Acoustic assessment of the seasonal occurrence and behaviour of Antarctic blue whales *Balaenoptera musculus intermedia* in the southeastern Atlantic and Southern Oceans

by

Fannie Welcome Shabangu

Submitted in partial fulfilment of the requirements for the

degree of

Doctor of Philosophy (Zoology)

in the

Faculty of Natural and Agricultural Sciences

University of Pretoria

Pretoria

South Africa

February 2018

Declaration

I, …Fannie Welcome Shabangu…… declare that the thesis/dissertation, which I hereby submit for the degree …………PhD Zoology…………..… at the University of Pretoria, is my own work and has not previously been submitted by me for a degree at this or any other tertiary institution.

SIGNATURE: ……………………………..
DATE: 13/02/2018

The whales do not sing because they have an answer, they sing because they have a song

—— **Gregory Colbert** ——

To my daughter and son:

Fanisa Philisile and Fanela Katekile Shabangu

And to my late mother:

Tryphina Veronica Sethole

Acoustic assessment of the seasonal occurrence and behaviour of Antarctic blue whales *Balaenoptera musculus intermedia* in the southeast Atlantic and Southern Oceans

Student: Fannie W. Shabangu

Supervisor: Professor Kenneth P. Findlay

Department: Zoology and Entomology, University of Pretoria

Degree: Doctor of Philosophy (Zoology/Mammalogy)

Summary

With catches of over 360,000 individuals, Antarctic blue whales *Balaenoptera musculus intermedia* were harvested to near extinction by commercial whaling in the past century. Antarctic blue whales are an important ecological component of marine ecosystems as they ensure the circulation of nutrients in the pelagic environment making such nutrients accessible for primary production. However, their recoveries; distributions; migrations; large-scale response to environmental variabilities are poorly known. This thesis explored the distribution, seasonal occurrence, behaviour and response of Antarctic blue whales to environmental conditions in the high and low latitudes. I used Antarctic circumpolar acoustic data collected from sonobuoys deployed in the austral summers of 1997 through 2009 during the International Whaling Commission's Southern Ocean Whale and Ecosystem Research (IWC SOWER) line-transect surveys. I also used recent acoustic data from three autonomous acoustic recorders (AARs) deployed between 2014 and 2015; two of these AARs were deployed on oceanographic moorings in the low latitudes and one AAR was deployed on a dedicated mooring in the high latitudes.

Characteristic Z-call and feeding associated D-call of Antarctic blue whales; and sometimes low frequency downsweeping ~28-15 Hz eastern Antarctic fin whale *B. physalus* calls, were detected using an automated detection template and visual verification methods. I used random forest model to determine pattern of environmental preferences, spatial occurrence and behaviour of Antarctic blue whales. Distance to southern boundary of the Antarctic Circumpolar Current, latitude, longitude and distance from the nearest Antarctic shores were the main geographic predictors of blue whale call occurrence and behaviour during IWC SOWER cruises. Satellite derived sea surface height (SSH), wind stress, wind direction, water depth, sea surface temperature (SST), chlorophyll-a and wind speed were important environmental predictors of blue whale occurrence and behaviour during IWC SOWER cruises. Antarctic blue whale call occurrence and call rates varied significantly in response to inter-annual variabilities of those environmental predictors during those cruises.

Migratory Antarctic blue and fin whales were acoustically detected in South African waters between May and August with fin whales present till November. Diel call rate patterns of both whale species varied between seasons. Wind speed, SSH, SST, chlorophyll-a, time of the day and Ekman upwelling index were important predictors of Antarctic blue and fin whale call occurrence and behaviour off the South African west coast. Off the Maud Rise, Antarctica, call occurrences and rates of Antarctic blue whales peaked in March and were detected throughout the whole year suggesting asynchronous migrations to the low latitudes and part of the population remaining in the Maud Rise during winter. Fin whale calls were only detected in January and March. Wind speed, distance to the sea ice extent, sea surface height, sea surface temperature and time of the day were important predictors of Antarctic blue and fin whale call occurrence and behaviour.

Information emerging from this thesis will improve the management and conservation of these highly depleted species. This thesis provides the first acoustic recordings of Antarctic blue and fin whales in the southern Benguela ecosystem; and provides preliminary information on which to concentrate further research effort to investigate abundance, distribution and seasonality of these large baleen whale populations in both high and low latitudes.

Acknowledgements

Firstly, I would like to express my sincere and heartfelt gratitude to my supervisor, Prof Ken Findlay, for taking me on as a doctoral student to study this interesting and fascinating field of marine mammals, and for introducing me to Antarctic research and passive acoustic monitoring. From Ken, I have learned so much about marine mammals in the past four years as he challenged me to think like a "whale expert". I thank the late Prof Peter Best for providing me with many useful references and for the wise advice he provided over the short time I got to interact with him. I am grateful to Meredith Thornton for the exceptional technical assistance at sea and for our friendly chats about life in general, her view of life touched me and her passion of marine mammals definitely rubbed onto me. I thank Profs Armanda Bastos and Marthan Bester for their great assistance with the University of Pretoria's administrative matters relating to my thesis; they made things easier for me from the remote Cape Town.

I am very grateful to Dr Kathleen Stafford for introducing me to the software for analysing passive acoustic data, for providing innumerable relevant references and for numerous fruitful e-mail conservations. I am deeply indebted to Dr Dawit Yemane for spending a lot of his precious time to teach me how to process the environmental data in R and for his generous assistance and introduction to the building of machine learning models I used in most of my thesis chapters and resultant papers. For those reasons, I am endlessly grateful for his statistical advice and guidance; and I hope I have absorbed a significant amount of his statistical wisdom. I thank Brendan Boule for his kind assistance with the decimation of sonobuoy acoustic data. I am profoundly grateful to Marcel du Plessis and many oceanographers (at the University of Cape Town, Council of Scientific and Industrial Research, and Department of Environmental Affairs) for numerous enlightening discussions about environmental conditions in the Southern Ocean and Atlantic Ocean- a field I was less familiar with.

I would like to greatly thank the International Whaling Commission (IWC) for allowing me to use the passive acoustic data collected during the Southern Ocean Whale and Ecosystem Research (SOWER) cruises and to those who collected the data during these cruises. Drs Chris Clark, Paul Ensor and Kate Stafford are thanked for kindly providing the IWC SOWER data. The South African National Antarctic Programme; National Research Foundation (NRF); Department of Agriculture, Forestry and Fisheries (DAFF); and the Department of Environmental Affairs are thanked for funding my field trips without which Chapters 5 and 6 would not have been possible. Every member of the IWC's Southern Ocean Research Partnership (SORP) Acoustic Trends Working Group is thanked for the encouragements to deploy autonomous acoustic recorders in Antarctica and South Africa. I am very grateful to NRF for funding the South African Blue Whale Project and for funding my travel to attend the 2013 SORP meeting in Paris, France. I thank the South African Network for Coastal and Oceanic Research for awarding me the travel grant to attend the 2016 American Cetacean Society's 15th International Conference, Monterey, USA. I also thank the Society of Marine Mammalogy (SMM) for awarding me the travel grant to attend the 2017 SMM Biennial Conference on the Biology of Marine Mammals, Halifax, Canada. I learned a lot about different techniques to study marine mammals at the above conferences.

Many thanks to my managers at DAFF for allowing me time to pursue this doctoral degree; I really appreciate this capacity building opportunity. I also thank my colleagues at DAFF for their enthusiastic support and many stimulating conversations about my research. Amongst others mentioned above, Kirsty Venter, Ove Fabriciussen, Ian Thompson, Sinekhaya Bilana, Jarred Voorneveld, Jethan d'Hotman and Chris Wilkinson are warmly thanked for their selfless assistance with the preparation, deployment and recovery of the autonomous acoustic recorders in Antarctica and South Africa. My sincere thanks go to the captains and crew of the RV *SA Agulhas II* and RV *Algoa* for their outstanding service during the deployment and recovery of the autonomous acoustic recorders. I am incredibly grateful to Marcel van den

Berg; Bradley Blows and oceanographers of the South Atlantic Meridional Overturning Circulation project for modifying their oceanographic moorings to accommodate autonomous acoustic recorders used to collect acoustic data for my research. I am grateful to Catherine Boucher for her kind and professional graphic assistance. Special thanks to Drs Sheldon Dudley and Taryn Morris for editing certain chapters of this thesis. I also thank the three anonymous examiners for providing useful comments and suggestions on the first edition of this thesis.

I am beyond words grateful to my parents and siblings for their invaluable support, love and encouragement throughout my scientific career building journey, I am the man I am today because of you. I am thankful to my in-laws for their never-ending support especially for babysitting during the last few months of concluding this thesis; you are the best family-in-law a son-in-law can ever ask for. To my daughter and son, Fanisa and Fanela, for more than you can ever imagine; I love you so much and you inspire to be the best I can be at everything. You gave me reasons to take breaks in the middle of the night to attend to your childhood “discomforts”; you give my life a steadfast direction. My deepest gratitude goes to my beloved wife, Primrose Shabangu, for being my best friend, listener and counsellor of endless frustrations and problems that I encountered in the past four years. I thank you my love for singlehandedly taking care of our family while I was away for extended periods of time at sea to collect data for this thesis. Thank you wifey for supporting me throughout my daring dream to obtain a doctoral degree, and I am also appreciative of your patience and understanding while I spent countless hours at home in front of the computer preparing this masterpiece.

Finally, but by no means least, I thank my Heavenly Father for answering many of my prayers and for the privilege to study his amazing creature, the blue whale. His love and kindness are continuously so marvellous to me.

Table of Contents

List of Tables

List of Figures

List of Research Outputs (Emanating from this research)

Peer-reviewed book chapters and papers

Shabangu, F.W. and Findlay, K.P. 2014. Passive acoustic monitoring of marine mammals in South Africa, with special reference to Antarctic blue whales. *In:* Funke, N., Claassen, M., Meissner, R. and Nortje, K. (eds). Reflections on the state of research and development in the marine and maritime sectors in South Africa: 153-173 (Chapter 8 of book). Pretoria: Council for Scientific and Industrial Research.

Shabangu, F.W., Yemane, D., Stafford, K.M., Ensor, P. and Findlay, K.P. 2017. Modelling the effects of environmental conditions of the acoustic occurrence and behavior of Antarctic blue whales. PLoS ONE 12(2): e0172705. doi:10.1371/journal.pone. 0172705.

Shabangu, F.W., Stafford, K.M., Findlay, K.P., Rankin, S., Ljungblad, D., Tsuda, Y., Morse, L., Clark, C.W., Kato, H., and Ensor, P. *In press*. Overview of the IWC SOWER cruise circumpolar acoustic survey data and analyses of Antarctic blue whale calls. Journal of Cetacean Research and Management’s IWC SOWER Special Issue.

Shabangu, F.W., Yemane, D. and Findlay, K.P. *In review.* Acoustic seasonality and behaviour of Antarctic blue and fin whales off the Maud Rise, eastern Weddell Sea. Polar Biology.

Shabangu, F.W., Findlay, K.P., Yemane, D., Stafford, K.M., van den Bergh, M. and Blows, B. *In review.* Seasonal occurrence and diel calling behaviour of Antarctic blue whales and fin whales off the west coast of South Africa. Journal of Marine Systems.

International Whaling Commission’s Scientific Committee Documents

Shabangu, F.W. and Findlay, K.P. 2014. *Overview of the IWC IDCR/SOWER cruise acoustic survey data*. Paper presented to the Scientific Committee of the International Whaling Commission, Bled, Slovenia, SC/65b/Forinfo18, 5 pp.

Findlay, K.P., Thornton, M., **Shabangu, F.W.**, Venter, K., Thompson, I., and Fabriciussen, O. 2014. *Report of the 2013/14 South African Antarctic blue whale survey, 000° - 020°E*. Paper presented to the Scientific Committee of the International Whaling Commission, Bled, Slovenia, SC/65b/SH01, 33 pp.

Popular articles

Shabangu, F.W., and Findlay, K.P. 2014. *Out of the blue – acoustic monitoring of southern African blue whales*. South African Network for Coastal and Oceanic Research, Newsletter Issue 204: 1-3.

Shabangu, F.W. 2014. *A whale biologist’s perspective of a whaling station*. South Georgia Newsletter, August 2014: 4- 6.

Shabangu, F.W., 2014. *Active and passive acoustic technology*. *In*: Grade 11 Marine Science Programme Booklet, South African Environmental Observation Network (SAEON) marine science and climate change: elevating excellence in school science, 3 pp.

Shabangu, F.W. 2014. *If you need me, call: Antarctic blue whale vocalization*. Fishing Industry News Southern Africa Magazine 15 (4): 20- 21.

