206–214.

Aguilar de Soto N, Madsen PT, Tyack P, Arranz P, Marrero J, Fais A, Revelli E, Johnson M (2012). No shallow talk: cryptic strategy in the vocal communication of Blainville's beaked whales. *Marine Mammal Science.* 28:E75–E92.

Akamatsu T, Wang D, Wang K, Li S, Dong S, Zhao X, Barlow J, Stewart B, Richlen M (2008). Estimation of the detection probability for Yangtze finless porpoises (*Neophocaena phocaenoides asiaeorientalis*) with a passive acoustic method. *The Journal of the Acoustical Society of America*, 123(6): 4403–4411.

Akamatsu T, Rasmussen MH, Iversen M (2014). Acoustically invisible feeding blue whales in Northern Icelandic waters. *The Journal of the Acoustical Society of America*, 136(2): 939–944.

Alldredge MW, Pollock KH, Simons TR (2006). Detection Probabilities from Multiple-Observer Point Counts. *The Auk,* 123(4): 1172-1182.

Alldredge MW, Pollock KH, Simons TR, Collazo JA, Shriner SA, Johnson DH (2007). Time-of-Detection Method for Estimating Abundance from Point-Count Surveys. *The Auk,* 124(2): 653-664.

Amundson CL, Royle JA, Handel CM (2014). A hierarchical model combining distance sampling and time removal to estimate detection probability during avian point counts. *The Auk*, 131(4): 476-494.

Anderson PK, Barclay RM (1995). Acoustic signals of solitary dugongs: physical characteristics and behavioral correlates. *Journal of Mammalogy.* 76(4): 1226 – 1237.

Au WWL. (1993). The Sonar of Dolphins. Springer, New York.

Au WWL, Mobley J, Burgess W, Lammers M, Natchtigall P (2000). Seasonal and diurnal trends of chorusing humpback whales wintering in waters off western Maui. *Marine Mammal Science*, 16(3): 530–544.

Au WWL, Pack AA, Lammers MO, Herman LM, Deakos MH, Andrews K (2006). Acoustic properties of humpback whale song. *The Journal of the Acoustical Ecology of America,* 120(2): 1103-1110.

Au WWL, Hastings M (2008). Principles of bioacoustics. New York: Springer. 679 p.

Australian Government, Department of the Environment and Energy (2018) *Australian Environment Protection and Biodiversity Conservation (EPBC) Act* (1999). Viewed: July 2018, from https://www.legislation.gov.au/Details/C2016C00777.

Balcazar NE, Tripovich JS, Klinck H, Nieukirk SL, Mellinger DK, Dziak RP, Rogers TL (2015). Calls reveal population structure of blue whales across the Southeast Indian Ocean and the Southwest Pacific Ocean. *Journal of Mammalogy*, 96(6): 1184-1193.

Ballinger GA (2004). Using Generalized Estimating Equations for Longitudinal Data Analysis. *Organizational Research Methods*, 7: 127–150.

Barlow J, Gisiner R (2006). Mitigating, monitoring and assessing the effects of anthropogenic sound on beaked whales. *Journal of Cetacean Research and Management,* 7(3): 239-249.

Barlow J, Calambokidis J, Falcone EA, Baker SC, Burdin AM, Clapham PJ, Ford JKB, Gabriele CM, LeDuc R, Mattila DK, Quinn II TJ, Rojas-Bracho L, Straley JM, Taylor BL, Urbán J, Wade P, Weller D, Witteveen BH, Yamaguchi M (2011). Humpback whale abundance in the North Pacific estimated by photographic capture - recapture with bias correction from simulation studies. *Marine Mammal Science,* 27(4):793 - 818.

Bart J, Earnst S (2002). Double Sampling to Estimate Density and Population Trends in Birds. *The Auk*, 119(1): 36–45.

Barua DK (2005). Beaufort Wind Scale, in*:* Finkl C. & Makowski C. (eds), *Encyclopedia of Coastal Science. Encyclopedia of Earth Science Series,* pp, 186-187. Springer, Cham.

Bearder SK (2007). A comparison of calling patterns in two nocturnal primates, *Otolemur crassicaudatus* and *Galago moholi* as a guide to predation risk. In: Gursky S.L, Nekaris K.A.I (eds), *Primate anti-predator strategies. Developments in Primatology: Progress and Prospects,* pp. 206-221. Springer, Boston, MA.

Belinsky KL, Hogle JL, Schmidt KA (2012). Veeries experience more varied acoustic competition at dawn than at dusk. *The Wilson Journal of Ornithology*, 124(2): 265–269.

Bellier E, Kéry M, Schaub M (2016). Simulation-based assessment of dynamic N - mixture models in the presence of density dependence and environmental stochasticity. *Methods in Ecology and Evolution,* 7: 1029-1040. doi: 10.1111/2041-210X.12572

Bender DJ, Bayne EM, Brigham RM (1996). Lunar Condition Influences Coyote (*Canis latrans*) Howling. *The American Midland Naturalist*, 136(2): 413–417.

Best PB (2000). Coastal distribution, movements and site fidelity of right whales *Eubalaena australis* off South Africa, 1969-1998. *South African Journal of Marine Science,* 22:1, 43-55. DOI: 10.2989/025776100784125618.

Bioacoustics Research Program (2014). Raven Pro: Interactive Sound Analysis Software (Version 1.5) [Computer Software]. Ithaca, NY. The Cornell Lab of Ornithology. Available from: http://www.birds.cornell.edu/raven

Bittle M, Duncan A. (2013). A review of current marine mammal detection and classification algorithms for use in automated passive acoustic monitoring. Proceedings of Acoustics 2013, 17-20 Novermber 2013, Victor Harbor, South Australia.

Blackwell SB, Richardson WJ, Greene CR, Streever B (2013). Bowhead Whale (*Balaena mysticetus*) Migration and Calling Behaviour in the Alaskan Beaufort Sea, Autumn 2001-04: An Acoustic Localization Study. *Arctic,* 60(3): 255-270.

Blumstein DT, Mennill DJ, Clemins P, Girod L, Yao K, Patricelli G, Deppe J, Krakauer A, Clark C, Cortopassi K, Hanser S, Mccowan B, Ali A, Kirschel A (2011). Acoustic monitoring in terrestrial environments using microphone arrays: Applications, technological considerations and prospectus. *Journal of Applied Ecology*, 48(3): 758–767.

Boisseau O (2005). Quantifying the acoustic repertoire of a population: the vocalizations of free ranging bottlenose dolphins in Fjordland, New Zealand. *Journal of the Acoustical Society of America*, 117(4): 2318–2329.

Boisseau O, Gillespie D, Leaper R, Moscrop A (2008). Blue (*Balaenoptera musculus*) and fin (*B. physalus*) whale vocalisations measured from northern latitudes of the Atlantic Ocean. *Journal of Cetacean Research and Management*, 10(1): 23–30.

Bolus (2013). Birdsong variation as a source of social information for migrating common yellowthroats. PhD thesis, University of Massachusetts Amherst. Available at: https://scholarworks.umass.edu/open_access_dissertations/778.

Borchers D (2012). A non-technical overview of spatially explicit capture-recapture models. *Journal of Ornithology*. 152(Suppl 2): 435-444.

Borissova I (2002). Geological framework of the Naturaliste Plateau. *Geoscience Australia Record*, 2002/20: 1–43.

Bort J, Van Parijs S, Stevick P, Summers E, Todd S (2015). North Atlantic right whale *Eubalaena glacialis* vocalization patterns in the central Gulf of Maine from October 2009 through October 2010. *Endangered Species Research*, 26(3): 271–280.

Branch T (2007). Abundance of Antarctic blue whales south of 60°S from three completecircumpolar sets of surveys. *Journal of Cetacean Research and Management,* 9(3): 253-262.

Branch TA, Stafford KM, Palacios DM, Allison C, Bannister JL, Burton CLK, Cabrera E, Carlson CA, Galletti Vernazzani B, Gill PC, Hucke-Gaete R, Jenner KCS, Jenner MNM, Matsuoka K, Mikhalev YA, Miyashita T, Morrice MG, Sturrock VJ, Tormosov D, Anderson R C, Baker AN, Best PB, Borsa P, Brownell Jr RL, Childerhouse S, Findlay KP, Gerrodette T, Ilangakoon AD, Joergensen M, Kahn B, Ljungblad DK, Maughan B, Mccauley RD, Mckay S, Norris TF, Oman Whale and Dolphin Research Group, Rankin S, Samaran F, Thiele D, Van Waerebeek K, Warneke RM (2007). Past and present distribution, densities and movements of blue whales *Balaenoptera musculus* in the Southern Hemisphere and northern Indian Ocena. *Mammal Reviews.* 37(2): 116 – 175.

Brandes TS (2008). Automated sound recording and analysis techniques for bird surveys and conservation. *Bird Conservation International*, 18:S163–S173.

Browning E, Gibb R, Glover–Kapfer P, Jones KE (2017). Passive Acoustic monitoring in ecology and conservation. WWF Conservation Technology Series 1(2). WWF – UK. Woking. United Kingdom. 74 p.

Buckland ST, Anderson DR, Burnham KP, Laake JL, Borchers DL, Thomas L (2001). Introduction to distance sampling: estimating abundance of biological populations. New York New York USA (Vol. 10). 448 p.

Burtenshaw JC, Oleson E, Hildebrand J, McDonald M, Andrew R, Howe B, Mercer J (2004). Acoustic and satellite remote sensing of blue whale seasonality and habitat in the Northeast Pacific. *Deep Sea Research Part II: Topical Studies in Oceanography*, 51(10–11): 967–986.

Calambokidis J, Barlow J (2004). Abundance of blue and humpback whales in the eastern North Pacific estimated by capture–recapture and line–transect methods. *Marine Mammal Science.* 21(1): 63 – 85.

Cato DH, Paterson R, Paterson P (2001). Vocalisation rates of migrating humpback whales over 14 years. *Memoirs of the Queensland Museum*, 47(2): 481–489.

Cato DH, McCauley R (2002). Australian research in ambient sea noise. *Acoustics Australia*, 30: 1-13.

Cerchio S, Andrianantenaina B, Lindsay A, Rekdahl M, Andrianarivelo N, Rasoloarijao T (2015). Omura's whales (*Balaenoptera omurai*) off northwest Madagascar: ecology, behaviour and conservation needs. *R. Soc. open sci*. 2(10):150301. doi: doi.org/10.1098/rsos.150301

Cerchio S, Dahlheim M (2001). Variation in feeding vocalizations of humpback whales Megaptera novaeangliae from southeast Alaska. *Bioacoustics* 11(4): 277-295.

Cerchio S, Jacobsen JK, Norris TF (2001). Temporal and geographical variation in songs of humpback whales, Megaptera novaeangliae: synchronous change in Hawaiian and Mexican breeding assemblages, *Animal Behaviour*, 62(2): 313-329.

Cerchio S, Strindberg S, Collins T, Bennett C, Rosenbaum H (2014). Seismic surveys negatively affect humpback whale singing activity off Northern Angola. *PLoS ONE*, 9(3): e86464. doi:10.1371/journal.pone.0086464.

Chandler R, Royle, JA, King DI (2011). Inference about density and temporary emigration in unmarked populations. *Ecology* 92(7): 1429-1435

Charif RA, Clapham PJ, Clark CW (2001). Acoustic detections of singing humpback whales in deep waters off the British Isles. *Marine Mammal Science*, 17(4): 751–768.

Charrier I, Harcourt RG (2006). Individual vocal identity in mother and pup Australian sea lion (*Neophoca cinerea*). *Journal of Mammalogy,* 87(5): 929-938.

Cholewiak DM (2008). Evaluating the role of song in the humpback whale (*Megaptera novaeangliae*) breeding system with respect to intra-sexual interactions. PhD thesis. Cornell University. United States of America. 159 pp.

Cholewiak DM, Sousa-Lima RS, Cerchio S (2013). Humpback whale song hierarchical structure: Historical context and discussion of current classification issues. *Marine Mammal Science*, 29(3): E312–332.

Chu C (1988). Dive times and ventilation patterns of singing humpback whales (*Megaptera novaeangliae*). *Canadian Journal of Zoology,* 66: 1322-1327.

Clapham PJ (1996). The social and reproductive biology of Humpback Whales: an ecological perspective. *Mammal Review*, 26: 27-49.

Clapham PJ, Mattila D (1990). Humpback whale songs as indicators of migration routes. *Marine Mammal Science,* (62)2: 155-160.

Clark CW (1982). The acoustic repertoire of the Southern right whale, a quantitative analysis. *Animal Behaviour*, 30(4): 1060–1071.

Clark CW (1990). Acoustic behavior of Mysticete Whales, in*:* Thomas JA, Kastelein RA (eds), *Sensory abilities of cetaceans*, pp. 571-583. Plenum Press, New York,

Clark CW, Clapham PJ (2004). Acoustic monitoring on a humpback whale (*Megaptera novaeangliae*) feeding ground shows continual singing into late spring. *Proceedings of the Royal Society B: Biological Sciences*, 271(1543): 1051–1057.

Clark CW, Ellison WT, Southall BL, Hatch L, Van Parijs SM, Frankel A, Ponirakis D (2009) Acoustic masking in marine ecosystems: Intuitions, analysis, and implication. *Marine Ecology Progress Series*, 395, 201-222

Clark CW, Brown MW, Corkeron P (2010). Visual and acoustic surveys for North Atlantic right whales, *Eubalaena glacialis*, in Cape Cod Bay, Massachusetts, 2001–2005: Management implications. *Marine Mammal Science*, 26(4): 837–854.

Coggins LG, Bacheler NM, Gwinn DC (2014). Occupancy models for monitoring marine fish: a Bayesian hierarchical approach to model imperfect detection with a novel gear combination. *PLoS ONE,* 9(9): e108302. doi: 10.1371/journal.pone.0108302.

Conway CJ, Eddleman WR, Anderson SH, Hanebury LR (1993). Seasonal Changes in Yuma Clapper Rail Vocalization Rate and Habitat Use. *The Journal of Wildlife Management*, 57(2): 282–290.

Conway CJ (2011). Standardized North American Marsh Bird Monitoring Protocol. *Waterbirds,* 34(3): 319-346.

Cooke JG (2018). *Balaenoptera musculus*. The IUCN Red List of Threatened Species 2018: e.T2477A50226195. Viewed June 2018, from http://dx.doi.org/10.2305/IUCN.UK.2018-2.RLTS.T2477A50226195.en

Cowx IG, Harvey JP, Noble RA, Nunn AD (2009). Establishing survey and monitoring protocols for the assessment of conservation status of fish populations in river Special Areas of Conservation in the UK. *Aquatic Conservation: Marine and Freshwater Ecosystems,* 19: 96-103.

Craig A, Herman L, Gabriele C, Pack A (2003). Migratory Timing of Humpback Whales (*Megaptera novaeangliae*) in the Central North Pacific Varies with Age, Sex and Reproductive Status. *Behaviour*, 140(8/9): 981–1001.

Croll DA, Clark CW, Calambokidis J, Ellison WT, Tershy BR (2001). Effect of anthropogenic low-frequency noise on the foraging ecology of Balaenoptera whales. *Animal Conservation*, 4: 13–27.

Croll DA, Clark CW, Acevedo A, Tershy B, Flores S, Gedamke J, Urban J (2002) Only male fin whales sing loud songs. *Nature,* 417:809

Dail D & Madsen L (2011). Models for Estimating Abundance from Repeated Counts of an Open Metapopulation. *Biometrics.* 64(2): 577-587.

Darling JD, Bérubé M (2001). Interactions of singing humpback whales with other males. *Marine Mammal Science,* 17(3): 570-584.

Darling JD, Jones ME, Nicklin CP (2006). Humpback whale song: do they organize males during the breeding season? *Behaviour.* 143(9): 1051-1101.

Darling JD, Acebes JMV, Yamaguchi M (2014). Similarity yet a range of differences between humpback whale songs recorded in the Philippines, Japan and Hawaii in 2006. *Aquatic Biology,* 21: 93 – 107.

Darling JD, Acebes JMV, Frey O, Urbán J, Yamaguchi M (2019). Convergence and divergence of songs suggests ongoing, but annually variable, mixing of humpback whale populations throughout the North Pacific. *Scientific Reports,* 9: 7002. doi: doi.org/10.1038/s41598-019-42233-7

Damara WA Pty. Ltd (2011). Shire of Busselton Coastal Erosion Study. Assessment of Climate Change Impacts. Final Report 96-00-01. Prepared for the Department of Transport. Western Australia. 68 p.

Dawbin WH (1966). The seasonal migratory cycle of humpback whales, in: Norris, K. S. (ed.), *Whales, dolphins, and porpoises*. Berkeley, California: University of California Press.

Dawbin WH (1997). Temporal segregation of humpback whales during migration in southern hemisphere waters. *Memoirs of the Queensland Museum*, 42:105–138.

Dawson DK, Efford MG (2009). Bird population density estimated from acoustic signals. *Journal of Applied Ecology*, 46(6): 1201–1209.

Deepayan S (2008). *Lattice: Multivariate Data Visualization with R*. Springer, New York. ISBN 978-0-387-75968-5

Dénes, FV, Silveira LF, Beissinger SR (2015). Estimating abundance of unmarked animal populations: Accounting for imperfect detection and other sources of zero inflation. *Methods in Ecology and Evolution*, 6(5): 543-556.

Department of biodiversity, Conservation and Attractions (2018). *Monitoring Standards - Why have standards for monitoring?* Viewed September 20 2018, from https://www.dpaw.wa.gov.au/plants-and-animals/monitoring/standards-and-protocols.

Department of the Environment and Energy (2018a). *Conservation Management Plan for the Blue Whale—A Recovery Plan under the Environment Protection and Biodiversity Conservation Act 1999*. Commonwealth of Australia 2018. 57 p.

Department of the Environment and Energy (2018b), *Australian Marine Parks. Geographe Park.* Viewed February 20 2018, from http://www.environment.gov.au/topics/marine/marine-reserves/south-west/geographe

Delarue J, Martin B, Hannay D (2013). Minke whale boing sound detection in the northeastern Chukchi Sea. *Marine Mammal Science* 29: E333-E341.

Di Sciara GN, Gordon J (1997). Bioacoustics: a tool for the conservation of cetaceans in the Mediterranean Sea. *Mar Freshw Behav Physiol,* 30:125–146.

Di Iorio L, Clark CW (2010). Exposure to seismic survey alters blue whale acoustic communication. *Biology Letters*, 6(1): 51–54.

Dombroski JRG, Parks SE, Groch KR, Flores PAC, Sousa-Lima RS (2016). Vocalizations produced by southern right whale (*Eubalaena australis*) mother-calf pairs in a calving ground off Brazil. *Journal of the Acoustical Society of America*. 140(3): 1850–1857. doi:10.1121/1.4962231

Doniol-Valcroze T, Berteaux D, Larouche P, Sears R (2007) Influence of thermal fronts on habitat selection by four rorqual whale species in the Gulf of St. Lawrence. *Marine Ecology Progress Ser*ies, 335: 207–216.

Dormann CF, McPherson JM, Araújo MB, Bivand R, Bolliger J, Carl G, Davies RG, Hirzel A, Jetz W, Kissling WD, Kühn I, Ohlemüller R, Peres-Neto PR, Reineking B, Schröder B, Schurr FM, Wilson R (2007). Methods to account for spatial autocorrelation in the analysis of species distributional data: a review. *Ecography,* 30: 609-628.