Shabangu, F.W. 2017. *Trip to Monterey Bay, California: Lessons and sentiments*. South African Network for Coastal and Oceanic Research, Newsletter Issue 214: 21-24.

Conference and symposium presentations (oral/poster)

Oral presentations

Shabangu, F.W., Findlay, K.P. and Best, P.B. *Acoustic estimations of Antarctic blue whale* Balaenoptera musculus intermedia *relative abundance and distribution using IWC sonobuoy data from 1995 to 2009*. 15th Southern African Marine Science Symposium (SAMSS), Stellenbosch University, South Africa, 15-18 July 2014.

Venter, K., Thornton, M., **Shabangu, F.W.**, Gregor, L., Best, P. and Findlay K.P. *The distribution of baleen whales found off the Queen Maud Land coast of Antarctica in relation to primary productivity and the availability of prey*. 21st Society of Marine Mammalogy's (SMM) Biennial Conference on Marine Mammals, San Francisco, USA, 13-18 December 2015.

Shabangu, F.W. *Potential effects of climate change on the distribution and acoustic behaviour of Antarctic blue whales.* 2nd Student Conference on Climate Change and Development, Kirstenbosch Botanical Gardens, Cape Town, South Africa, 18 March 2016.

Shabangu, F.W. and Findlay, K.P. *Acoustic monitoring of the recovery of large baleen whales in the Benguela ecosystem*. 4th African Marine Mammal Colloquium (AMMC), Kleinbaai, South Africa, 22- 27 May 2016.

Shabangu, F.W. and Findlay, K.P. *Acoustic monitoring of the recovery of blue and fin whales in the Benguela ecosystem*. Mammal Research Institute 50th Anniversary Symposium, Mopani Camp, Kruger National Park, South Africa, 12-16 September 2016.

Shabangu, F.W. and Findlay, K.P. *Acoustic monitoring of the recovery of Antarctic blue and fin whales in the Benguela ecosystem*. Benguela Symposium, University of Cape Town, Cape Town, South Africa, 15-18 November 2016.

Shabangu, F.W., Findlay, K.P., and Yemane, D. *Acoustic occurrence and behaviour of Antarctic blue and fin whales in South Africa and Antarctica*. South African Marine Science Symposium (SAMSS), Port Elizabeth, South Africa, 02-07 July 2017.

Shabangu, F.W., Findlay, K.P., Yemane, D., Stafford, K.M., van den Berg, M., and Blows, B. *Seasonal occurrence and diel calling behaviour of Antarctic blue whales and fin whales off the west coast of South Africa* [Invited]. Underwater Acoustics Conference and Exhibition (UACE), Skiathos, Greece, 3-8 September 2017.

Shabangu, F.W., Findlay, K.P., Yemane, D., Stafford, K.M., van den Berg, M., and Blows, B. *Seasonal occurrence and diel calling behaviour of Antarctic blue whales and fin whales off the west coast of South Africa*. 22nd Society of Marine Mammalogy's (SMM) Biennial Conference on Marine Mammals, Halifax, Nova Scotia, Canada, 22-27 October 2017.

Poster presentations

Shabangu, F.W., Findlay, K.P., Best, P.B., Ensor, P. and Stafford, K.M. *We hear them in thousands: Acoustic distribution and behavior of Antarctic blue whales*. 21st Society of Marine Mammalogy's (SMM) Biennial Conference on Marine Mammals, San Francisco, USA, 13-18 December 2015.

Shabangu, F.W., and Findlay, K.P. *Sounds of Antarctic blue and fin whales off the west coast of South Africa*. American Cetacean Society's 15th International Conference, Monterey, USA, 11-13 November 2016. Awarded 3rd place in the conference student poster contest.

News release and media coverage

Antarctic blue whales discovered off the South African west coast by Ansa Heyl, University of Pretoria Whale Unit News Release, 12 April 2016:

http://www.up.ac.za/en/whale-unit/news/post_2262110-antarctic-blue-whales-discovered-off-the-south-african-west-coast

Blue whales are back, humpbacks thriving in Cape by Claire Keeton, Sunday Times, 29 October 2017:

https://www.timeslive.co.za/sunday-times/lifestyle/travel/2017-10-29-cape-is-having-a-whale-of-a-time/

Chapter 1: General introduction and thesis structure

1.1 Taxonomy and nomenclature of blue whales

The term “blue whale” is an umbrella term used to describe four suggested subspecies of the family Balaenopteridae of suborder Mysticeti that live in different oceans and are made up of widely varying but large sizes (Jefferson *et al.* 1993; Bannister, 2002; Best, 2007a), including Northern Hemisphere blue whales, *B. m. musculus* (Linnaeus, 1758); Antarctic or "true" blue whales, *B. m. intermedia* (Burmeister, 1871); pygmy blue whale *B. m. brevicauda* (Ichihara, 1966); and the Indian Ocean blue whale *B. m. indica* (Blyth, 1859) (Reeves *et al.* 1998; Bannister, 2002). However, only the first three subspecies are currently recognized internationally (Rice, 1977, 1998; Reeves *et al.* 1998; Jefferson *et al.* 1993; Best, 2007a) as *B. m. indica* is currently considered an approximate synonym of *B. m. breivicauda* (Reeves *et al.* 1998; Rice, 1998).

Blue whales are generically named for their mottled blue-grey colour when underwater, mottling which tends to be dull grey in colour (Figure 1.1) when exposed in air (Mackintosh and Wheeler, 1929; Best, 2007a). The pattern of this distinctive mottling varies between individuals and is used to identify individual blue whales (Sears, 2002). The term blue whale originated from the Norwegian translation of 'Blaahval,' first used by the Norwegian whaler, Svend Foyn, and then later officially adopted by the Norwegian researcher, G.O. Sars, in 1875 (Allen, 1916).

Antarctic blue whale is the largest of all the whales; and is the largest animal ever known on the planet (Allen, 1916; Leatherwood *et al.* 1976; Best, 2007a). They range throughout the pelagic waters of the Southern Hemisphere where they may co-occur with the smaller subspecies, the pygmy blue whale; the key diagnostic features between the two are length, external features (particularly the general body shape and the shape of the blowhole), genetic profile, acoustic call types, and summer distribution (Best and Ross, 1989; Ljungblad *et al.*

1998; Branch *et al.* 2007b; Best, 2007a; Attard *et al.* 2016). Although they might be confused with fin whales *B. physalus* or sei whales *B. borealis*, they are much larger than these congeners with distinct morphological features (Leatherwood *et al.* 1976; Best and Ross, 1989; Jefferson *et al.* 1993). Hybridization is known to occur between blue and fin whales (Allen, 1916; Bérubé, 2002); and between the blue whale subspecies (Attard *et al.* 2012, 2016).

Figure 1.1. Antarctic blue whale at sea showing its mottling and characteristic small dorsal fin. This kind of image is used for photo identification studies of this species based on the mottling pattern.

The body shape of the Antarctic blue whale has generally been described as ‘torpedo-shaped’ depicting a comparatively narrower head (Figure 1.2), while pygmy blue whales are described as ‘tadpole-shaped’ depicting a comparatively wider head (Jefferson *et al.* 1993; Kato, 2002; Best, 2007a). Heads of males are relatively larger than of females, head length contributes about 19.5-20.5 % to the total body length (Mackintosh and Wheeler, 1929; Best, 2007a) despite females being larger in total length and mass.

Antarctic blue whales are the largest of blue whales with the largest recorded to be around 33 m long (measured from lower jaw projection to tips of flukes) with a 29.5 m female weighing 163 metric tons (Mackintosh and Wheeler, 1929; Mackintosh, 1942; Jefferson *et al.* 1993; Ballance, 2002; Best, 2007a). Best (2007a) notes however that few specimens of over 30 m have been reliably measured. On average, adult Antarctic blue whales can reach maximum lengths of 29 m (Jefferson *et al.* 1993). While the majority of the Northern Hemisphere subspecies *B. m. musculus* are 23-27 m long, with females growing larger than males (Jefferson *et al.* 1993). The pygmy subspecies is the smallest of the three, with biggest measuring around 24 m (Ichihara, 1966; Jefferson *et al.* 1993; Best, 2007a).

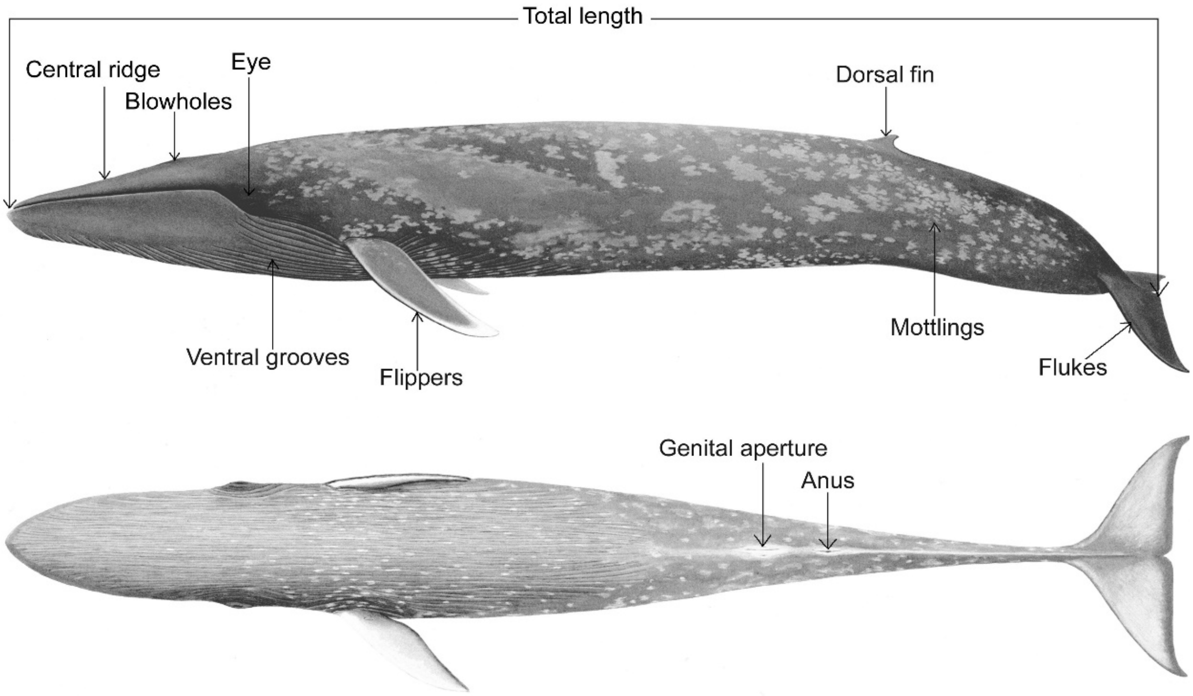


Figure 1.2. Lateral (top) and ventral (bottom) anatomical features of Antarctic blue whale. Figure adapted from Best (2007a).

Females of Antarctic blue whales are broadly recorded to reach sexual maturity at around 23.7 m while males mature sexually around 22.2 m at ages between 8-10 years (Mackintosh and Wheeler, 1929; Ichihara, 1966; Sears, 2002; Branch and Mikhalev, 2007). After reaching sexual maturity, female Antarctic blue whales give birth to a single calf every two to three years following a 10-12 month gestation period (Mackintosh and Wheeler, 1929; Mizroch *et al.* 1984; Klinowska, 1991; Sears, 2002). Newborn calves weigh 2-3 tons and measure 6-7 m long, weaned when approximately 16 m long at 6-8 months (Sears, 2002; Best, 2007a).

1.2 Distribution and migration of Antarctic blue whales

Blue whales are generally cosmopolitan in range, although generally not frequenting coastal waters (Mackintosh and Wheeler, 1929; Best, 2007a). Antarctic blue whales feed predominantly on small zooplankton, primarily the Antarctic krill *Euphausia superba* in

Antarctica (Bannister, 2002; Branch *et al.* 2007a) and on megalopa larvae when in the southern African region which qualifies them to be strict carnivores (Best, 1967). Feeding on low trophic level prey makes blue whales an important ecological component of the marine ecosystem as they therefore transfer nutrients within and between various elements and levels of the ecosystem (Leaper and Miller, 2011). Antarctic blue whale distribution during the austral summer is largely determined by food or prey availability and distribution (Mackintosh and Wheeler, 1929; Bannister, 2002; Branch *et al.* 2007a); and factors determining the winter distribution blue whales are currently poorly understood. A comprehensive and detailed analysis of the distribution of Antarctic blue whales was undertaken by Branch *et al.* (2007a), where they used multi-disciplinary data from catches, sightings, strandings, Discovery marking and recoveries, and acoustic recordings.