Double MC, Andrews-Goff V, Jenner KCS, Jenner MN, Laverick SM, Branch TA, Gales NJ (2014). Migratory Movements of Pygmy Blue Whales (*Balaenoptera musculus brevicauda*) between Australia and Indonesia as Revealed by Satellite Telemetry. *PloS ONE,* 9(4): e93578. doi: 10.1371/journal.pone.0093578

Double M, Gales N, Jenner KCS, Jenner MN (2010). Satellite tracking of south-bound female humpback whales in the Kimberley region of Western Australia. Final Report. Australian Marine Mammal Centre. 90 p.

Doyle LR, McCowan B, Hanser SF, Chyba C, Bucci T, Blue JE (2008). Applicability of Information Theory to the Quantification of Responses to Anthropogenic Noise by Southeast Alaskan Humpback Whales. *Entropy*, 10(2): 33–46.

Duarte A, Adams MJ, Peterson JT (2018). Fitting N-mixture models to count data with unmodeled heterogeneity: Bias, diagnostics, and alternative approaches. *Ecological modelling.* 374: 51-59.

Dudzinski KM, Thomas JA, Gregg JD (2009). Communication in marine mammals. In Perrin W.F, Würsig B, Thewissen J.G.M (Eds.). *Encyclopedia of Marine Mammals* (2nd ed.), pp. 260-269. Academic Press, London.

Dunlop RA (2016). Changes in vocal parameters with social context in humpback whales: considering the effect of bystanders. *Behavioral Ecology and Sociobiology*, 70(6): 857–870.

Dunlop RA, Noad MJ, Cato DH, Stokes D (2007). The social vocalization repertoire of east Australian migrating humpback whales (*Megaptera novaeangliae*). *The Journal of the Acoustical Society of America*, 122(5): 2893–2905.

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

Dunlop RA, Cato DH, Noad MJ (2010). Your attention please: increasing ambient noise levels elicits a change in communication behaviour in humpback whales (*Megaptera novaeangliae*). *Proceedings of the Royal Society B: Biological Sciences*, 277(1693): 2521–2529.

Dunlop RA, Noad MJ, Cato DH, Stokes D (2013). Source levels of social sounds in migrating humpback whales (*Megaptera novaeangliae*). *The Journal of the Acoustical Society of America*, 134(1): 706–714.

Edds PL (1988). Characteristics of finback *Balaenoptera physalus* vocalizations in the St. Lawrence Estuary. *Bioacoustics*, 1(2–3): 131–149.

Edds-Walton PL (1997). Acoustic communication signals of mysticete whales. *Bioacoustics*, 8(1–2): 47–60.

Erbe C (2013). Underwater passive acoustic monitoring & noise impacts on marine fauna – a workshop report. *Acoustics Australia,* (41(1): 113-119.

Erbe C, Verma A, McCauley R, Gavrilov A, Parnum I (2015). The marine soundscape of the Perth Canyon. *Progress in Oceanography*, 137: 38–51.

Erbe C, McCauley R, Gavrilov A, Madhusudhana S, Verma A. (2016). The underwater soundscape around Australia. *Proceedings of Acoustics 2016*, 9-11 November 2016, Brisbane, Australia.

Erbe C, Dunlop R, Jenner KCS, Jenner M, McCauley R, Parnum I, Parsons M, Rogers T, Salgado Kent CP (2017). Review of Underwater and In-Air Sounds Emitted by Australian and Antarctic Marine Mammals. *Acoustics Australia,* 45(2): 179-241.

Ersts P, Rosenbaum HC (2003). Habitat preference reflects social organization of humpback whales (*Megaptera novaeangliae*) on a wintering ground. *Journal of Zoology.* London 260: 337-345.

Etnoyer P, Canny D, Mate BR, Morgan LE, Ortega-Ortiz JG, Nichols WJ (2006). Sea-surface temperature gradients across blue whale and sea turtle foraging trajectories off the Baja California Peninsula, Mexico. *Deep Sea Research Part II: Topical Studies in Oceanography,* 53: 340–358.

Farnsworth GL, Pollock KH, Nichols JD, Simons TR, Hines JE, Sauer JR (2002). A removal model for estimating detection probabilities from point-count surveys. *The Auk*, 119(2): 414–425.

Farnsworth GL, Nichols JD, Sauer JR, Fancy SG, Pollock H, Shriner S, Simons TR (2005). Statistical Approaches to the Analysis of Point Count Data: A Little Extra Information Can Go a Long Way 1, USDA Forest Service Gen. Technical. Report. PSW-GTR. 191. 8pp.

Félix F (2004). Assessment of the level of surface activity in humpback whales during the breeding season. *Latin American Journal of Aquatic Mammals,* 3(1): 25-36.

Ficetola GF, Barzaghi B, Melotto A, Muraro M, Lunghi E, Canedoli C, Lo Parrino E, Nanni V, Silva-Rocha I, Urso A, Carretero MA, Salvi D, Scali S, Scarì G, Pennati R, Andreone F, Manenti R (2018). Open N -mixture models reliably estimate the abundance of small vertebrates. *Scientific Reports, 8: 10357.* doi: 10.1038/s41598-018-28432-8 1

Field SA, O'Connor PJ, Tyre AJ, Possingham HP (2007). Making monitoring meaningful. *Austral Ecology,* 32(5): 485-491.

Fiske I, Chandler R (2011). unmarked: An R Package for Fitting Hierarchical Models of Wildlife Occurrence and Abundance. *Journal of Statistical Software,* 43(10): 1-23.

Fichtel C, Manser M (2010). Vocal communication in social groups. In: Kappeler, P.M. (ed.), *Animal behavior: evolution and mechanisms,* pp. 29-54. Springer-Verlag Berlin Heidelberg.

Fournet ME, Matthews LP, Gabriele CM, Mellinger DK, Klinck H (2018). Source levels of foraging humpback whale calls. *The Journal of the Acoustical Society of America,* 143(2): EL105-EL111.

Fournet ME, Szabo A, Mellinger DK (2015). Repertoire and classification of non-song calls in Southeast Alaskan humpback whales (*Megaptera novaeangliae*). *The Journal of the Acoustical Society of America*, 137(1): 1–10.

Fox J, Weisberg S (2011). *An {R} Companion to Applied Regression*, Second Edition. Sage publications, Thousand Oaks CA. 608 p.

Frankel AS, Clark C, Gabriele C (1995). Spatial-distribution, habitat utilization, and social interactions of humpback whales, *Megaptera-novaeangliae*, off Hawaii, determined using acoustic and visual techniques. *Canadian Journal of Zoology*, 73(6): 1134–1146.

Frick WF (2013). Acoustic monitoring of bats, considerations of options for long-term monitoring. *Therya,* 4(1): 69-78.

Fuller RA, Warren PH, Gaston KJ (2007). Daytime noise predicts nocturnal singing in urban robins. *Biology letters,* 3(4): 368-370.

Gannon DP (2008). Passive Acoustic Techniques in Fisheries Science: A Review and Prospectus. *Transactions of the American Fisheries Society*, 137(2): 638–656.

Garland EC, Goldizen AW, Rekdahl ML, Constantine R, Garrigue C, Hauser ND, Poole M, Robbins J, Noad MJ (2011). Dynamic Horizontal Cultural Transmission of Humpback Whale Song at the Ocean Basin Scale. *Current Biology: CB*, 21(8): 687–691.

Garland EC, Berchok CL, Castellote M (2015). Temporal peaks in beluga whale (*Delphinapterus leucas*) acoustic detections in the northern Bering, northeastern Chukchi, and western Beaufort Seas: 2010-2011. *Polar Biology*, 38(5): 747–754.

Gastwirth JL, Gel YR, Hui WLW, Lyubchich V, Miao W, Noguchi K (2017). Lawstat: Tools for Biostatistics, Public Policy, and Law. R package version 3.1. https://CRAN.R-project.org/package=lawstat

Gavrilov AN, McCauley RD, Salgado-Kent C, Tripovich J, Burton C (2011). Vocal characteristics of pygmy blue whales and their change over time. *Journal of Acoustical Society of America*, 130(6): 3651–3660.

Gavrilov AN, McCauley RD (2013). Acoustic detection and long-term monitoring of pygmy blue whales over the continental slope in southwest Australia. *The Journal of the Acoustical Society of America*, 134(3): 2505–2513.

Gavrilov AG, Parsons MJG (2014). A Matlab tool for the characterisation of underwater sound (CHORUS). *Acoustics Australia*, 42(3): 190-196.

Gedamke J, Costa DP, Dunstan A (2001). Localization and visual verification of a complex minke whale vocalization. *The Journal of the Acoustical Society of America,* 109(6): 3038-3047.

Gedamke J, Gales N, Hildebrand J, Wiggins S (2007). Seasonal occurrence of low frequency whale vocalisations across eastern Antarctic and southern Australian waters, February 2004 to February 2007. *Report of the International Whaling Commission*, SC/59/SH5 (February 2004): 1–11.

Genz A, Bretz F, Miwa T, Mi X, Leisch F, Scheipl F, Hothorn T (2016). mvtnorm: Multivariate Normal and t Distributions. R package version 1.0-5.

Gerber LR, Beger M, McCarthy MA, Possingham HP (2005). A theory for optimal monitoring of marine reserves. *Ecology Letters,* 8(8): 829-837.

Gillespie D (2004). Detection and classification of right whale calls using an ‘Edge’ detector operating on a smoothed spectrogram. *Canadian Acoustics,* 32(2): 39-47.

Guan S, Takemura A, Koido T (1999). An introduction to the structure of humpback whale, *Megaptera novaeangliae*, song off Ryukyu Islands, 1991/ 1992. *Aquatic Mammals*, 25.1: 35–42.

Guidino C, Llapapasca MA, Silva S, Alcorta B, Pacheco AS (2014). Patterns of spatial and temporal distribution of humpback whales at the southern limit of the southeast pacific breeding area. *PloS ONE, 9(11):* e112627*.* doi: 10.1371/journal.pone.0112627

Halekoh U, Højsgaard S, Yan J (2006). The R package geepack for Generalized Estimated Equations. *Journal of Statistical Software,* 15(2): 1-11.

Halkias XC, Paris S, Glotin H (2013). Classification of mysticete sounds using machine learning techniques. *The Journal of the Acoustical Society of America,* 134(5): 3496 – 3505.

Hannay DE, Delarue J, Mouy X, Martin BS, Leary D, Oswald JN, Vallarta J (2013). Marine mammal acoustic detections in the northeastern Chukchi Sea, September 2007–July 2011. *Continental Shelf Research.* 67: 127-146.

Hardin J, Hilbe J (2013). Generalized Estimating Equations, Second Edition. Chapman and Hall/CRC, New York. 279 p.

Hatch L, Clark, C, Merrick R, Van Parijs S, Ponirakis D, Schwehr K, Thompson M, Wiley David (2008). Characterizing the Relative Contributions of Large Vessels to Total Ocean Noise Fields: A Case Study Using the Gerry E Studds Stellwagen Bank National Marine Sanctuary. *Environmental management*. 42: 735-752. doi: 10.1007/s00267-008-9169-4.

Hedley SL, Bannister JL, Dunlop RA (2011). Abundance estimates of Breeding Stock ‘D’ humpback whales from aerial and land-based surveys off Shark Bay, Western Australia, 2008. *Journal of Cetacean Research and Management*, Special issue 3: 209–21

Helble TA (2013). Site specific passive acoustic detection and densities of humpback whale calls off the coast of California. PhD Thesis. University of California, San Diego, California, USA.

Helble TA, D’Spain, Hildebrand J, Campbell R, Heaney K (2013). Site specific probability of passive acoustic detection of humpback whale calls from single fixed hydrophones. *The Journal of the Acoustical Society of America*, 134: 2556-2570.

Helweg DA, Herman LM (1994). Diurnal Patterns of Behaviour and Group Membership of Humpback Whales (*Megaptera novaeangliae*) Wintering in Hawaiian Waters. *Ethology*, 98(3–4): 298–311.

Herman LM (2017). The multiple functions of male song within the humpback whale (*Megaptera novaeangliae*) mating system: review, evaluation, and synthesis. *Biological reviews,* 92(3): 1795 – 1818.

Hildebrand JA (2009). Anthropogenic and natural sources of ambient noise in the ocean. *Marine Ecology Progress Series*. 395(7): 5-20.

Hinkle DE, Wiersma W, Jurs SG (1994). Applied statistics for the behavioral sciences. 3rd edition. Boston: Houghton Mifflin.

Hofmeyr-Juritz LH, Best PB (2011). Acoustic behaviour of southern right whales in relation to numbers of whales present in Walker Bay, South Africa. *African Journal of Marine Science*, 33(3): 415–427.

Halekoh R, Højsgaard S, Yan J (2006). The R Package geepack for Generalized Estimating Equations. *Journal of Statistical Software.* 15(2): 1-11.

Herbst CT (2016). Biophysics of Vocal Production in Mammals. In: Suthers R., Fitch W., Fay R., Popper A. (eds) *Vertebrate Sound Production and Acoustic Communication*. Springer Handbook of Auditory Research, vol 53. Springer, Cham. p. 159 – 189.

Højsgaard S (2006). The doBy package. *R News*, 6(2) (May 2006): 47-49.

Ichikawa K, Akamatsu T, Shinke T, Sasamori K, Miyauchi Y, Abe Y, Adulyanukosol K, Arai N (2009). Detection probability of vocalizing dugongs during playback of conspecific calls. *The Journal of the Acoustical Society of America*, 126(4): 1954–1959.

International Whaling Commission (2016a). Report of the standing working group on conservation management plans. IWC/66/CCRep06. 19 pp.

International Whaling Commission (2016b). Report of the Conservation Committee. IWC/66/Rep05. 31 pp.

International Whaling Commission (2018). *Status of whales.* Viewed 10th of June 2018, from https://iwc.int/status

Irvine LM, Mate BR, Winsor MH, Palacios DM, Bograd SJ, Costa DP, Bailey H (2014) Spatial and Temporal Occurrence of Blue Whales off the U.S. West Coast, with Implications for Management. *PLoS ONE,* 9(7): e102959. doi:10.1371/journal.pone.0102959

Irvine L, Salgado Kent C (2017). The distribution and relative abundance of humpback whale (*Megaptera novaeangliae*) calves within the Ningaloo Marine Park, Western Australia between June and August 2016. Report to the Department of Parks and Wildlife, Western Australia. 49 pp.

Isaac D, Marler P (1963). Ordering of sequences of singing behavior of Mistle thrushes in relationship to timing. *Animal Behaviour* 11:179–188.

Jenner KCS, Jenner MNM, McCabe KA (2001). Geographical and temporal movements of humpback whales in Western Australian waters. *APPEA Journal,* 41: 749-765.

Jenner C, Jenner M, Burton C, Sturrock V, Salgado Kent C, Morrice M, Attard C, Moller L, Double MC (2008). Mark recapture analysis of pygmy blue whales from the Perth Canyon, Western Australia 2000–2005. Paper presented to the Scientific Committee of the International Whaling Commission: SC/60/SH16.

Jones, G.J, Sayigh LS (2002). Geographic variation in rates of vocal production of free-ranging bottlenose dolphins. *Marine Mammal Science*, 18(2): 374–393.

Kellner KF, Swihart RK (2014). Accounting for imperfect detection in ecology: a quantitative review. *PloS ONE,* 9(10): E111436. doi: 10.1371/journal.pone.0111436

Kendall WL, Nichols JD, Hines JE (1997). Estimating temporary emigration using capture–recapture data with Pollock's robust design. *Ecology*, 78: 563–578.

Kéry M (2018). Identifiability in N-mixture models: a large-scale screening test with bird data. *Ecology.* 99(2): 281-288.

Kéry M, Royle JA (2016). Applied hierarchical modeling in ecology: analysis of distribution, abundance and species richness in R and BUGS. Vol. 1, Prelude and static models. Amsterdam: Elsevier. 783 p.

Kimura S, Akamatsu T, Wang K, Wang D, Li S, Dong S, Arai N. (2009). Comparison of stationary acoustic monitoring and visual observation of finless porpoises. *The Journal of the Acoustical Society of America*, 125(1), 547-553.

Kumar A (2003). Estimation of abundance of blue whale calls off Central California using a seafloor-mounted hydrophone. Master Thesis. College of Science and Mathematics. California State University, Fresno, California. USA.

Kuperman AW, Roux P. (2014). Underwater acoustics. In: Rossing TD (ed). *Springer Handbook of Acoustics.* Springer, USA. pp: 157-209.

Küsel ET, Mellinger DK, Thomas L, Marques TA, Moretti D, Ward J (2011). Cetacean population density estimation from single fixed sensors using passive acoustics. *The Journal of the Acoustical Society of America,* 129(6): 3610-3622.

Kwon E, Houghton LM, Settlage RE, Catlin DH, Karpanty SM, Fraser JD (2018). Estimating transient populations of unmarked individuals at a migratory stopover site using generalized N-mixture models. *Journal of Applied Ecology, in press*. doi: 10.1111/1365-2664.13243

La VT, Nudds TD (2016). Estimation of avian species richness: biases in morning surveys and efficient sampling from acoustic recordings. *Ecosphere,* 7(4): e01294.

Laake JL, Collier BA, Morrison ML, Wilkins RN (2011). Point-based mark-recapture distance sampling. *Journal of Agricultural, Biological, and Environmental Statistics*, 16(3): 389–408.

Lahoz-Monfort JJ, Guillera-Arroita G, Wintle BA (2014). Imperfect detection impacts the performance of species distribution models. *Global Ecology and Biogeography,* 23: 504-515.

Lammers MO, Brainard RE, Au WW, Mooney TA, Wong KB (2008). An ecological acoustic recorder (EAR) for long-term monitoring of biological and anthropogenic sounds on coral reefs and other marine habitats. The Journal of the Acoustical Society of America, 123(3), 1720-1728.

Langlois TJ, Harvey ES, Fitzpatrick B, Meeuwig JJ, Shedrawi G, Watson DL (2010). Cost-efficient sampling of fish assemblages: comparison of baited video stations and diver video transects. *Aquatic Biology,* 9: 155–168.

Laundre JW (1981). Temporal Variation in Coyote Vocalization Rates. *The Journal of Wildlife Management*, 45(3): 767.

Leary CJ, Garcia AM, Knapp R (2008). Density-dependent mating tactic expression is linked to stress hormone in Woodhouse's toad. *Behavioral Ecology*, 19: 1103-1110.

Lesage V, Barrette C, Kingsley MCS, Sjare B (1999). The effect of vessel noise on the vocal behavior of belugas in the St. Lawrence river estuary, Canada. *Marine Mammal Science*, 15(1): 65–84.

Lima A, Le Pendu Y (2014). Evidence for signature whistles in Guiana dolphins (*Sotalia guianensis*) in Ilhéus, northeastern Brazil. *The Journal of the Acoustical Society of America,* 136(6): 3178-3185.

Lingnau R, Bastos RP (2007). Vocalizations of the Brazilian torrent frog Hylodes heyeri (Anura: Hylodidae): Repertoire and influence of air temperature on advertisement call variation. *Journal of Natural History*, 41(17–20): 1227–1235.

Link W (2018). On the robustness of N-mixture models. *Ecology,* 99(7): 1547-1551.

Lucas JR, Schraeder A, Jackson C (1999). Carolina Chickadee (Aves, Paridae, *Poecile carolinensis*) Vocalization Rates: Effects of Body Mass and Food Availability under Aviary Conditions. *Ethiopian Journal of Environmental Studies and Management*, 105(6): 503–520.