Antarctic blue whales are commonly distributed throughout the Antarctic (high latitude) in austral summer and migrate to southern African region, Australia and South America (low latitude) in winter while a small proportion of the population spend their winter in the Antarctic (e.g. Rice and Scheffer, 1968; Mizroch *et al.* 1984; Jefferson *et al.* 1993; Branch *et al.* 2007a; Samaran *et al.* 2013, Širović *et al.* 2009, Thomisch *et al.* 2016). The distribution of Antarctic blue whales on the high latitude feeding grounds is fairly-well understood due to the extent of the modern whaling of blue whales that occurred in the region last century (Mizroch *et al.* 1984; Branch *et al.* 2007a). The distribution of the majority of blue whales in the Antarctic is in the ice edge region in close correspondence to the dense concentrations of krill (Branch *et al.* 2007a). However, the migration routes and distribution of this species off South-western and South-eastern African regions are still not well established (Branch *et al.* 2007a; Figueiredo and Weir, 2014; Leroy *et al.* 2016).

An understanding of the behaviour and movement of Antarctic blue whales on their calving and wintering regions will fill a large information gap in the ecology of this species. Based on the extensive land based catch histories, Best (1998) suggested from catch records that the west coast of South Africa and Namibia are potential overwintering grounds and migration route of the Antarctic blue whale. Catches of large pregnant females close to term or recently pregnant or ovulating whales are suggestive that the southern African region is important for this species as the calving and mating ground (Best and Ross, 1989; Best, 1998). Recent acoustic recordings also confirm the west coast of South Africa as overwintering ground of Antarctic blue whales (This Study - Chapter Five).

1.3 Population history and status

Antarctic blue whales were once considered one of the most abundant large whale species that ever existed but were harvested to near extinction by the modern whaling (Clapham *et al.* 1999; Clapham and Baker, 2002; Branch *et al.* 2007a). This iconic species is presently considered by the International Union for the Conservation of Nature and Natural Resources (IUCN) to be a Critically Endangered large whale population due to these high catches that occurred during the whaling decades (1904-1973) (Klinowska, 1991; Jefferson *et al.* 1993; Rice, 1998; Clapham *et al.* 1999). Some 360,000 Antarctic blue whales were caught in the Southern Hemisphere (Branch *et al.* 2004), which accounted for 99.2% of blue whales caught south of 52°S (Branch *et al.* 2007b). This blue whale subspecies was consequently diminished to 0.7% (95% confidence interval (CI): 0.3%–1.3%) of the pre-exploitation abundance (of 239,000 (95% CI: 202,000-311,000)) by the time whaling ceased (Branch *et al.* 2004). Antarctic blue whales contributed 90.4% of the total worldwide catches of blue whales (Branch *et al.* 2008); and also contributed over 90% of the whaling catches in the Southern Whaling Stations in Southern Georgia and South Africa between 1904 and 1928 when combined with fin whales (Mackintosh and Wheeler, 1929).

It is estimated that only about 1-3% of their pre-whaling population size remained in 1996; the pre-exploitation population of this species was 239,000 (95% CI: 202,000-311,000) and after whaling was depleted to 360 (95% CI: 150-840) (Branch *et al.* 2004). The latest Antarctic blue whale population assessment over the period 1973-1996 was conducted in

1996 based on Bayesian modelling which demonstrated that this whale stock is nonetheless increasing at an annual rate of 8.2% for its population size at that time of 1,700; with lowest estimated 95% CI population size value of 860 and highest 95% CI of 2,900 (Branch *et al.* 2004). Branch *et al.* (2004) maintain that because the population of Antarctic blue whale is at its lowest ever recorded critical biomass; there should be a rapid recovery due to biological changes in population growth rate and reproductive behaviour. Thus, the life-history parameters of Antarctic blue whales are one of the key factors influencing their recovery rate as these large whales are long lived and become sexually mature at a much older age compared to other blue whale subspecies (Sears, 2002; Branch *et al.* 2007b).

The International Whaling Commission (IWC), established in 1946 under the International Convention for the Regulation of Whaling, was responsible for regulating whaling, overseeing the research on whale stocks and setting quotas (Best and Ross, 1989; Clapham and Baker, 2002). Prior to the IWC establishment, whaling regulations were carried out by the International League of Nations (in the 1930s) and regional regulations such as the limitation of humpback whale catches in 1917 (Christol *et al.* 1972; Tønnessen and Johnsen, 1982). Blue whales were of greater economic value than other whales due to their huge size that produced greater oil yields than any other whale species (Mackintosh and Wheeler, 1929), a catch management matrix known as the blue-whale-unit introduced in the 1930s where a whale of a smaller species might be worth one-half or one-third of a blue-whale-unit (Small, 1971). For example, one blue whale was equivalent to 2 fin whales, 2.5 humpback whales, or 6 sei whales (Parsons *et al.* 2012). The higher incentives paid to whalers for catching blue whales than any other species further exacerbated the population decline in the Antarctic and resulted in blue whale being commonly more targeted than any other whale species that occurred in the same area (Mackintosh and Wheeler, 1929; Jefferson *et al.* 1993). This led to smaller whale species being allocated unsustainable quotas that were two to three times higher than the quota for blue whales (Mackintosh, 1942). In the southern African region, whalers targeted blue whales after the severe exploitation and collapse of the more coastal humpback whales *M. novaeangliae* stock between 1908 and 1917 (Best, 1994, 1998; Findlay, 2001). Blue whale catches (both Antarctic and pygmy blue whales) contributed 20% towards the total 1.8 million whales caught during the last century in the Southern Hemisphere.

Open boat whaling (1750-1930), modern land whaling station (1904 onwards - e.g., Donkergat, Durban, and South Georgia), and modern pelagic whaling (stern slipway 1920s onwards) were practiced in the Southern Hemisphere (Best and Ross, 1989; Clapham and Baker, 2002). Depending on the season of harvest, Antarctic and pygmy blue whale were caught by modern whaling in both Antarctica and low latitudes waters; summer catches occurred in the Antarctic and winter catches occurred in the southern African region, South America and Australia (Mackintosh and Wheeler, 1929; Best, 1998). In the Southern Ocean, most Antarctic blue whale catches were landed in South Georgia with few in the South Shetlands and South Orkneys; the Antarctic pelagic whaling industry was operated by the Norwegian and British governments (Mackintosh and Wheeler, 1929; Mackintosh, 1942; Branch *et al.* 2008).

Antarctic blue whale catches from the South Atlantic and South Western Indian Oceans were made off South Africa (Saldanha Bay, Cape Hangklip, Durban, Mossel Bay and Plettenberg Bay), Namibia (Luderitz and Walvis Bay), Angola (Baia Dos Tigres, Porto Alexandre, Mossamedes, Elephant Bay, and Lobito), with low numbers taken off Congo, Mozambique (Linga Linga, Quelimane and Angoche), and Madagascar (Tønnessen and Johnsen, 1982; Best, 1998; Branch *et al.* 2008). The extent of Antarctic blue whale catches from the southern African region was relatively low compared with the Antarctic catches for the whole whaling era (Mackintosh and Wheeler, 1929; Best, 1998; Branch *et al.* 2008), although some of the highest catches were in the low latitudes. Southern Hemisphere modern whaling was initaited in 1904 (Figure 1.3) by the Norwegian sea captain and whaler, Carl Anton Larsen, and continued till its closure in the mid-1980s (Allen, 1916; Clapham and Baker, 2002; Branch *et al.* 2007).

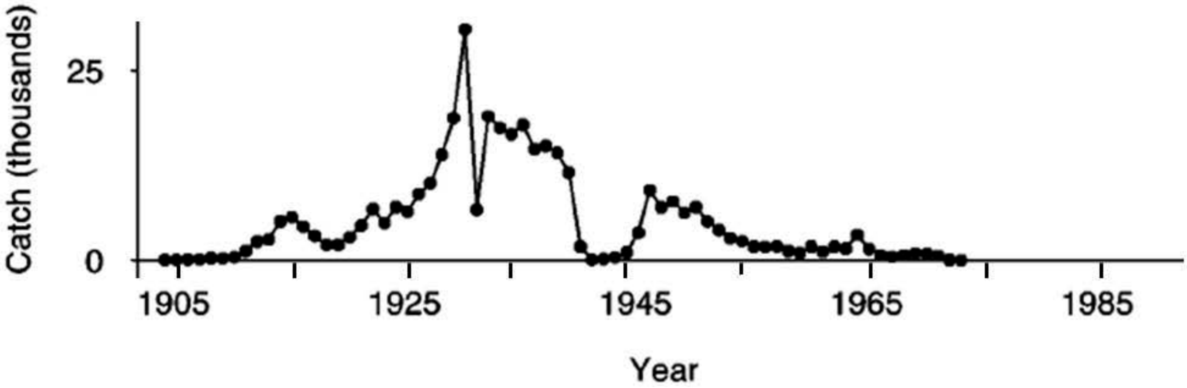


Figure 1.3. Annual catches of blue whales in the Southern Hemisphere reflecting the discovery, exploitation, and consequent crash of the species. Source: Hilborn *et al.* (2003).

When Larsen arrived back from the Antarctic in Buenos Aires, Argentina, in 1903, he exclaimed "…..bot I ask youse ven I am here vy don't yousetake dese vales at your doors – dems vary big vales and I seen dem in houndreds and tousends" (Tønnessen and Johnsen, 1982). Larsen's observation indicates that large populations of baleen whales including blue, fin and humpback whales were available in the Southern Ocean (Clapham and Baker, 2002). The introduction of powerful steam vessels and harpoon guns in the modern whaling era radically altered whaling processes by facilitating the harvesting of faster swimming, large Antarctic blue whales (Mackintosh and Wheeler, 1929; Clapham *et al.* 1999; Clapham and Baker, 2002)), although modern whaling was limited to the close proximity of land stations for the first approximately 20 years. The introduction of stern slipway in the mid-1920s opened pelagic whaling because now whales could be dragged onto the deck of factory ships for processing even in bad weather conditions (Best and Ross, 1989). The introduction of factory ships further opened pelagic whaling as there was no limit to how far from land the whalers could operate and process unspoiled whale carcasses (Clapham and Baker, 2002).

The Antarctic blue whale stock was exploited to below 1% of its pre-whaling population size to cause the collapse of the stock in the 1960s (Branch *et al.* 2004). Whale stocks suffered from the "tragedy of the commons," where as a non-rival and non-excludable resource if one fleet did not catch a particular whale, another could catch it, therefore there was little incentive to whale sustainably for the future because this is an open resource enjoyed by everyone (Hardin, 1968). Turning the commons into private goods and restricting exploitation freedom by rules and laws generally avoids the “tragedy” (Hardin, 1968). For example, there were no strict whaling regulations implemented in the southern African region between 1908-1930 to manage the quantity, species, sexual maturity state or size of harvested whales (Best and Ross, 1989; Best, 1994). In the southern African region, the main objectives of the whaling industry were to potentially maximize economic profitability and employment, and reduce conflicts while compromising the biological productivity of whale stocks (Best and Ross, 1989; Hilborn, 2007). The introduction of the 200 nautical miles exclusive economic zones (EEZs) in the mid-1970s gave sovereignty to coastal nations and certainly improved the worldwide management and conservation of marine resources (Best and Ross, 1989; Dankel *et al.* 2008).

Best and Ross (1989) believed that the IWC should have ideally limited the resurrection of whale harvesting after World War II (1939-1945) to protect the already over-depleted whale species. Nevertheless, whaling of blue whales continued officially until the 1965/1966 whaling season even though the stock size was decimated by this time when the IWC protected it from hunting (Best and Ross, 1989; Best, 1993; IWC, 1995; Clapham *et al.* 1999; Branch *et al.* 2004, 2007a). From 1964-1973, the pelagic whaling fleet of the Union of Soviet Socialist Republics (USSR) continued with the illegal hunting of Antarctic blue whale, killing an additional 852 Antarctic blue whales and 8,000 pygmy blue whales to those declared (Zemsky *et al.* 1995; Yablokov *et al.* 1998; Clapham *et al.* 1999).

It should be noted that the majority of the catch statistics do not include the unreported mortality of struck and lost animals (Best, 2007b; Branch *et al.* 2008). A further bias not considered in those catch statistics is the uncertainty and discrepancy imposed by species identification and unstandardized length measurements experienced during the earlier years of whaling (Best, 1994; Branch *et al.* 2007b).