Lucke K (2014). Noise logger overview. (One size does not fit all). *IMARES internal report*, 44 pp.

Luczkovich JJ, Mann DA, Rountree RA (2008). Passive Acoustics as a Tool in Fisheries Science. *Transactions of the American Fisheries Society,* 137(2): 533-541.

Ma BB, Nystuen JA, Lien RC (2005). Prediction of underwater sound levels from rain and wind. *The Journal of the Acoustical Society of America*, 117(6): 3555–3565.

McDonald MA, Fox CG (1999). Passive acoustic methods applied to fin whale population density estimation. *The Journal of the Acoustical Society of America,* 105(5): 2643-2651.

Marcoux M, Auger-Méthé M, Chmelnitsky EG, Ferguson SH, Humphries MM (2011). Local Passive Acoustic Monitoring of Narwhal Presence in the Canadian Arctic: A Pilot Project. *Arctic*, 64(3): 307–316.

Marques T, Thomas L, Ward J, DiMarzio N, Tyack PL (2009). Estimating cetacean population density using fixed passive acoustic sensors: an example with Blainville's beaked whales. *The Journal of the Acoustical Society of America*, 125(4): 1982–1994.

Marques TA, Munger L, Thomas L, Wiggins S, Hildebrand JA (2011). Estimating North Pacific right whale *Eubalaena japonica* density using passive acoustic cue counting. *Endangered Species Research*, 13(3): 163–172.

Marques TA, Thomas L, Martin SW, Mellinger DK, Jarvis S, Morrissey RP, Ciminello CA, DiMarzio N (2012). Spatially explicit capture-recapture methods to estimate minke whale density from data collected at bottom-mounted hydrophones. *Journal of Ornithology,* 152 (Supl 2): S445-S455. doi: 10.1007/s10336-010-0535-7

Marques TA, Thomas L, Martin SW, Mellinger DK, Ward JA, Moretti DJ, Harris D, Tyack PL (2013). Estimating animal population density using passive acoustics. *Biological Reviews*, 88(2): 287–309.

Martin J, Kitchens WM, Hines JE (2007). Importance of well-designed monitoring programs for the conservation of endangered species: Case study of the snail kite. *Conservation Biology*, 21(2): 472–481.

Martin SW, Marques TA, Thomas L, Morrissey RP, Jarvis S, DiMarzio N, Moretti D, Mellinger DK (2013). Estimating minke whale (*Balaenoptera acutorostrata*) boing sound density using passive acoustic sensors. *Marine Mammal Science*, 29(1): 142–158.

Matthews JN, Brown S, Gillespie D, Johnson MP, RcLanaghan R, Moscrop A, Nowacek DP (2001). Vocalisation rates of the North Atlantic right whale (*Eubalaena glacialis*). *Journal of Cetacean Research and Management*, 3(3): 271-282.

Matthews LP, McCordic JA, Parks SE (2014). Remote Acoustic Monitoring of North Atlantic Right Whales (*Eubalaena glacialis*) Reveals Seasonal and Diel Variations in Acoustic Behavior. *PLoS ONE*, 9(3): e91367. doi: 10.1371/journal.pone.0091367

McCallum DA (2005a). The relationship between cue abundance and cue availability, and its impact on detectability during point count surveys: a Monte Carlo simulation study. Report presented to Patuxent Wildlife & Research Center Breeding Bird Survey. Laurel Maryland. 23 pp. Available at: http://www.appliedbioacoustics.com/research/reports/Cue abundance and availability final.pdf

McCallum D (2005b). A conceptual guide to detection probability for point counts and other count-based survey methods. *US Forest Service General Technical Report PSW-GTR-149*, Albany, California, USA.

McCarthy MA, Moore JL, Morris WK, Parris KM, Garrard GE, Vesk PA, Rumpff L, Giljohann KM, Camac JS, Bau SS, Friend T, Harrison B, Yue B (2012). The influence of abundance on detectability. *Oikos,* 122(5): 717-726.

McCauley RD (2012). Fish choruses from the Kimberley, seasonal and lunar links as determined by long term sea noise monitoring. *Proceedings of the Acoustical Society of Australia*, (November), Fremantle, Western Australia; 21-23 November.

McCauley RD, Jenner C, Bannister JL, Cato DH (2001). Blue whale calling off the Western Australian coast. *The Journal of the Acoustical Society of America*, 109(5): 2391.

McCauley RD, Jenner CK (2010). Migratory patterns and estimated population size of pygmy blue whales (*Balaenoptera musculus brevicauda*) traversing the Western Australian coast based on passive acoustics. In: Reports of the 62nd International Whaling Commission Annual Meeting. Agadir, Morocco.

McCauley RD, Thomas F, Parsons MJG, Erbe C, Cato DH, Duncan AJ, Gavrilov A, Parnum I, Salgado-Kent CP (2017). Developing an Underwater Sound Recorder: The Long and Short (Time) of It. *Acoustics Australia*, 45(2): 301-311.

McDonald MA, Calambokidis J, Teranishi, Hildebrand JA (2001). The acoustic calls of blue whales off California with gender data. *Journal of the Acoustical Society of America*, 109(4): 1728-1735.

McDonald MA, Mesnick SL, Hildebrand JA (2006). Biogeographic characterization of blue whale song worldwide: Using song to identify populations. *Journal of Cetacean Research and Management,* 8 (1):55-65.

McKenna MF (2011). Blue Whale Response to Underwater Noise from Commercial Ships. PhD thesis. University of California, San Diego, United States of America. 218 p.

Meelup Regional Park. 2018. *About Meelup Regional Park.* Visited February 20 2018, from http://meeluppark.com/

Melcón ML, Cummins AJ, Kerosky SM, Roche LK, Wiggins SM, Hildebrand JA (2012). Blue Whales Respond to Anthropogenic Noise. *PLoS ONE*, 7(2): e32681. doi: 10.1371/journal.pone.0032681

Mellinger D, Clark C (2003). Blue whale (*Balaenoptera musculus*) sounds from the North Atlantic. The *Journal of Acoustical Society of America*, 114(2): 1108-1119.

Mellinger DK, Nieukirk SL, Matsumoto H, Heimlich SL, Dziak RP, Haxel J, Fowler M, Meinig C, Miller HV (2007). Seasonal occurrence of North Atlantic right whale (*Eubalaena glacialis*) vocalizations at two sites on the Scotian shelf. *Marine Mammal Science*, 23(4): 856–867.

Mellinger DK, Küsel ET, Thomas L, Marques TA (2009). Taming the Jez monster: Estimating fin whale spatial density using acoustic propagation modeling. *The Journal of the Acoustical Society of America,* 126(4): 2229.

Mellinger DK, Küsel ET, Harris D, Thomas L, Matias L (2014). Estimating singing fin whale population density using frequency band energy. *The Journal of the Acoustical Society of America*, 136(4): 2275.

Mercado III E, Herman L, Pack A (2003). Stereotypical sound patterns in humpback whale songs: Usage and function. Aquatic Mammals, 29(1), 16.

Milner-Gulland EJ, Rowcliffe M (2007). Conservation and sustainable use: a handbook of techniques. Oxford University Press; Oxford, UK, 328 p.

Mobley JR, Herman LM, Frankel AS (1988) Responses of wintering humpback whales (*Megaptera novaeangliae*) to playbacks of winter and summer vocalizations and synthetic sound. *Behavioral Ecology Sociobiology*, 23:211–223

Monnahan CC, Branch TA, Stafford KM, Ivashchenko YV, Oleson EM (2014). Estimating Historical Eastern North Pacific Blue Whale Catches Using Spatial Calling Patterns. *PLoS ONE*, 9(6): e98974. doi: 10.1371/journal.pone.0098974

Moore SE, Stafford KM, Dahlheim ME, Fox CG, Braham HW, Polovina JJ, Bain DE (1998). Seasonal variation in reception of fin whale calls at five geographic areas in the north pacific. *Marine Mammal Science,* 14(3): 617-627.

Morano JL, Rice A, Tielens J, Estabrook B, Murray A, Roberts B, Clark C (2012). Acoustically detected year-round presence of right whales in an urbanized migration corridor. *Conservation Biology*, 26(4): 698-707.

Morete ME, Bisi TL, Rosso S (2007). Temporal pattern of humpback whale (*Megaptera novaeangliae*) group structure around Abrolhos Archipielago breeding region, Bahía, Brazil. *Journal of the Marine Biological Association of the United Kingdom,* 87(1): 87-92.

Morgan J, Daugherty R, Hilchie A, Carey B (2003). Sample size and modelling accuracy of decision tree based data mining tools. *Academy of Information and Management Sciences Journal*, 6(2): 77-92.

Moscrop A, Matthews J, Gillespie D, Leaper R (2004). Development of passive acoustic monitoring systems for Northern right whales. *Canadian Acoustics,* 32(2): 17-22.

Mulder BS, Noon BR, Spies TA, Raphael MG, Palmer CJ, Olsen AR, Reeves GH, Welsh HH (1999). The strategy and design of the effectiveness monitoring program for the Northwest Forest Plan. USDA Forest Service, Pacific Northwest Forest Station, *General Technical Report PNW–GTR–437.* 138 p.

Munger LM, Wiggins SM, Moore SE, Hildebrand JA (2008). North Pacific right whale (*Eubalaena japonica*) seasonal and diel calling patterns from long-term acoustic recordings in the southeastern Bering Sea, 2000–2006. *Marine Mammal Science,* 24(4): 795–814.

Murn C, Holloway GJ (2006). Using areas of known occupancy to identify sources of variation in detection probability of raptors: taking tie lowers replication effort for surveys. *Royal Society Open Science,* 3(10): 160368. doi: 10.1109/ICCVW.2017.352

Murray A, Cerchio S, McCauley R, Jenner CS, Razafindrakoto Y, Coughran D, McKay S, Rosenbaum H (2012). Minimal similarity in song suggest limited exchange between humpback whales (*Megaptera novaeangliae*) in the southern Indian Ocean. *Marine Mammal Science* 28(1): E41-E57.