Numerous theoretical and empirical observations provide evidence that life-history parameters of fisheries stocks were altered in the direction of rapid harvest-evolution to sustain their populations over time (Conover, 2000; Heino and Godø, 2004; Jørgensen *et al.* 2007). The theory of life-history shows that elevated mortality from exploitation generally promotes the evolution of a strategy of an earlier sexual maturation at small size and increased reproductive effort (Conover, 2000; Branch and Mikhalev, 2007; Jørgensen *et al.* 2007). Since fishing mortalities are commonly extremely selective with respect to size, sex, maturity, behavioural patterns and activity, and spatial location (Heino and Godø, 2004). Thus, the incurred mortality will impose genetic hereditary traits changes on the exploited populations even if the species is harvested at the maximum sustainable yield (Conover, 2000; Jørgensen *et al.* 2007). However, there are no signs of evolutionary genetic changes due to whaling in Antarctic and pygmy blue whales but low genetic diversity between Australian pygmy blue whales due to climate change (Attard *et al.* 2015)

Some species tend to be more affected by the exploitation than others in the same community (Heino and Godø, 2004). The heavily depleted species will therefore have higher population growth rate than their less depleted cohabitants as dictated by their gross recruitment rate and survival rate to maturity (Best, 1993). Although no length confinements were implemented in the earlier years of whaling, whalers were size selective and catch statistics indicate that size selectivity varied due to the spatial availability of whales (Best, 1998, 2007a, 2007b; Punt *et al.* 2003; Branch *et al.* 2007b, 2008). Another indication of selectivity in the whale fishery is the apparent greater harvesting of females than males, especially the pregnant females due to their large sizes that yielded more oil (Best and Ross, 1989).

In theory, as a population decreases more resources should be available *per capita* to improve growth (Branch *et al.* 2004); nevertheless, if the freshly accessible resources are not utilized, species replacement may occur as other competing species in the ecosystem will exhaust such resources as density-dependent resource competition is decreased (Heino and Godø, 2004). The developing Antarctic krill fishery is currently commercially exploiting Antarctic blue whale prey from the ecosystem (Hewitt *et al.* 2002), albeit at levels below the recommended total allowable catch. Therefore, the Scientific Committee of the IWC and Convention for the Conservation of Antarctic Marine Living Resources (CCAMLR), the organization responsible for managing Antarctic krill fishery, should join forces for the conservative and precautionary management of these two interacting species in a co-management approach as recommended by Leaper and Miller (2002).

For a heavily depleted population such as that one of Antarctic blue whale (99% depletion), the most recent estimated growth rate of 8.2% p.a. (Branch, 2007) is a good indication that the population is increasing rapidly as the above population growth rate broadly exceeds the average baleen whale growth rate of 6.7% p.a. (Branch *et al.* 2004). However, Antarctic blue whale populations are still faced with a wide variety of threats that might affect their recovery ranging from environmental to anthropogenic activities including: pollution, climate change, ship strikes, ambient noise, and fishing gear entanglement (Conover, 2000; Leaper and Miller, 2011). These should be included to fully understand the inherent dynamics of the whale populations.

The current low Antarctic blue whale population abundance means that it is challenging to monitor the recovery of blue whales from visual line-transect surveys, as surveys are costly and prone to logistically difficult research operations including inclement weather (Branch *et al.* 2007; Kelly *et al.* 2012; Thomas and Marques, 2012). Furthermore, blue whales seem to disperse over large areas during their winter breeding migrations in the low latitudes so that wide-ranging areas would need to be surveyed to attain the required sample sizes for population estimation (Samaran *et al.* 2013; Leroy *et al.* 2016). Fortunately, acoustic research can play an important role here.

1.4 Vocalizations of Antarctic blue whales

Antarctic blue whales produce powerful sounds that can be detected hundreds to thousands kilometres from the calling animals (Cummings and Thompson, 1971; Stafford *et al.* 1998; Širović *et al.* 2007). These whales produce two kinds of calls; the socialising and long-distance communication call supposedly only produced by males, referred to as Z-call, and the contact calls potentially feeding associated, produced by both sexes known as the D-call (Ljungblad *et al.* 1998; Rankin *et al.* 2005; Oleson *et al.* 2007). Acoustic detections indicate that Antarctic blue whales are present year-round in the Antarctic and low latitudes (Širović *et al.* 2007; Samaran *et al.* 2013; Leroy *et al.* 2016; Thomisch *et al.* 2016); and that some might be feeding in their overwintering grounds (Chapter 5). Passive acoustic monitoring proves to be a reliable, cost-effective and relatively easy method to potentially investigate Antarctic blue whales' recovery (as carried out for North Pacific right whales by Marques *et al.* (2011)), distribution, migration routes and behaviour in their inclement and remote high latitude feeding grounds to their low latitude overwintering grounds (Thomisch *et al.* 2016; Leroy *et al.* 2016; Chapters 5 and 6).

1.5 Objectives and aims of this study

This study used passive acoustic monitoring to research the distribution and acoustic behaviour of Antarctic blue whale off the Antarctic; and estimated seasonal occurrence of these animals both in the Antarctic and South Africa. Although seasonal occurrence and acoustic behaviour of fin whales are studied in some chapters; the main focus of this thesis was to improve our knowledge and understanding of Antarctic blue whale biology and ecology. Fin whale calls were considered in some chapters as these low frequency sounds overlap with the low frequency range of blue whale calls.

The broad aim of this thesis was to acoustically describe and assess the distribution, seasonal occurrence and behaviour of Antarctic blue whales in the South-eastern Atlantic Ocean and

Southern Ocean. In turn, I also evaluated the effects of environmental conditions (i.e. chlorophyll-a, sea surface temperature, sea surface height, wind speed, wind direction, wind stress, distance to the Antarctic shoreline, distance to the southern boundary of the Antarctic Circumpolar Current, distance to the ice extent, sea ice concentration, Ekman upwelling index, time of the day, months, latitude, longitude and water depth) on the multi-year acoustic call occurrence and call rate behaviour of Antarctic blue whales in areas of the Southern Ocean and off the west coast of South Africa. This is the first study of its kind to consider environmental factors influencing acoustic occurrence and behaviour of blue whales in the Southern Hemisphere. I, here, quantitatively determined through ensemble modelling that Antarctic blue whales are vulnerable to environmental variability and to climate change in the long term as they respond to environmental changes. Herein, I also highlight the preferred and important habitats of blue whales during the austral summer. This work enhances our understanding of the acoustic occurrence and behaviour of Antarctic blue whales in the high and low latitudes; and also significantly contributes towards the limited literature on Antarctic blue whale passive acoustic monitoring.

The detailed specific objectives of this study are:

- To provide an overview of passive acoustic data collected during the International Whaling Commission’s Southern Whale and Ecosystem Research (IWC SOWER) circumpolar cruises from 1997 to 2009 and provide the metadata on available acoustic data (Chapter 3);
- To develop a time-series of blue whale acoustic spatial occurrence and behaviour from the circumpolar passive acoustic data collected in the Southern Hemisphere (Chapters 2 and 4);
- To determine the seasonal occurrence and behaviour of Antarctic blue and fin whales in the Southern Ocean and South-eastern Atlantic Ocean using autonomous acoustic recorders (Chapters 5 and 6);

- To model the effects of environmental conditions on the long term and seasonal occurrence and behaviour of blue and fin whales in the Southern Ocean and South-eastern Atlantic Ocean (Chapters 4-6);
- To implement a call identification technique for estimating the number of blue and fin whale calls and thereby to determine the types of calls produced by blue and fin whales in their feeding grounds and overwintering grounds (Chapters 3-6);
- To determine the overwintering ground of blue whales off the west coast of South Africa (Chapter 5); and
- To validate the advantages of using passive acoustics for monitoring and tracking the low population of blue whales and other large baleen whales in the high and low latitudes (Chapters 2-6).

1.6 Thesis structure

This thesis structure follows a progression of firstly, a review and provision of the background, applications, limitations and advantages of passive acoustic monitoring (Chapter Two); followed by an in-depth overview of acoustic data from the IWC SOWER circumpolar surveys (Chapter Three); then an investigation of environmental conditions influencing the circumpolar occurrence and behaviour of blue whales (Chapter Four); lastly studies into the seasonal occurrence and behaviour of Antarctic blue and fin whales in the high and low latitudes (Chapters Five and Six).

In Chapter Two, I investigate a method to improve our ability to remotely, cost effectively and reliably monitor the recovery of marine mammals especially the heavily depleted Antarctic blue whales. I consider the importance of passive acoustic monitoring for blue whales and other marine mammals in South Africa and elsewhere through an easy-to-understand approach of explaining all the principles, applications, limitations, and advantages of the method. I also discuss the estimation of whale density and factors determining the detectability and audibility of marine mammal sounds by including mathematical formulae that illustrate all important factors and processes involved in passive acoustic monitoring. I lastly highlighted that as a relative emerging methodology, a number of crucial challenges have to be overcome before passive acoustic monitoring reaches the same level of maturity as visual surveys.

Chapter Three investigates the passive acoustic data collected during the IWC SOWER cruises between 1997 and 2009 to acoustically monitor the recovery and distinguish *in situ* between pygmy and Antarctic blue whale subspecies in the Southern Ocean. After intensive efforts to reconcile all the acoustic data from those cruises, I found that only 62% of all the collected acoustic data are currently accessible and the rest of the data appear unavailable. This work also describes sounds of other marine mammals present within the IWC SOWER. I conclude this chapter by giving recommendations for managing future data from such extensive large-scale (i.e. both temporal and spatial) acoustic surveys.

In Chapter Four, I use random forest regression model to investigate the effects of environmental conditions on the multi-year acoustic call occurrence and call rate behaviour of Antarctic blue whales in different areas of the Southern Ocean. Environmental conditions considered were chlorophyll-a, sea surface temperature, sea surface height, wind speed, wind direction, wind stress, distance to the Antarctica shoreline, distance to the southern boundary of the Antarctic Circumpolar Current, latitude, longitude and water depth. This novel and comprehensive analyses of such a large suite of environmental conditions provide the basis to assess the vulnerability of Antarctic blue whales to long and short term changes in environmental conditions. I also demonstrate the caveats of the automated template detector algorithm on multi-year acoustic data.

Chapter Five provides the first recorded acoustic evidence of Antarctic blue and fin whales overwintering off the west coast of South Africa; and the first evidence that Antarctic blue whales might be feeding in the Atlantic Ocean. In this chapter, I assess the seasonal diel acoustic behaviour of blue and fin whales; and the broad seasonal occurrence of both species.

I highlight the ecological importance of both whale species in the Benguela ecosystem. I determine the influences of environmental conditions (chlorophyll-a, sea surface temperature, sea surface height, wind speed, Ekman upwelling index and time of the day) on the seasonal occurrence and behaviour of these whales using the random forest model. Results of this work provide preliminary information to concentrate further research effort to investigate abundance, distribution and seasonality of these large baleen whale populations in the Benguela ecosystem while highlighting the importance of monitoring these Antarctic whales in the low latitudes.

In Chapter Six, I use acoustic data collected at the seamount of Maud Rise, Antarctica, to determine the seasonal occurrence and diel behaviour of blue and fin whales in their feeding ground. Wind speed, distance to the ice extent, sea ice concentration, sea surface temperature, sea surface height and time of the day explained the seasonal occurrence and behaviour of these whales. I confirm that not all blue whales migrate to the low latitudes in winter but part of the population is continuously present off the Maud Rise whereas fin whales were seasonally present.

And Chapter 7 offers conclusions and implications of research presented in this thesis while suggesting future work and technologies to monitor large baleen whales in low and high latitudes.

Since the thesis chapters comprise published or to be published papers there is some repetition between chapters, particularly in the methods and background. Although contents remain the same, journal published manuscripts have been edited to a thesis version and some minor textual alterations were made subsequent to publication.

1.7 References

Allen, G.M. 1916. The whalebone whales of New England. Memoirs of Boston Society of Natural History 8(2): 107–322.

Attard, C.R.M., Beheregaray, L.B., Jenner, K.C.S., Gill, P.C., Jenner, M.-N., Morrice, M.G., Robertson, K.M., and Moller, L.M. 2012. Hybridization of Southern Hemisphere blue whale subspecies and a sympatric area off Antarctica: Impacts of whaling or climate change? Molecular Ecology, doi: 10.1111/mec.12025.

Attard, C.R.M., Beheregaray, L.B., Jenner, K.C.S., Gill, P.C., Jenner, M.-N.M., Morrice, M.G., Teske, P.R., Möller, L.M. 2015. Low genetic diversity in pygmy blue whales is due to climate-induced diversification rather than anthropogenic impacts. Biology Letters 11: 20141037.

Attard, C.R.M., Beheregaray, L.B., and Möller, L.M. 2016. Towards population-level conservation in the critically endangered Antarctic blue whale: the number and distribution of their populations. Scientific Reports 6: 22291.

Baker, C.S. and Clapham, P.J. 2004. Modelling the past and future of whales and whaling. TRENDS in Ecology and Evolution 19(7): 365–371.

Ballance, L.T. 2002. Cetacean ecology. *In:* Perrin,W.F., Wursig, B. and Thewissen, J.G.M. (eds) Encyclopedia of marine mammals. Academic Press, California. pp. 208–214.

Bannister, J.L. 2002. Baleen Whales, Mysticetes. *In:* Perrin, W.F., Wursig B. and Thewissen, J.G.M., (eds) Encyclopedia of marine mammals. Academic Press, California. pp. 62–72.

Bérubé, M. 2002. Hybridism. *In:* Perrin, W.F., Wursig B. and Thewissen, J.G.M. (eds) Encyclopedia of marine mammals. Academic Press, California. pp. 596–600.

Best, P.B. 1967. Distribution and feeding habits of baleen whales off the Cape Province. Investigational Report, Division of Sea Fisheries of South Africa 57:1-44.

Best, P.B. 1993. Increase rates in severely depleted stocks of baleen whales. ICES Journal of Marine Science 50: 169–186.

Best, P.B. 1994. A review of the catch statistics for modern whaling in southern Africa, 1908-1930. Paper SC/44/O 16 (Revised), Report of International Whaling Commission 44: 467–485.

Best, P.B. 1998. Blue whales off Namibia - a possible wintering ground for the Antarctic population. Paper SC/50/CAWS14 presented to the IWC Scientific Committee, April 1998, Muscat, Oman. 10 pp.

Best, P.B. 2007a. Whales and dolphins of the Southern African subregion. Cambridge University Press, Cape Town, South Africa. 338 pp.

Best, P.B. 2007b. Assessing struck-and-lost rates in early modern whaling: examination of firsthand accounts. Paper SC/62/O2 presented to the IWC Scientific Committee, June 2010, Agadir, Morocco. 6 pp.

Best, P.B., and Ross, G.J.B. 1989. Whales and whaling. *In:* Payne, A.I.L., and Crawford, R.J.M. (eds) Oceans of Life of southern Africa. pp. 315–338.

Blyth, E. 1859. On the great rorqual of the Indian Ocean, with notices of other cetals, and of the Syrenia or marine pachyderms. Journal of the Asiatic Society of Bengal 28: 481–98.

Branch, T.A. 2007. Abundance of Antarctic blue whales south of 60°S from three complete circumpolar sets of surveys. Journal of Cetacean Research and Management 9: 253–262.

Branch, T.A. and Mikhalev, Y. 2007. Female length at sexual maturity for pygmy and Antarctic blue whales based on Soviet ovarian corpora, 1961-72. Paper SC/59/SH7 submitted to the IWC Scientific Committee, June 2007, Anchorage, Alaska, USA. 14 pp.

Branch, T.A., Matsuoka, K. and Miyashita, T. 2004. Evidence for increases in Antarctic blue whales based on Bayesian modelling. Marine Mammal Science 20 (4): 726–754.

Branch, T.A., Stafford, K.M., Palacios, D.M., Allison, C., Bannister, J.L., Burton, C.L.K., Cabrera, E., Carlson, C.A., Vernazzani, B.G., Gill, P.C., Hucke-Gaete, R., Jenner, K.C.S., Jenner, M.N.M., Matsuoka, K., Mikhalev, Y.A., Miyashita, T., Morrice, M.G., Nishiwaki, S., Sturrock, V.J., Tormosov, D., Anderson, R.C., Baker, A.N., Best, P.B., Borsa, P., Brownell, R.L., Childerhouse, S., Findlay, K.P., Gerrodette, T., Ilangakoon, A.D., Joergensen, M., Kahn, B., Ljungblad, D.K., Maughan, B., McCauley, R.D., McKay, S., Norris, T.F., Whale, O., Rankin, S., Samaran, F., Thiele, D., Van Waerebeek, K. and Warneke, R.M. 2007a. Past and present distribution, densities and movements of blue whales *Balaenoptera musculus* in the Southern Hemisphere and northern Indian Ocean. Mammal Review 37(2): 116–175.

Branch, T.A., Abubaker, E.M.N., Mkango, S., and Butterworth, D.S. 2007b. Separating southern blue whale subspecies based on length frequencies of sexually mature females. Marine Mammal Science 23: 803–833.

Branch, T.A., Allison, C. Mikhalev, Y.A., Tormosov, D., Brownell, Jr. R.L. 2008. Historical catch series for Antarctic and pygmy blue whales. Paper presented to the Scientific Committee of the International Whaling Commission, Santiago, Chile, SC/60/SH9, 11 pp.

Burmeister, H. 1871. Del Año 1871 (In Spanish). Boletin del Museo Publico de Buenos Aires 1871: 11–20.

Christol, C.Q., Schmidhauser, J.R. and Totten, G.O. 1976. The Law and the Whale: Current Developments in the International Whaling Controversy. Case W. Res. J. Int'l L. 8: 149–167.

Clapham, P.J., Young, S.B. and Brownell Jr, R.L. 1999. Baleen whales: conservation issues and the status of the most endangered populations. Mammal Society, Mammal Review 29: 35–60.

Clapham, P.J. and Baker, C.S. 2002. Modern whaling. *In:* Perrin, W.F., Wursig B. and Thewissen, J.G.M. (eds) Encyclopedia of marine mammals. Academic Press, California. pp. 1328-1332.

Conover, D.O. 2000. Darwinian fishery science. *In:* Brownman, H.I. (ed) 'Evolution' of fisheries science. Marine Ecology Progress Series 208: 303–307.

Cummings, W.C., and Thompson, P.O. 1971. Underwater sounds from the blue whale, Balaenoptera musculus. Journal of the Acoustical Society of America 50: 1193–1198.

Dankel, D., Skagen, D., and Ulltang, Ø. 2008. Fisheries management in practice: review of 13 commercially important fish stocks. Reviews in Fish Biology and Fisheries 18: 201–233.

Figueiredo, I. and Weir, C.R. 2014. Blue whales (*Balaenoptera musculus*) off Angola: recent sightings and evaluation of whaling data. African Journal of Marine Science 36(2): 269–278.

Findlay, K.P. 2001. A review of humpback whale catches by modern whaling operations in the Southern Hemisphere. Memoirs of the Queensland Museum 47(2): 411–420.

Hardin, G. 1968. The tragedy of the commons. Science 162: 1243–1248.

Heino, M. and Godø, O.R. 2002. Fisheries-induced selection pressures in the context of sustainable fisheries. Interim Report 2(22): 1–20.

Hewitt, R.P., Watkins, J.L., Naganobu, M., Tshernyshkov, P., Brierley, A.B., Demer, D.A., Kasatkina, S., Takao, Y., Goss, C., Malyshko, A., Brandon, M.A., Kawaguchi, S., Siegel, V., Trathan, P.N., Emery, J.H., Everson, I., and Miller, D.G.M. 2002. Setting a precautionary catch limit for Antarctic krill. Oceanography 15(3): 26–33.

Hilborn, R., Branch, T.A., Ernst, B., Magnusson, A., Minte-Vera, C.V., Scheuerell, M.D., and Valero, J.L. 2003. State of the world's fisheries. Annu. Rev. Environ. Resour. 28: 359–399.

Hilborn, R. 2007. Defining success in fisheries and conflicts in objectives. Marine Policy 31: 153–158.

Ichihara, T. 1966. The pygmy blue whale, *Balaenoptera musculus brevicauda*, a new subspecies from the Antarctic. *In:* Norris, K.S. (ed) Whales, dolphins, and porpoises. University of California Press, Berkeley and Los Angeles, CA. pp. 79–111.

IWC (1995) Forty-Fifth Report of the International Whaling Commission. Reports of the International Whaling Commission, 45. 462 pp.

Jefferson, T.A., Leatherwood, S. and Webber, M.A. 1993. FAO species identification guide. Marine mammals of the world. Rome, FAO. 320 pp.

Jørgensen, C., Enberg, K., Dunlop, E.S., Arlinghaus, R., Boukal, D.S., Brander, K., Ernande, B., Gårdmark, A., Johnston, F., Matsumura, S., Pardoe, H., Raab, K., Silva, A., Vainikka, A., Dieckmann, U., Heino, M., and Rijnsdorp, A.D. 2007. Managing evolving fish stocks. Science 318: 1247–1248.

Kato, H. 2002. Japan Progress Report on cetacean research June 2001 to April 2002. Paper SC/54/ProgRep Japan presented to the IWC Scientific Committee, April 2002, Shimonoseki, Japan. 14 pp.

Kelly, N., Miller, B., Peel, D., Double, M.C., De la Mare, W. and Gales, N. 2012. Strategies to obtain a new circumpolar abundance estimate for Antarctic blue whales: survey design and sampling protocols. Paper presented to the Scientific Committee of the International Whaling Commission, Panama City, Panama, SC/64/SH10.

Klinowska, M. 1991. Dolphins, Porpoises and Whales of the World: The IUCN Red Data Book. IUCN - The World Conservation Union, Gland, Switzerland. 429 pp.

Leaper, R. and Miller, C. 2011. Review management of Antarctic baleen whales amid past exploitation, current threats and complex marine ecosystems. Antarctic Science: 1–27.

Leatherwood, S., Caldwell, D.K. and Winn, H.E. 1976. Whales, dolphins, and porpoises of the western North Atlantic: A guide to their identification. U.S. Dept. of Commerce, NOAA Tech. Rep. NMFS Circ. 396. 176 pp.

Leroy, E.C., Samaran, F., Bonnel, J., and Royer, J.-Y., 2016. Seasonal and Diel Vocalization Patterns of Antarctic Blue Whale (*Balaenoptera musculus intermedia*) in the Southern Indian Ocean: A Multi-Year and Multi-Site Study. PLoS ONE 11(11): e0163587. doi:10.1371/journal.pone.0163587

Linnaeus, C. 1758. System nature, 10th Edition (In Latin). Laurentii Salvii: Holmiae.

Ljungblad, D.K., Clark, C.W. and Shimada, H. 1998. A comparison of sounds attributed to pygmy blue whales (*Balaenoptera musculus brevicauda*) recorded south of the Madagascar Plateau and those attributed to 'true' blue whales (*Balaenoptera musculus*) recorded of Antarctica. Report of the International Whaling Commission 48: 439–42.

Mackintosh, N.A. 1942. The southern stocks of whalebone whales. Discovery Reports 22: 197–300.

Mackintosh, N.A. and Wheeler, J.F.G. 1929. Southern blue and fin whales. Discovery Reports I: 259–540.

Marques, T.A., Thomas, L., Munger, L., Wiggins, S., and Hildebrand, J.A. 2011. Estimating North Pacific right whale (Eubalaena japonica) density using passive acoustic cue counting. Endangered Species Research 13: 163–172.

Marques, T.A., Thomas, L., Martin, S., Mellinger, D., Ward, J., Moretti, D., Harris, D. and Tyack, P. 2013. Estimating animal population density using passive acoustics. Biological Reviews 8: 287–309.

Mizroch, S.A., Rice, D.A. and Breiwick, J.M. 1984. The blue whale, *Balaenoptera musculus*. Marine Fisheries Review 46(4): 15–19.

Oleson, E.M., Calambokidis, J., Barlow, J. and Hildebrand, J.A. 2007. Blue whales visual and acoustic encounter rates in the Southern California Bight. Marine Mammal Science 23(3): 574–597.

Parsons, E.C.M., Bauer, A., McCafferty, D., Simmonds, M.P., and Wright, A.J. 2012. An introduction to marine mammal biology and conservation. Jones & Bartlett Publishing, Sudbury, MA.

Punt, A.E., Breiwick, J.M., George, J.C. 2003. Including age- and length-composition information in the assessment of the B-C-B Seas stock of bowhead whales. Paper SC/55/BRG10 presented to the IWC Scientific Committee, May 2003, Berlin (unpublished). 12 pp.

Rankin, S., Ljungblad, D., Clark, C., and 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, Antarctica. Journal of Cetacean Research and Management 7: 13–20.

Reeves R.R., Clapham, P.J. Brownell, Jr., R.L. and Silber, G.K. 1998. Recovery plan for the blue whale (*Balaenoptera musculus*). National Marine Fisheries Service, Silver Spring, MD. 42 pp.

Rice, D.W. 1977. A list of the marine mammals of the world. NOAA Technical Report NMFS SSRF-771: 1–15.

Rice, D.W. 1998. Marine mammals of the world: Systematics and distribution. Society for Marine Mammalogy Special Publication No. 4, Allen Press Inc, Lawrence, KS. 231 pp.

Rice, D.W. and Scheffer, V.B. 1968. A list of the marine mammals of the world. United States Fish and Wildlife Service Special Scientific Report- -Fisheries No. 579: 1–16.

Samaran, F., Stafford, K.M., Branch, T.A., Gedamke, J., Royer, J.-Y., Dziak, R.P. and Guinet, C. 2013. Seasonal and geographic variation of southern blue whale subspecies in the Indian Ocean. PLoS ONE 8(8): e71561.