Mussoline S, Risch, D, Hatch L, Weinrich M, Wiley D, Thompson M, Corkeron P, Van Parijs S (2012). Seasonal and diel variation in North Atlantic right whale up-calls: implications for management and conservation in the northwestern Atlantic Ocean. *Endangered Species Research*, 17(1): 17–26.

Nichols JD, Hines JE, Sauer JR, Fallon JE, Heglund PJ (2000). A Double-Observer Approach for Estimating Detection Probability and Abundance from Point Counts. *The Auk,* 117(2): 393-408. doi: 10.2307/4089721.

Noad MJ, Cato DH (2007). Swimming speeds of singing and non-singing humpback whales during migration. *Marine Mammal Science*, 23(3): 481–495

Noad MJ, Dunlop RA, Mack AK (2017). Changes in humpback whale singing behavior with abundance: Implications for the development of acoustic surveys of cetaceans. *The Journal of the Acoustical Society of America*, 142(3): 1611–1618.

Norris KS, Goodman RM, Villa-Ramirez B, Hobbs L (1977) Behavior of California gray whale, *Eschrichtius robustus*, in southern Baja California, Mexico. *Fisheries Bulletin,* 75: 159–172

Norris TF, McDonald M, Barlow J (1999). Acoustic detections of singing humpback whales (*Megaptera novaeangliae*) in the eastern North Pacific during their northbound migration. *The Journal of the Acoustical Society of America*, 106(1): 506–514.

Nowacek DP, Casper BM, Wells RS, Nowacek SM, Mann DA (2003). Intraspecific and geographic variation of West Indian Manatee (*Trichechus manatus spp.)* vocalizations (L). *Journal of the Acoustical Society of America* 114(1): 66 – 69.

Nowacek DP, Bröker K, Donovan G, Gailey G, Racca R, Reeves RR, Vedenev A, Weller D, Southall BL (2013). Responsible Practices for Minimizing and

Monitoring Environmental Impacts of Marine Seismic Surveys with an Emphasis on Marine Mammals. *Aquatic Mammals*, 39(4): 356–377.

Odom KJ, Mennill DJ (2010). A Quantitative Description of the Vocalizations and Vocal Activity of the Barred Owl. *The Condor*, 112(3): 549–560.

Oedekoven CS, Buckland ST, Mackenzie ML, Evans KO, Burger LW (2013). Improving distance sampling: accounting for covariates and non-independency between sampled sites. *Journal of Applied Ecology*, 50: 786–793.

Oldham C, Lavery P, McMahon K, Pattiaratchi C, Chiffings T (2010). Seagrass wrack dynamics in Geographe Bay, Western Australia, (April), *Report presented to Department of Transport, Shire of Busselton*. 214. Edith Cowan University, University of Western Australia, DHI Australia. Available at: http://www.ecu.edu.au/__data/assets/pdf_file/0003/393753/Seagrass-Wrack-Dynamics-LR.pdf

Oleson EM, Calambokidis J, Barlow J, Hildebrand JA (2007). Blue whale visual and acoustic encounter rates in the southern California bight. *Marine Mammal Science*, 23(3): 574–597.

Oleson EM, Calambokidis J, Burgess WC, McDonald MA, LeDuc CA, Hildebrand JA (2007). Behavioral context of call production by eastern North Pacific blue whales. *Marine Ecology Progress Series*, 330: 269–284.

Oleson EM, Wiggins SM, Hildebrand JA (2007). Temporal separation of blue whale call types on a southern California feeding ground. *Animal Behaviour,* 74(4): 881-894.

Oña J, Garland EC, Denkinger J (2016). Southeastern Pacific humpback whales (*Megaptera novaeangliae*) and their breeding grounds: distribution and habitat preference of singers and social groups off the coast of Ecuador. *Marine Mammal Science,* 33(1): 219-235.

Pace F, Benard F, Glotin H, Adam O, White P (2010). Subunit definition and analysis for humpback whale call classification. *Applied Acoustics,* 71(11): 1107-1112.

Pan W (2001). Akaike’s information criterion in generalized estimating equations. *Biometrics,* 57(1): 120-125.

Parsons MJG, Salgado Kent CP, Recalde-Salas A, McCauley RD (2016). Fish choruses off Port Hedland, Western Australia. *Bioacoustics*, 4622(September): 1–18.

Parsons MJG, Holley D, McCauley RD (2013). Source levels of dugong (*Dugong dugon*) vocalizations recorded in Shark Bay. *The Journal of the Acoustical Society of America*, 134(3): 2582 – 2588.

Parks SE, Clark CW, Tyack PL (2007). Short- and long-term changes in right whale calling behavior: The potential effects of noise on acoustic communication. *The Journal of the Acoustical Society of America*, 122(6): 3725-3731.

Parks SE, Searby A, Célérier A, Johnson MP, Nowacek DP, Tyack PL (2011) Sound production behavior of individual North Atlantic right whales: implications for passive acoustic monitoring. *Endangered Species Research*, 15:63–76.

Pattiaratchi C (2007). Understanding areas of high productivity within the South-west Marine Region. *Report prepared for the Department of the Environment, Water, Heritage and the Arts*. School of Environmental Systems Engineering, University of Western Australia. Western Australia. 53 p.

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

Payne, R (1978). Behavior and vocalizations of humpback whales (*Megaptera* sp.). In: Norris KS, Reeves RR (eds). *Report on a workshop on problems related to humpback whales (Megaptera novaeangliae) in Hawaii*. NTIS, PB-280 794, Report no. MMC-77/03: 56–78.

Payne R, Guinee L (1983). Humpback whale (Megaptera novaeangliae) songs as an indicator of “stocks”. R. Payne (Editor). In: *Communication and Behavior of Whales.* Westview Press, Boulder, CO. pp: 333-358.

Payne K, Tyack P, Payne R (1983). Progressive changes in the songs of humpback whales (*Megaptera novaeangliae*): A detailed analysis of two seasons in Hawaii. In: Payne R (ed.), *Communication and Behavior of Whales,* pp. 9–57, Boulder, CO: Westview Press.

Picciulin M, Sebastianutto L, Codarin A, Calcagno G, Ferrero EA (2012). Brown meagre vocalization rate increases during repetitive boat noise exposures: A possible case of vocal compensation. *The Journal of Acoustical Society of America*, 132(5): 3118–3124.

Pollock KH, Nichols JD, Simons TR, Farnsworth GL, Bailey LL, Sauer JR (2002). Large scale wildlife monitoring studies: statistical methods for design and analysis. *Environmetrics*, 13(2): 105–119.

Ponce D, Thode AM, Guerra M, Urban RJ, Swartz S (2012). Relationship between visual counts and call detection rates of gray whales (*Eschrichtius robustus*) in Laguna San Ignacio, Mexico. *The Journal of Acoustical Society of America*, 131(4): 2700–2713.

Propped DS, Finch E (2017). Vocalizing during gaps in anthropogenic noise is an uncommon trait for enhancing communication in songbirds. *Journal of Ecoacoustics*, 1: TLP16D.

Radford CA, Jeffs AG, Tindle CT, Montgomery JC (2008). Temporal patterns in ambient noise of biological origin from a shallow water temperate reef. *Oecologia*, 156(4): 921–929.

Ramp C, Delarue, J, Palsbøll PJ, Sears R, Hammond PS (2015). Adapting to a warmer ocean - Seasonal shift of baleen whale movements over three decades. *PLoS ONE*, 10(3): e0121374. doi:10.1371/journal.pone.0121374.

Rankin S, Ljungblad D, Clark C, Kato H (2005). Vocalisations of Antarctic blue whales, *Balaenoptera musculus intermedia*, recorded during the 2001/2002 and 2002/2003 IWC/SOWER circumpolar cruises, Area V, Antarctic. *Journal of Cetacean Research and Management,* 7(1): 13-20.

Rankin S, Norris TF, Smultea MA, Oedekoven C, Zoidis AM, Silva E, Rivers J (2007). A Visual Sighting and Acoustic Detections of Minke Whales, *Balaenoptera acutorostrata* (Cetacea: Balaenopteridae), in Nearshore Hawaiian Waters. *Pacific Science,* 61(3): 395-398.

Rasmussen K, Panama DC, Calambokidis J, Steiger GH (2012). Distribution and migratory destinations of humpback whales off the Pacific coast of Central America during the boreal winters of 1996 – 2003. *Marine Mammal Science,* 28(3): E267 – E279.

Recalde-Salas A, Salgado Kent CP, Parsons MJG, Marley SA, McCauley RD (2014). Non-song vocalizations of pygmy blue whales in Geographe Bay, Western Australia. *The Journal of the Acoustical Society of America*, 135(5): EL213-218.

Redfern JV, Ferguson MC, Becker EA, Hyrenbach KD, Good C, Barlow J, Kaschner K, Baumgartner MF, Forney KA, Ballance LT, Fauchald P, Halpin

P, Hamazaki T, Pershing AJ, Qian SS, Read A, Reilly SB, Torres L, Werner F (2006). Techniques for cetacean-habitat modeling. *Marine Ecology Progress Series,* 310: 271-295.

Reilly SB, Bannister JL, Best PB, Brown M, Brownell Jr RL, Butterworth DS, Clapham PJ, Cooke J, Donovan GP, Urbán J, Zerbini AN (2008). *Megaptera novaeangliae.* The IUCN Red List of Threatened Species 2008: e.T13006A3405371. Viewed June 2018, from http://dx.doi.org/10.2305/IUCN.UK.2008.RLTS.T13006A3405371.en

Rekdahl ML, Dunlop RA, Noad MJ, Goldizen AW (2013). Temporal stability and change in the social call repertoire of migrating humpback whales. *Journal of Acoustical Society of America*, 133(3): 1785-1795.