Sears, R. 2002. Blue whale *Balaenoptera musculus*. *In:* Perrin, W.F., Wursig B. and Thewissen, J.G.M. (eds) Encyclopedia of marine mammals. Academic Press, California. p. 112–116.

Širović, A., Hildebrand, J.A., and Wiggins, S.M. 2007. Blue and fin whale call source levels and propagation range in the Southern Ocean. Journal of the Acoustical Society of America 122: 1208–1215.

Širović, A., Hildebrand, J.A., Wiggins, S.M., Thiele, D. 2009. Blue and fin whale acoustic presence around Antarctica during 2003 and 2004. Marine Mammal Science 25(1):125–136.

Small, G.L. 1971. The blue whale. Columbia University Press, New York.

Stafford, K.M., Fox, C.G., and Clark, D.S. 1998. Long-range acoustic detection and localization of blue whale calls in the northeast Pacific Ocean. Journal of the Acoustical Society of America 104: 3616–3625.

Thomas, L. and Marques, T.A. 2012. Passive acoustic monitoring for estimating animal density. Acoustics Today l8(3): 35–44.

Thomisch, K., Boebel, O., Clark, C.W.. Hagen, W., Spiesecke, S., Zitterbart, D.P., and Van Opzeeland, I., 2016. Spatio-temporal patterns in acoustic presence and distribution of

Antarctic blue whales *Balaenoptera musculus intermedia* in the Weddell Sea. Endangered Species Research 30: 239–253.

Tønnessen, J.N., and Johnsen, A.O. 1982. The history of modern whaling. C. Hurst & Company, London, UK. 818 pp.

Yablokov, A.V., Zemsky, V.A., Mikhalev, Y.A., Tormosov, V.V., and Berzin, A.A. 1998. Data on Soviet whaling in the Antarctic in 1947–1972 (population aspects). Russian Journal of Ecology 29: 38–42.

Zemsky, V.A., Berzin, A.A., Mikhaliev, Y.A. and Tormosov, D.D. 1995. Soviet Antarctic pelagic whaling after WWII: review of actual catch data. Reports of the International Whaling Commission 45:131-135.

Chapter 2: Passive acoustic monitoring of marine mammals in South Africa, with special reference to Antarctic blue whales

Published as: Shabangu, F.W. and Findlay, K. 2014. Passive acoustic monitoring of marine mammals in South Africa, with special reference to Antarctic blue whales. In: Funke, N., Claassen, M., Meissner, R. and Nortje, K. (eds). Reflections on the state of research and development in the marine and maritime sectors in South Africa: 153-173 (Chapter 8 of book). Pretoria: Council for Scientific and Industrial Research.

2.1 Introduction

Marine mammals are an important predator component of marine ecosystems, both through the ecosystem roles they play in the bottom up forcing through the transfer of nutrients in and between various elements of the ecosystem, and through the top-down forcing of the system structure through predation (Huang *et al.* 2011; Leaper and Miller, 2011). Antarctic blue whales *Balaenoptera musculus intermedia* are one of the top predators that feed directly on the low-trophic-level prey in the krill-based trophic ecosystem of the Southern Ocean (Mackintosh, 1942; Nicol *et al.* 2008).

There are four proposed blue whale subspecies that occur in different oceans (Jefferson *et al.* 1993; Bannister, 2002; Best, 2007). These are the northern hemisphere blue whale *B. m. musculus* (Linnaeus, 1758), the Antarctic blue whale *B. m. intermedia* (Burmeister, 1871), the pygmy blue whale *B. m. brevicauda* (Ichihara, 1966) and the Indian Ocean blue whale *B. m. indica* (Blyth, 1859). However, presently, only the first three subspecies are recognised internationally (Reeves *et al.* 1998; Jefferson *et al.* 1993; Best, 2007), as there is a broad uncertainty in morphologically distinguishing *B. m. indica* from other subspecies. It is therefore considered an approximate synonym of *B. m. brevicauda* (Reeves *et al.* 1998; Rice, 1998). The Antarctic blue whale is the biggest of the blue whale subspecies, growing up to 30 metres and weighing up to 163 metric tons (Mackintosh and Wheeler, 1929; Best, 2007).

Blue whales have a cosmopolitan distribution, although they do not frequent coastal low-latitude waters (Mackintosh and Wheeler, 1929; Best, 2007). Antarctic blue whales are widely distributed in the Southern Hemisphere (Best, 2007; Širovic *et al.* 2009; Samaran *et al.* 2013). Like other large Southern Ocean baleen whales, the majority of Antarctic blue whales migrate seasonally between summer high-latitude feeding grounds and winter breeding grounds in low-latitude waters, although the exact locations of such breeding grounds remain unknown (Jefferson *et al.* 1993; Best, 2007; Double *et al.* 2014). It has been shown from passive acoustic monitoring (PAM) studies that Antarctic blue whales are present in the Antarctic throughout the winter months due to part of the population migrating to the so-called 'overwintering/breeding grounds' in the mid and low latitudes (Stafford *et al.* 2004), since part of the population remain in the feeding ground at the high latitudes all year-round (Širovic *et al.* 2009; Samaran *et al.* 2013). Then again, vocalisation of Antarctic blue whales are recorded all year-round on the breeding grounds (Stafford *et al.* 2004; Širovic *et al.* 2009; Samaran *et al.* 2013).

Antarctic blue whales primarily filter feed on zooplankton prey, chiefly Antarctic krill *Euphausia superba* (Best, 2007; Branch *et al.* 2007). Little or no feeding is thought to occur during winter migrations and their distribution during the austral summer is particularly determined by prey distribution (Best, 2007; Branch *et al.* 2007). Year-round passive acoustic recordings show that Antarctic blue whales may feed on their breeding grounds and move in between low latitude regions in a season, possibly to make use of available food resources in those regions (Samaran *et al.* 2013).

The International Union for the Conservation of Nature (IUCN) considers Antarctic blue whales – once considered to be one of the most abundant large whale species (Clapham *et al.* 1999; Clapham and Baker, 2002) – to be Critically Endangered. This is due to their heavy exploitation through whaling during the last century (Klinowska, 1991; Jefferson *et al.* 1993; Rice, 1998; Clapham *et al.* 1999). Based on catch statistics (Figure 2.1a), it is clear that

Antarctic blue whales were harvested at unsustainable rates that exceeded the maximum sustainable yield (MSY) by great margins (Best and Ross, 1989). With some 360,000 blue whales caught in the Southern Hemisphere during the last century (Clapham and Baker, 2002), Branch *et al.* (2004) estimated in 1996 that modern whaling had reduced the Southern Ocean blue whale population from a pristine 239,000 (95% confidence interval: 202,000-311,000) to a low of 360 (150-840) animals (Figure 2.1b) before being protected by the International Whaling Commission (IWC) in 1965. Currently, it is estimated that 1-3% of the pristine Antarctic blue whale population remains. The population is estimated to increase at a rate of 8.2% (95% CI: 1.7-15.3%) per annum (Branch *et al.* 2004).

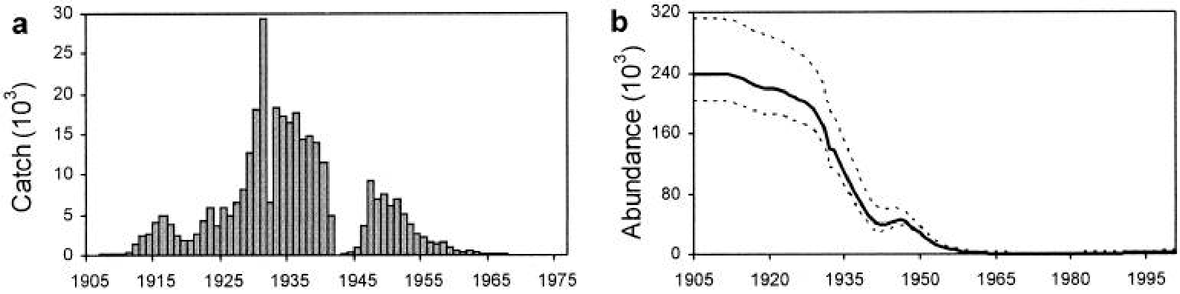


Figure 2.1. Multi-decadal patterns of catches (a) and abundance estimated by logistic models (b) of the Antarctic blue whale in the Southern Hemisphere showing the discovery, exploitation and subsequent collapse of the species (adapted from Branch *et al.* 2004).

It is currently difficult from sighting surveys to monitor the population recovery of Antarctic blue whales, which were so extensively decimated by commercial whaling (Branch *et al.* 2007). The difficulty with sighting surveys is that trained observers can only see Antarctic blue whales for a short period of time when these mammals surface to breathe, and those sighting surveys can only be done in daylight during adequate weather conditions (Mellinger and Barlow, 2003; Thomas and Marques, 2012). Such monitoring ideally requires an absolute abundance or at least a relative abundance estimation over a sufficiently long period for a population trend estimation to be apparent over the confidence limits of the abundance estimates (Buckland and York, 2002; Branch *et al.* 2007).

Absolute abundance is the actual number of whales estimated in a spatial unit, while relative abundance gives the relative indices of abundance, which may be used to estimate trends when constant proportions of the population are estimated each year (Buckland and York, 2002). Abundance estimations of Antarctic blue whales have been and still are centred on visual line-transect surveys or mark-recapture methodologies (Oleson *et al.* 2007; Kelly *et al.* 2012), both of which may be subject to costly and logistically difficult research operations (Buckland and York, 2002; Kelly *et al.* 2012; Thomas and Marques, 2012). Furthermore, factors affecting the reliability of data (for example, limited population sizes, and the surfacing or aggregation behaviour of the Antarctic blue whale leading to avalability bias) and factors affecting data collection (for example, weather or sighting conditions leading to perception bias) may increase the confidence limits of estimates compromising the required data to estimate population trends in the Southern Ocean (Branch *et al.* 2004, 2007; Kelly *et al.* 2012).

PAM can be used to estimate the relative abundance of vocalising animals as Antarctic blue whales are particularly vocal. It can also be used to provide information on behaviour and distribution. The use of PAM to estimate Antarctic blue whale abundance is an emerging methodology and a number of issues still need to be addressed before the method will be as mature as visual surveys in South Africa and worldwide. The South African Blue Whale Project (SABWP) is an initiative of the Mammal Research Institute’s Whale Unit based at the University of Pretoria, which aims to investigate the distribution and relative abundance of the Antarctic blue whale using both sighting survey and PAM methods in South African and associated Antarctic waters. The SABWP conducts research over a range of spatial and temporal scales, which contribute to the international management and conservation of these marine mammals. However, relatively low levels of PAM research have been done in South Africa. The work of the SABWP is pioneering many of the deep-water PAM studies to follow. In this chapter, a remote and autonomous acoustic method is presented that can provide indices of relative abundance and therefore population trends of marine mammals, with particular reference to Antarctic blue whales as the most severely depleted large whale species that occurs in South African waters. It should be noted that PAM has considerable application to other baleen species that occur in South African waters, including fin whales *B. physalus*.

2.2 Sound in the sea

Acoustics research is the science that examines the physical properties of sound. The research into sounds produced by living organisms is often referred to as bioacoustics (Au and Hastings, 2008). The ocean is by no means a quiet environment. Sounds are produced by a number of sources, including the following:

- Natural events, such as rain, wind, seismic events or ice (Urick, 1983; Au and Hastings, 2008; Zimmer, 2011)
- Marine animals that are often very vocal and produce diverse loud and/or soft sounds (Urick, 1983; Zimmer, 2011)
- Man-made noise sources, such as shipping or other anthropogenic activities (Urick, 1983; Au and Hastings, 2008)

Urick (1983) states that, as early as 1490, Leonardo da Vinci discovered that “If you cause your ship to stop, and place the head of a long tube in the water and place the outer extremity to your ear, you will hear ships at a great distance from you.” It was therefore from this rather simplistic observation that modern hydrophones and transducers were developed to study and explore the marine world (Urick, 1983; Simmonds and MacLennan, 2005).

Sound comprises waves of energy moving through a medium as oscillations of particles in that medium. Important characteristics of a sound include its frequency, or rate of oscillation, which is measured in Hertz (Hz), period (the duration of an oscillation cycle in seconds (s)) and wavelength (the length of a single oscillation in metres). A decibel (dB) is the unit of measurement of the acoustic intensity of a sound. Acoustic energy is the energy in a sound wave. The power of a wave is the energy measured over a period of time. Acoustic intensity is the acoustical power per unit area in the direction of propagation. The energy, power and intensity of a sound wave are proportional to the mean square pressure. Acousticians consequently refer to ratios of pressure or pressure squared, using a standard reference pressure against which sounds can be measured. A reference pressure of 1 µPa is used for water, whereas 20 µPa is used for air.

When comparing the relative intensities of two sounds, their responses are logarithmic, which is why sound intensities (*I*) are measured on a logarithmic scale (in decibels) as:

$$Intensity\_levels(dB) = 10\log\frac{I}{I_0} \tag{1}$$

where I_0 is the reference intensity.

As intensity is proportional to pressure squared, the sound pressure level (SPL) of sound pressure (P) is defined as:

$$SPL(dB) = 20\log\frac{P}{P_0} \tag{2}$$

where P_0 is the reference pressure, e.g., 1 µPa for water.

The principles applied in acoustics are similar to those applied in light, since both physical processes are subject to absorption, reflection and scattering. Both comprise energy waves that travel through a medium and follow elementary laws of physics (Mobley, 1994; Simmonds and MacLennan, 2005). However, the heterogeneous properties of water disrupt the basic linearity principle of a perfect wave transmitting energy through a homogeneous ‘lossless’ medium explained in most physics textbooks (Mobley, 1994; Simmonds and MacLennan, 2005). Thus, electromagnetic, thermal, light, chemical and other forms of energy attenuate very quickly in turbid waters due to scattering and absorption (Urick, 1983;

Tyack and Miller, 2002; Au and Hastings, 2008). Providentially, sound propagates faster and weakens less in water than in air (Tyack and Miller, 2002).

2.3 Acoustic research of marine mammals

Sound is important to marine mammals as they use it for communication, searching for prey, navigation, and to avoid unfavourable conditions or predators (Purves, 1967; Kenshalo, 1967; Tyack, 1998, 1999; Sears, 2002; Mellinger and Clark, 2003; Simmonds and MacLennan, 2005; Zimmer, 2011). Consequently, many marine mammals have evolved hearing and mental capacity to detect and interpret acoustic signals with good sensitivity and accurate localisation of the waterborne sound (Ketten, 1992, 1994; Au and Hastings, 2008) and many have specialised sound-generating organs (Kenshalo, 1967; Frankel, 2002; Au and Hastings, 2008). However, the hearing sensitivities of marine mammals are generally not well understood, with best hearing sensitivities often assumed around the frequencies at which the animal vocalises (Ketten, 1992; Ketten, 1994; Frankel, 2002).

Several balaenopteridae species of mysticete (or baleen) whales produce high-energy, low-frequency (< 100 Hz) or infrasonic (< 20Hz) sounds (Ketten, 1992, 1994; Sears, 2002; Mellinger and Clark, 2003; Au and Hastings, 2008; Zimmer, 2011). Antarctic blue and other baleen whales have larynxes like humans, but unlike humans, lack vocal cords to produce sound, thus these mammals are presumed to recycle air in their bodies (presumably the lungs) to vocalise (Frankel, 2002; McDonald *et al.* 2009). Antarctic blue whales and other baleen whales use sound for “long range contacts, assembly calls, sexual advertisement, greeting, spacing, threat and individual identification” (Dudzinski *et al.* 2002). Odontocetes (toothed whales and dolphins) produce higher-frequency (ultrasonic) whistles and broadcast clicks using the upper portion of the head, called the dorsal bursae, and the nasal passage, called the phonic lips, while directing the sound through the melon that combines vibrations produced by both the dorsal bursae and phonic lips (Frankel, 2002). Whistles are used mainly for social interaction and clicks for echolocation (Au and Hastings, 2008). Non-cetacean marine mammals like seals are said to produce underwater sounds comparable to those of their terrestrial relatives via the vibrations of their throats without emitting air through their mouths (Frankel, 2002).

2.3.1 Applications of passive acoustic monitoring

The use of passive acoustic techniques for estimating the abundance, behaviour and distribution of marine mammals has many advantages over the conventional abundance estimation methods (Urick, 1983; Simmonds and MacLennan, 2005; Au and Hastings, 2008; Zimmer, 2011). Models of Peel *et al.* (2014) depicted the fact that real-time acoustic tracking can result in increased encounters and subsequent photographic captures of Antarctic blue whales by two to four extra times compared to conventional visual transect surveys. Furthermore, based on the modelling of sighting rates, Kelly *et al.* (2012) argue that the sole utilisation of the line-transect survey design is not the best method of estimating the circumpolar abundance of Antarctic blue whales, but that mark-recapture using acoustics as a supplementary tool would provide better results. For instance, some areas might be logistically difficult for sighting surveys because they are remote, not accessible to direct observation, too expensive or difficult to survey (Best, 1993).

PAM can be used as a cost-effective method to monitor and track both the population and individuals in such areas (McDonald *et al.* 2006a; Mellinger *et al.* 2007; Van Parijs *et al.* 2009; Marques *et al.* 2013). PAM can be carried out as real-time or archival, manual or autonomous operations over a considerable duration (Van Parijs *et al.* 2009). Recording equipment can be mounted on stationary platforms, such as oceanographic moorings, or on moving/drifting platforms, such as research vessels or wave gliders (Bobbitt *et al.* 1997; Boisseau *et al.* 2008; Baumgartner *et al.* 2013). Real-time PAM has been conducted as part of the Listening to the Deep Ocean Environment (LIDO) project (André *et al.* 2011) and, more recently, from ocean gliders (Baumgartner *et al.* 2013). Digital acoustic recording tags (DTAGs) are used to monitor the behaviour of marine mammals and their response to sound stimuli, as archival sensors onboard the suction cup tags measure the dive cycles, 3D orientation and movement of the animals (Tyack, 2011). Instruments of this kind are unavailable in South Africa and the SABWP aims to conduct such research in the near future.

Sonobuoys are sound-receiving buoys primarily used by the military to detect submarines, and relay detected sounds to research platforms via ultra-high frequency (UHF) or very high frequency (VHF) transmission (Zimmer, 2011). These have been utilised in PAM whale research (McDonald, 2004; Rankin *et al.* 2005; Oleson *et al.* 2007; Miller *et al.* 2012, 2014a, 2014b). Sonobuoys with differential frequency analysis and ranging (DIFAR) enable estimations of the vocalising marine mammal's bearing relative to the sonobuoy and the surveying research vessel that can be used to track the animal in real time (McDonald, 2004; Rankin *et al.* 2005; Oleson *et al.* 2007; Miller *et al.* 2012, 2014a). The advantage of this type of sonobuoy is that acoustic research can be conducted simultaneously with visual surveys, for example, to improve the probabilities of encountering vocalising and non-vocalising animals for abundance estimation (Rankin *et al.* 2005; Oleson *et al.* 2007; Miller *et al.* 2012; Peel *et al.* 2014).

The abovementioned acoustic research techniques have particular advantages and disadvantages. Their choice of use is often specific to sites or species. For example, acoustic recorders towed behind research vessels may be limited for large baleen whales, as the low-frequency calls of whales are masked by the underwater noise of the ship's propellers at the same frequency (5-500 Hz) (Au and Hastings, 2008). However, these recorders are particularly valuable for the monitoring of odontocete cetaceans that vocalise at a high frequency, such as sperm whales *Physeter macrocephalus* (Thode *et al.* 2002; Mellinger *et al.* 2003).

2.3.2 Factors determining the detectability of marine mammal sounds

The speed of sound in seawater is approximately 1,500 m s^{-1}. When assuming constant temperature and increasing static pressure, this speed will increase by 1% for each 1,000 m of depth, while a 1 °C increase in temperature will result in a 2% increase in sound speed (Rossing, 2007). Sound refraction and reflection occur at both the surface and the seafloor due to sound speed changes, with these directional changes resulting in waveguides at different ocean depths (Urick, 1983; Simmonds and MacLennan, 2005; Rossing, 2007). Sound transmitted in both the upward and downward angles tends to propagate towards the minimum sound velocity region from its source and refract towards the depth of its source after hitting the surface and bottom boundaries (Urick, 1963; Rossing, 2007; Au and Hastings, 2008). During World War II (1939-1945), Ewing and Worzel (Urick, 1963) discovered a deep sound channel in which sound waves could travel long distances. This channel, known as the sound fixing and ranging (SOFAR) channel (Urick, 1963, 1983; Medwin and Clay, 1998; Rossing, 2007) occurs at shallower depths in high latitudes and at deep depths in low latitudes due to sound waves bending towards the lower sound velocity region caused by the temperature or depth profile (Urick, 1983; Rossing, 2007; Au and Hastings, 2008). Antarctic blue whales and other baleen whales are thought to use the SOFAR channel for transmitting sounds over great distances, since the sound at this axis encounters the least geometric spreading loss compared to surface or bottom reflection (Urick, 1983; Au and Hastings, 2008; Samaran *et al.* 2010b).

During World War II, military engineers developed the sound navigation and ranging (sonar) equation (Equation 3), with the aim of determining the maximum range of sonar equipment (Urick, 1983). The sonar equation models the functions of source level, transmission loss and received levels over the sound travel path (under the source-path-receiver model introduced earlier). Numerous parameters that affect the performance of the underwater sonar model were therefore conveniently and logically merged into small units in the sonar equation. In turn, the equation accommodates the effects of the propagation medium, target and the equipment itself (Urick, 1983). In a biological context, the sonar equation therefore addresses the acoustic energy reception in the animal’s *in situ* setting, given that they record received levels (Urick, 1983; Tyack, 1998; Au and Hastings, 2008). Given that the aim of research relating to PAM is to listen to sounds produced by animals, biologists are primarily concerned with the transmission loss from the animal of interest (Tyack, 1998; Au and Hastings, 2008).

The simple passive acoustic sonar model of evaluating sound propagation in water is measured in dB re 1 µPa as:

$$RL = SL - TL \qquad (3)$$

where RL is the received level, SL is the source level at 1 m from the source and TL is the transmission loss.

The intensity levels of acoustic signals weaken as sound propagates farther from the source through a medium due to transmission loss caused by spreading, absorption, scattering, reflection and rarefaction (Urick, 1983; Tyack, 1998; Swift, 2004). The majority of energy in any given acoustic wave is concentrated at the centre of the sound source, hence, as the sound propagates to a range (r), the acoustic energy will be spread in all directions over the sphere’s area of $4\pi r^2$ (Tyack, 1998; Swift, 2004). Thus, the signal intensity is expected to decrease exponentially with distance from the calling animal or sound source. This is called spherical or geometrical spreading (Tyack, 1998; Lurton, 2002; Swift, 2004; Simmonds and MacLennan, 2005).

The transmission loss due to spherical spreading is calculated as follows:

$$TL = a \log r = 10 \log \frac{I}{I_{ref}} = 10 \log \frac{4\pi r^2}{4\pi r_{ref}^2} = 20 \log \frac{r}{r_{ref}} \qquad (4)$$

where a is the environment-dependent absorption coefficient, I is the intensity of the signal, and I_{ref} is the intensity at the reference source. Širovic, *et al.* (2007) found in the Southern Ocean under spherical spreading considerations a is estimated to be 17.8 dB/m. For South Africa, a is undetermined, but it should be much less than 17.8 dB/m as the water is warmer around the coast.

Spherical spreading assumes that sound propagates through a uniform or homogenous environment (Swift, 2004) and occurs until the sound hits a boundary with a different acoustic property, such as the sea surface, seafloor or waters of different densities, where the sound waveform will refract in a plane according to Snell's Law and cylindrical spreading results (Tyack, 1998; Swift, 2004). Simple cylindrical spreading models contain or limit spreading by the seafloor and sea surface so that the sound energy spreads in a cylindrical fashion over the cylinder's cross-sectional area of $2\pi r$ where the sound energy will not be restricted by planes. Cylindrical spreading is therefore calculated in the form of:

$$TL = 10\log\frac{I}{I_{ref}} = 10\log\frac{2\pi r}{2\pi r_{ref}} = 10\log\frac{r}{r_{ref}} \tag{5}$$

While the spreading of sound in the water column defined in Equation 4 and Equation 5 weakens the acoustic signal, the conversion of sound to heat results in further loss of sound. This is known as absorption or attenuation (Tyack, 1998; Lurton, 2002, Shabangu *et al.* 2014). However, Tyack (1998) agrees with Cummings and Thompson (1971) that, for species like Antarctic blue whales, no significant absorption loss should be encountered as these animals transmit acoustic signals at very low frequencies, for example, less than 1 dB per 100 m will be lost to absorption for a 100 Hz frequency signal.

The ability of a hydrophone to detect an animal's call depends on the received call level in relation to the noise levels (NL) (Tyack, 1998; Au and Hastings, 2008). NL is expressed in dB re 1 µPa^2/Hz (Swift, 2004; Au and Hastings, 2008). Therefore, the modified passive acoustic sonar equation will take the following form:

$$DT = SL - TL - (NL - DI) \tag{6}$$

where DT is the detection threshold (dB) and will obviously vary for each animal species, and DI is the directivity index of the receiving hydrophone (measured in degrees) relative to the direction of the vocalising animal from the hydrophone.