Rehm EM, Baldassarre GA (2007). Temporal variation in detection of marsh birds during broadcast of conspecific calls. *Journal of Field Ornithology*, 78(1): 56–63.

Rice AN, Tielens JT, Estabrook BJ, Muirhead CA, Rahaman A, Guerra M, Clark CW (2014). Variation of ocean acoustic environments along the western North Atlantic coast: A case study in context of the right whale migration route. *Ecol. Inform.*, 21: 89–99.

Richardson WJ, Greene Jr CR, Malme CI, Thomson DH (1995). Marine Mammals and noise. Academic Press, Inc.

Richman NI, Gibbons JM, Turvey ST, Akamatsu T, Ahmed B, Mahabub E, Smith B, Jones J (2014). To See or Not to See: Investigating Detectability of Ganges River Dolphins Using a Combined Visual-Acoustic Survey. *PLoS ONE*, 9(5): e96811. doi: 10.1371/journal.pone.0096811

Riddle JD, Pollock KH, Simons TR (2010). An unreconciled double-observer method for estimating detection probability and abundance. *The Auk,* 127(4): 841-849.

Riera A, Ford JK, Chapman NR (2013). Effects of different analysis techniques and recording duty cycles on passive acoustic monitoring of killer whales. *The Journal of the Acoustical Society of America.* 135(3): 2393 – 2404.

Risch D, Corkeron PJ, Ellison WT, Van Parijs SM (2012). Changes in Humpback Whale Song Occurrence in Response to an Acoustic Source 200 km Away. *PLoS ONE,* 7(1): e29741. doi:10.1371/journal.pone.0029741

Risch D, Clark CW, Dugan PJ, Popescu M, Siebert U, Van Parijs SM (2013). Minke whale acoustic behavior and multi-year seasonal and diel vocalization patterns in Massachusetts Bay, USA. *Marine Ecology Progress Series*, 489: 279–295.

Rowell TJ, Schärer MT, Appeldoorn RS, Nemeth MI, Mann DA, Rivera JA (2012). Sound production as an indicator of red hind density at a spawning aggregation. *Marine Ecology Progress Series*, 462: 241–250.

Rowell TJ, Demer DA, Aburto-Oropeza O, Cota-Nieto JJ, Hyde JR, Erisman BE (2017). Estimating fish abundance at spawning aggregations from courtship sound levels. *Scientific Reports*, 7(1): 3340. doi: 10.1038/s41598-017-03383-8

Royle JA (2004). N-Mixture models for estimating population size from spatially replicated counts. *Biometrics.* 60(March): 108-115.

R Development Core Team (2012). R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria.

RStudio Team (2016). RStudio: Integrated Development for R. RStudio, Inc., Boston, MA. Available at: http://www.rstudio.com/

Salden DR (1988). Humpback Whale Encounter Rates Offshore of Maui, Hawaii. *The Journal of Wildlife Management*, 52(2): 301–304.

Salgado Kent C, Gavrilov A, Recalde-Salas A, Burton C, McCauley R (2012). Passive Acoustics Monitoring of baleen whales in Geographe Bay, Western Australia. In: *Proceedings of the Acoustical Conference of the Australian Acoustical Society*, p.148. Acoustics 2012, Acoustics, Development and the Environment. Fremantle.

Salgado Kent C, Jenner C, Jenner M, Bouchet P, Rexstad E (2012). Southern Hemisphere breeding stock “D” humpback whale population estimates from North West Cape, Western Australia. *Journal of Cetacean Research and Management*, 12(1): 29–38.

Salgado Kent C, Burton C, Recalde-Salas A, Marley S, Kniest E. (2014). Defining the significance of resting and migratory areas in a key habitat in Australia’s southwest for baleen whales. *Report presented to The International Fund of Animal Welfare (IFAW). Project CMST 1199*. Curtin University. Perth

Samaran F, Stafford KM, Branch TA, Gedamke J, Royer JY, Dziak RP, Guinet C (2013). Seasonal and geographic variation of southern blue whale subspecies in the Indian Ocean. *PLoS ONE*, 8(8): e71561. doi: 10.1371/journal.pone.0071561

Sanchez JN, Hudgens BR (2015). Interactions between density, home range behavior, and contact rates in the Channel Island fox (*Urocyon littoralis*). *Ecology and Evolution,* 5(12): 2466 – 2477.

Sarkar D (2008). Lattice: Multivariate Data Visualization with R. Springer. New York. 90 p.

Sasahara K, Cody ML, Cohen D, Taylor CE (2012). *PloS ONE,* 7(9): e44436. doi: 10.1371/journal.pone.0044436

Stafford KM, Lydersen C, Wiig Ø, Kovacs KM (2018). Extreme diversity in the songs of Spitsbergen's bowhead whales. *Biology Letters,* 14: 20180056*.* doi: http://dx.doi.org/10.1098/rsbl.2018.0056*.*

Sauvé CC, Beauplet G, Hammil MO, Charrier I (2015). Mother–pup vocal recognition in harbor seals: influence of maternal behavior, pup voice and habitat sound properties. *Animal Behaviour,* 105(2): 109-120.

Sayigh LS, Esch HC, Wells RS, Janik VM (2007). Facts about signature whistles of bottlenose dolphins *Tursiops truncatus*. *Animal Behaviour.* 75(6): 1631-1642.

Sayigh LS (2014). Cetacean acoustic communication. In: Witzany G (eds). *Biocommunication of animals,* pp.275 - 297. Springer, Dordrecht.

Scott TA, Lee PY, Greene GC, McCallum A (2005). Singing rate and detection probability: An example from the Least Bell's Vireo (*Vireo belli pusillus*). USDA Forest Service Gen. Tech. Rep- PSW-GTR-191. 2005.

Scott-Hayward LAS, Oedekoven CS, Mackenzie ML, Walker CG, Rexstad E (2013). User Guide for the MRSea Package: Statistical Modelling of bird and cetacean distributions in o shore renewables development areas. University of St. Andrews contract for Marine Scotland; SB9 (CR/2012/05).

Seger KD, Thode AM, Urbán-R J, Martínez-Loustalot P, Jiménez-López ME, López-Arzate D (2016). Humpback whale-generated ambient noise levels provide insight into singers' spatial densities. *The Journal of the Acoustical Society of America*, 140(3): 1581–1597.

Shabangu FW, Yemane D, Stafford KM, Ensor P, Findlay KP (2017). Modelling the effects of environmental conditions on the acoustic occurrence and behaviour of Antarctic blue whales. *Plos ONE*, 12(2): e0172705. doi: 10.1371/journal.pone.0172705

Silber GK (1986). The relationship of social vocalizations to surface behavior and aggression in the Hawaiian humpback whale (*Megaptera novaeangliae*). *Canadian Journal of Zoology* 64(10): 2075–2080.

Simao SM, Moreira SC (2005). Vocalizations of a female humpback whale in Arraial do Cabo (Rj, Brazil). *Marine Mammal Science*, 21(1), 150–153.

Simard Y, Roy N, Gervaise C (2008). Passive acoustic detection and localization of whales: Effects of shipping noise in Saguenay-St. Lawrence Marine Park. *Journal of Acoustical Society of America*, 123(6): 4109–4117.

Sinsch U, Joermann G (1989). Vocalization and Mating Behavior of the Marsupial Frog, *Gastrotheca marsupiata* (Dumeril and Bibron, 1841) (Amphibia: Hylidae). *Copeia*, 3: 755–760.

Širović A, Hildebrand JA, Wiggins SM, McDonald MA, Moore SE, Thiele D (2004). Seasonality of blue and fin whale calls and the influence of sea ice in the Western Antarctic Peninsula. *Deep Sea Research Part II: Topical Studies in Oceanography*, 51(17–19): 2327–2344.

Širović A, Rice A, Chou E, Hildebrand JA, Wiggins SM, Roch MA (2015). Seven years of blue and fin whale call abundance in the Southern California Bight. *Endangered Species Research*, 28 (1): 61–76.

Smith JN, Goldizen AW, Dunlop RA, Noad MJ (2008). Songs of male humpback whales, *Megaptera novaeangliae*, are involved in intersexual interactions. *Animal Behaviour*, 76: 467–477.

Smultea MA (1994). Segregation by humpback whale (*Megaptera novaeangliae*) cows with a calf in coastal habitat near the island of Hawaii. *Canadian Journal of Zoology,* 72(5): 805–811.

Sólymos P, Matsuoka SM, Bayne EM, Lele SR, Fontaine P, Cumming SG, Stralberg D, Schmiegelow FKA, Song SJ (2013). Calibrating indices of avian density from non-standardized survey data: making the most of a messy situation. *Methods in Ecology and Evolution,* 4(11): 1047-1058. doi: 10.1111/2041-210X.12106

Sousa-Lima RS, Paglia AP, Da Fonseca GAB (2002). Signature information and individual recognition in the isolation calls of Amazonian manatees, *Trichechus inunguis* (Mammalia: Sirenia). *Animal Behaviour,* 63(2): 301-310.

Sousa-Lima RS, Clark CW (2008). Modelling the effect of boat traffic on the fluctuation of humpback whale singing activity in the Abrolhos National Marine Park, Brazil *Canadian Acoustics,* 36(1): 174-181.

Sousa-Lima RS, Norris TF, Oswald JN, Fernandes DP (2013). A Review and Inventory of Fixed Autonomous Recorders for Passive Acoustic Monitoring of Marine Mammals. *Aquatic Mammals,* 39(1): 23-53.

Staaterman E, Paris CB, DeFerrari HA, Mann DA, Rice AN, D'Alessandro EK (2014). Celestial patterns in marine soundscapes. Mar*ine Ecology Progress Series*, 508: 17-32.

Stanistreet J, Risch D, van Parijs S (2013). Passive acoustic tracking of singing humpback whales (*Megaptera novaeangliae*) on a Northwest Atlantic feeding ground. *PLoS One* 8(4): e61263. doi: 10.1371/journal.pone.0061263

Stanistreet JE, Nowacek DP, Read AJ, Baumann-Pickering S, Moors-Murphy HB, Van Parijs SM (2016). Effects of duty-cycled passive acoustic recordings on detecting the presence of beaked whales in the northwest Atlantic. The *Journal of the Acoustical Society of America Express Letters.* 140 (1): EL31. doi: 10.1121/1.4955009.

Stafford KM, Moore SE, Fox CG (2005). Diel variation in blue whale calls recorded in the eastern tropical Pacific. *Animal Behaviour*, 69(4): 951–958.

Stafford KM, Citta J, Moore S, Daher M, George J (2009). Environmental correlates of blue and fin whale call detections in the North Pacific Ocean from 1997 to 2002. *Marine Ecology Progress Series*, 395: 37–53.

Stafford KM, Chapp E, Bohnenstiel DR, Tolstoy M (2011). Seasonal detection of three types of "pygmy" blue whale calls in the Indian Ocean. *Marine Mammal Science*, 27(4): 828–840.

Stafford KM, Lydersen C, Wiig Φ, Kovacs KM (2018). Extreme diversity in the song of Spitsbergen's bowhead whales. *Biology letters,* 14(4): 20180056. doi: 10.1098/rsbl.2018.0056.

Stimpert AK, Au W, Parks S, Hurst T, Wiley D (2011). Common humpback whale (*Megaptera novaeangliae*) sound types for passive acoustic monitoring. *The Journal of the Acoustical Society of America*, 129(1): 476–482.

Stimpert AK, Peavey LE, Friedlaender AS, Nowacek DP (2012) Humpback whale song and foraging behavior on an Antarctic feeding ground. *PLoS One,* 7: e51214

Stirling I, Thomas JA (2003). Relationships between underwater vocalizations and mating systems in Phocid seals. *Aquatic Mammals,* 29(2): 227–246.

Stowell D, Plumbley MD (2014). Automatic large-scale classification of bird sounds is strongly improved by unsupervised feature learning. *PeerJ.* 2: e488. doi:10.7717/peerj.488.

Thomas PO, Reeves RR, Brownell RL (2015). Status of the world's baleen whales. *Marine Mammal Science*, 32(2): 682–734. DOI: 10.1111/mms.12281

Thomisch K, Boebel O, Zitterbart DP, Samaran F, Van Parijs S, Van Opzeeland I (2015). Effects of subsampling of passive acoustic recordings on acoustic metrics. *The Journal of the Acoustical Society of America*, 138(1): 267–278.

Thompson PO, Cummings WC, Ha SJ (1986). Sounds, source levels, and associated behavior of humpback whales, Southeast Alaska. *The Journal of the Acoustical Society of America*, 80(3): 735–740.

Thompson WL (2002). Towards Reliable Bird Surveys: Accounting for Individuals Present but Not Detected. *The Auk*, 119(1): 18–25.

Tiemann CO, Martin SW, Mobley JR (2006). Aerial and acoustic marine mammal detection and localization on navy ranges. *IEEE Journal of Oceanic Engineering*, 31(1): 107–119.

Tozer D, Drake K, Falconer CM (2016). Modeling detection probability to improve marsh birds surveys in southern Canada and the Great Lakes states. *Avian Conservation Ecology,* 11 (2): art3. doi: 10.5751/ACE-00875-110203

Tripovich J, Klinck H, Nieukirk S, Adams T, Mellinger D, Balcazar N, Klinck K, Hall E, Rogers T (2015). Temporal segregation of the Australian and Antarctic blue whale call types (*Balaenoptera musculus* spp.). *Journal of Mammalogy*, 96(3): 603–610.

Tulloch VJD, Plagányi ÉE, Matear R, Brown CJ, Richardson AJ (2018). Ecosystem modelling to quantify the impact of historical whaling on Southern Hemisphere baleen whales. *Fish and Fisheries*. 19:117–137.

Tyack PL (1981). Interactions between Singing Hawaiian Humpback Whales and Conspecifics Nearby. *Behavioral Ecology and Sociobiology*, 8(2): 105–116.

Tyack PL (1983) Differential response of humpback whales, *Megaptera novaeangliae,* to playback of song or social sounds. *Behavioral Ecology and Sociobiology,* 13: 49–55.

Tyack PL, Miller EH (2002). Vocal anatomy, acoustic communication and echolocation. *In:* Hoelzel R. (ed.). *Marine mammal biology: an evolutionary approach,* pp. 142 – 173. John Wiley & Sons.

Van Parijs S, Southall B. Convenors and Workshop Co-Chairs (2007). Report of the 2006 NOAA National Passive Acoustics Workshop: Developing a Strategic Program Plan for NOAA's Passive Acoustics Ocean Observing System (PAOOS), Woods Hole, Massachusetts, 11–13 April 2006. U.S. Dep. Commerce, NOAA. Tech. Memo. NMFS – F / SPO-81, 64 p.

Van Parijs SM, Clark CW, Sousa-Lima RS, Parks SE, Rankin S, Risch D, Van Opzeeland IC (2009). Management and research applications of real-time and archival passive acoustic sensors over varying temporal and spatial scales. *Marine Ecology Progress Series*, 395: 21–36.

Verfuss UK, Gillespie D, Gordon J, Marques TA, Miller B, Plunkett R, Theriault JA, Tollit DJ, Zitterbart DP, Hubert P, Thomas L (2018). Comparing methods suitable for monitoring marine mammals in low visibility conditions during seismic surveys. *Marine Pollution Bulletin.* 126:1-18.

Vesely D, McComb BC, Vojta CD, Suring LH, Halaj J, Holthausen RS, Zuckerberg B, Manley PM (2006). Development of protocols to inventory or monitor wildlife, fish, or rare plants. Department of Agriculture, Forest Service. General Technical Report. WO-72. Washington, DC: U.S. 100 p.

Videsen SKA, Bejder L, Johnson M, Madsen PT (2017). High suckling rates and acoustic crypsis of humpback whale neonates maximise potential for mother–calf energy transfer. *Functional Ecology,* 31(8): 1561-1573.

Vu ET, Risch D, Clark C, Gaylord S, Hatch L, Thompson M, Wiley D, Van Parijs S (2012). Humpback whale song occurs extensively on feeding grounds in the western North Atlantic Ocean. *Aquatic Biology*, 14(2): 175–183.

Wang K, Wang D, Akamatsu T, Li S, Xiao J (2005). A passive acoustic monitoring method applied to observation and group size estimation of finless porpoises. *The Journal of the Acoustical Society of America*, 118(2): 1180-1185.

Ward JA, Len T, Jarvis S, Dimarzio N, Moretti D, Marques TA, Dunn C, Claridge D, Hartvig E, Tyack, P (2012). Passive acoustic density estimation of sperm whales in the Tongue of the Ocean, Bahamas. *Marine Mammal Science,* 28(4): 444-455.

Watkins WA (1981). Activities and underwater sounds of fin whales. *Scientific Reports of the Whales Research Institute*, 33:83–117

Western Australia Planning Commission, Department of Planning (2011). Regional Hot Spots Land Supply Update. *Published by the Western Australia Planning Commission,* State of Western Australia. 177 p.

Wickham H (2007). Reshaping data with the reshape package. *Journal of Statistical Software*, 21(12). doi: 10.18637/jss.v021.i12.

Wickham H (2009). ggplot2: Elegant Graphics for Data Analysis. Springer-Verlag New York. R Package version 2.2.1.

Wickham H (2012). Stringr: Simple, Consistent Wrappers for Common String Operations. R package version 1.3.1.

Wiggins SM, Oleson EM, McDonald MA, Hildebrand JA (2005). Blue whale (*Balaenoptera musculus*) diel call patterns offshore of Southern California. *Aquatic Mammals*, 31(2): 161.

Wilke CO (2017). Cowplot: Streamlined Plot Theme and Plot Annotations for 'ggplot2'. R package version 0.8.0.

Williams R, Clark CW, Ponirakis D, Ashe E (2014). Acoustic quality of critical habitats for three threatened whale populations. *Animal Conservation*, 17: 174–185. doi:10.1111/acv.12076

Winn HE, Bischoff WL, Taruski AG (1973). Cytological sexing of cetaceans. *Marine Biology.* 23: 343-346.

Winn HE, Beamish P, Perkins PJ (1979). Sounds of two entrapped humpback whales (*Megaptera novaeangliae*) in Newfoundland. *Marine Biology*, 55(2): 151-155.

Winn HE, Thompson TJ, Cummings WC, Hain J, Hudnall J, Hays H, Steiner WW (1981). Song of the humpback whale – Population comparisons. *Behavioural Ecology and Sociobiology,* 8(1): 41 – 46.

Woodley TH, Gaskin DE (1996). Environmental characteristics of North Atlantic right and fin whale habitat in the lower Bay of Fundy, Canada. *Canadian Journal of Zoology,* 74:75–84.

Würsig B, Dorsey EM, Fraker MA, Payne RS, Richardson WJ (1985). Behavior of bowhead whales, *Balaena mysticetus* summering in the Beaufort Sea: A description. *Fish. Bull,* 83(3): 357–377

Zimmer WM (2011). Passive acoustic monitoring of cetaceans. Cambridge University Press. Cambridge. doi: doi.org/10.1017/CBO9780511977107

Zoidis AM, Smultea MA, Frankel AS, Hopkins JL, Day A, McFarland AS, Whitt A, Fertl D (2008). Vocalizations produced by humpback whale (*Megaptera novaeangliae)* calves recorded in Hawaii. *The Journal of the Acoustical Society of America*, 123(3): 1737–1746.

Zuur A, Leno EN, Walker N, Saveliev AA, Smith GM (2009). Mixed Effects Models and Extensions in Ecology with R. Springer – Verlang New York. First Edition. 412 p.

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