Au and Hastings (2008) propose that, provided marine mammals have a specific acoustic detection system with a boundary specified by a direct filtering bandwidth, Equation 6 could be revised to incorporate the filter effects in the sonar equation to fit the new measurement system as follows:

$$DT_A = SL - TL - (NL - DI + \Delta f) \tag{7}$$

where DT_A is the new detection threshold of the system and Δf is the filter bandwidth of the system.

This is calculated as follows:

$$\Delta f = \frac{2^n - 1}{2^{n/2}} fc \tag{8}$$

where n is 1/3, 1/2, or 1 for a 1/3-octave, 1/2-octave, or 1-octave band, respectively. Octave bands are commonly utilised sets of frequency bands with fc (the centre frequency of the band). A one-octave bandwidth has an upper band frequency twice the lower band frequency, while a one-third octave band is a frequency band where the upper band-edge frequency is the lower band-edge frequency multiplied by the cube root of two.

Au and Hastings (2008) further explain that if DT_A equals zero, the mammal hearing system would only detect the signal half the time due to equal intensities between the received signals and received ambient or background noise. This defines the animal's critical ratio of the auditory system. However, a DT_A of 3 dB would enable the animal to easily detect a signal because the signal intensity will be twice as strong as the ambient noise intensity. This principle can also be applied to acoustic systems to determine the transmission loss that can be tolerated by a hydrophone without missing any signal detections (Tyack, 1998; Au and Hastings, 2008).

Marine mammals can tolerate transmission loss to a certain degree where they can hear a signal. The transmission loss threshold is calculated as follows:

$$TL = SL - (NL - DI + 10\log\Delta f) \tag{9}$$

Following the computation of the amount of transmission loss an animal can tolerate in Equation 9, the probability of a signal being detected can be mathematically computed as the signal-to-noise ratio (SNR) expressed in a subtraction form:

$$SNR = RL - NL \tag{10}$$

SNR is not only determined by RL, but also by external environmental noise and any internal noise in the receiver (Tyack, 1998).

The source level, frequency and bandwidth of a call are the most crucial acoustic parameters. However, their significance is determined by the transmission range and ambient noise (Tyack, 1998; Xiaohong *et al.* 2012). For a receiver (hydrophone or sonobuoy) to receive the most prominent SNR, an animal must transmit sound at a carrier frequency and bandwidth of the receivers' detection capabilities (Xiaohong *et al.* 2012). The receiver can therefore be designed to correspond with the frequency and time characteristics of the animal of interest, and if the receiver bandwidth is tuned effectively to fit the signal bandwidth, the noise spectrum level outside the frequency range of interest will be reduced (Tyack, 1998). Building on from the octave bands in Equation 9, the frequency band (W) among the ambient noise spectrum levels of the energy and at distinct frequencies can be calculated in the following form:

$$Band\_level = Spectrum\_Level + 10\log W \tag{11}$$

For the minimisation of the integration effects of signals throughout a given time period within a given receiver, the integration time must be well matched to the duration of an animal signal (Tyack, 1998). For example, a fin whale can produce an infrasonic pulse that lasts for 1 second and contains 20 cycles (Tyack, 1998).

Therefore, if the receiver integration time (t_{int}) is longer than a given short pulse (t_{pulse}),the effective source level of the sound signal (SL_{eff}) will be biased in the following equation:

$$SL_{eff} = SL + 10\log\frac{t_{pulse}}{t_{\text{int}}} \tag{12}$$

The SL_{eff} is important to determine the detection range and the distance the sound will travel. Another factor that determines the detection range or source level of the vocalisation is the size of the animal. Bigger animals will generally produce higher-intensity sounds (Tyack, 1999).

2.3.3 Antarctic blue whale density estimation

Although challenging, once factors affecting the detectability of a signal are addressed and considered, the estimation of Antarctic blue whale density based on PAM is possible if both the cue rates per individual and group sizes are known (Marques *et al.* 2013). PAM density estimation is an ongoing research area, with working algorithms required for each vocalising species based on the species' acoustic behaviour (Thomas and Marques, 2012). Density (D)

is generally defined as the number of animals in a given area, and calculated by the following formula:

$$D = \frac{n}{a} \tag{13}$$

where n is the whale number/count, and a is the survey area. Given that the area surveyed by the recording instrument is known for the assumed source level, the abundance can be estimated from density as $n = D \times a$ (Marques *et al.* 2009). Since n detected in the area a is now known, the abundance ($\hat{D}$) can be estimated as:

$$\hat{D} = \frac{n}{a\hat{P}} \tag{14}$$

where $\hat{P}$ is the probability of a whale sound being detected by the PAM recorder, which is dependent on source and noise levels as shown above in Section 3.2.

The estimated density of blue whales over time ($\hat{D}_t$) can be determined from PAM by upgrading Equation 14 through the consideration of further parameters:

$$\hat{D}_t = \frac{n_c(1-\hat{c})}{K\pi w^2 \hat{P} T \hat{r}} \tag{15}$$

where n_c is the number of calls, $\hat{c}$ is the estimated amount of false positive detections, K is the number of replicate recorders used, w is the distance away from the recorder where vocalising whales are assumed not to be detected, T is the time, and $\hat{r}$ is the estimated call rate.

Thomas and Marques (2012) and Marques *et al.* (2009, 2013) provide methods of estimating cetacean density from PAM data collected through arrays of hydrophones. Call rates, sound propagation and the frequency and source level of calls are important for the determination of blue whale density. PAM data recorded through DIFAR sonobuoys during the IWC's International Decade of Cetacean Research (IDCR) and Southern Ocean Whale and Ecosystem Research (SOWER) cruises have bearing on detected calling animals to determine number of calling animals in an area, but single instruments were usually deployed at the time. Thus, the above density estimation mechanisms are adequate for experiments with replicates extending to large spatial and temporal scales. These are also applicable to a single recorder, while some additional errors are introduced (Kusel *et al.* 2011; Thomas and Marques, 2012; Marques *et al.* 2013).

2.3.4 Antarctic blue whale calls

Blue whales produce calls with high source levels (around 188 dB re 1 µPa at 1 m) (Cummings and Thompson, 1971; Au and Hastings, 2008). Antarctic blue whales are the loudest blue whale subspecies with a mean source level of 189±3 dB re 1 µPa at 1 m over the 25-29 Hz range (Širovic *et al.* 2007). However, there is a spread on the variability of measurements of the source levels for Antarctic blue whales. Samaran *et al.* (2010a) reported source levels of 179±5 dB re 1 µPa at 1 m over frequencies of 17-30 Hz. The most recent preliminary source level measurements by Miller *et al.* (2014a) are 182-185±2 dB re 1 µPa over 25-29 Hz. Antarctic blue whales produce two types of calls that are both frequency- and amplitude- modulated, namely Z- and D-calls (Figure 2.2 and Figure 2.3). The frequency of frequency- modulated calls changes over time (Frankel, 2002). Individual units of stereotypical patterns of frequency-modulated sounds are called 'calls' and the repetitive sequence of stereotyped three-unit low-frequency calls are called 'songs' (Rankin *et al.* 2005; McDonald *et al.* 2006a). The Z-call is so named because the shape of the call resembles the alphabetic letter 'Z' when viewed on the spectrogram (Figure 2.2b). The Z-call is only produced by Antarctic blue whales and is presumably used by males to find mates.

McDonald *et al.* (2006a) found that these highly vocal cetaceans produce population-specific sounds, and identified nine song types of blue whales from around the world. Antarctic blue whales' Z-calls are characterised by the distinct long-duration (8-12 seconds), 28 Hz first tonal sounds (Figure 2.2b1), followed by a second relatively short- duration (2-5 seconds) sound downsweeping from 28 Hz to 19 Hz (Figure 2.2b). A third component is an 8- to 12-second (Figure 2.2b3) slightly frequency-modulated tone between 20 Hz and 18 Hz (Ljungblad *et al.* 1998; Rankin *et al.* 2005). This call is also believed to be a contact call usually produced intermittently by a single whale or a group of travelling whales (Edds-Walton, 1997; McDonald *et al.* 2006a). The average intercall interval (pause time between calls) in a series of calls is estimated to be 48.5±2.8 seconds for Antarctic blue whales (Stafford *et al.* 2004). A decline in the tonal frequencies of this Antarctic blue whale song has been observed lately (McDonald *et al.* 2009).

Sound produced at these low frequencies can travel hundreds to thousands of kilometres from the source, but these low-frequency sounds are susceptible to noise due to poor target definition and separation (Urick, 1983; Rossing, 2007; Zimmer, 2011; Miller *et al.* 2012). The frequency range of the signal transmits useful information from the transmitter to the recipient (Tyack and Miller, 2002; Au and Hastings, 2008).

Only male Antarctic blue whales are thought to sing (Z-calls) and little is known about female blue whale vocalisation (Tyack, 1998; McDonald *et al.* 2001, 2006a; Samaran *et al.* 2013). However, Oleson *et al.* (2007) observed that both sexes of northern hemisphere blue whales vocalise during feeding, producing a call more variable in duration and frequency, called the D-call. Antarctic blue whales' D-calls are shown in Figure 2.3. This higher-frequency call is likely used for short-distance communication, and could be used to advertise the presence of food to conspecific animals. D-calls range in frequency from 22 Hz to 106 Hz (Thompson *et al.* 1996; Rankin *et al.* 2005). The D-call is a general, worldwide blue whale call that is not population-specific and has been observed from different feeding areas like the gulfs of California and Mexico (Thompson *et al.* 1996), as well as the Cortez and Tanner Banks and the Southern California Bight (Oleson *et al.* 2007).

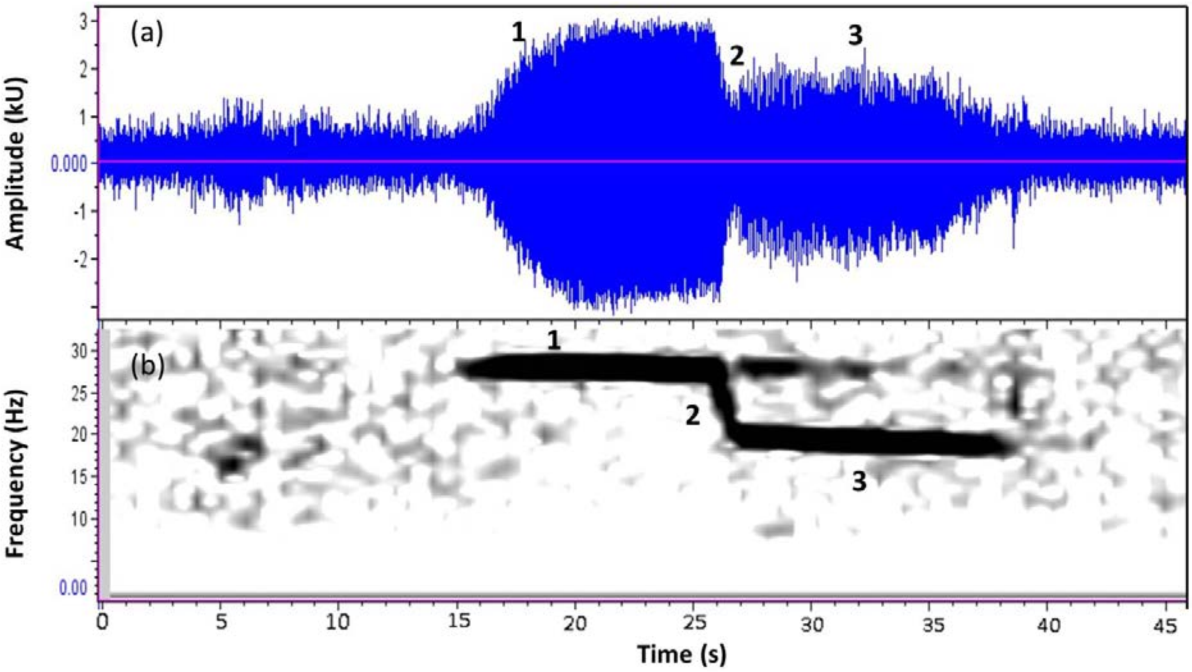


Figure 2.2. A typical Antarctic blue whale Z-call illustrating the wave form amplitude modulation (a), with the corresponding frequency modulation and duration of each unit of this three-unit call (b). The 28 Hz unit is the high-energy component of the call as it has the highest amplitude compared to the other two components of the call as shown by the amplitude values. The amplitude is presented here in a thousand unit, also known as a kilo unit (kU), of the dimensionless sample values. Data was collected during the 2001/02 IWC SOWER cruise.

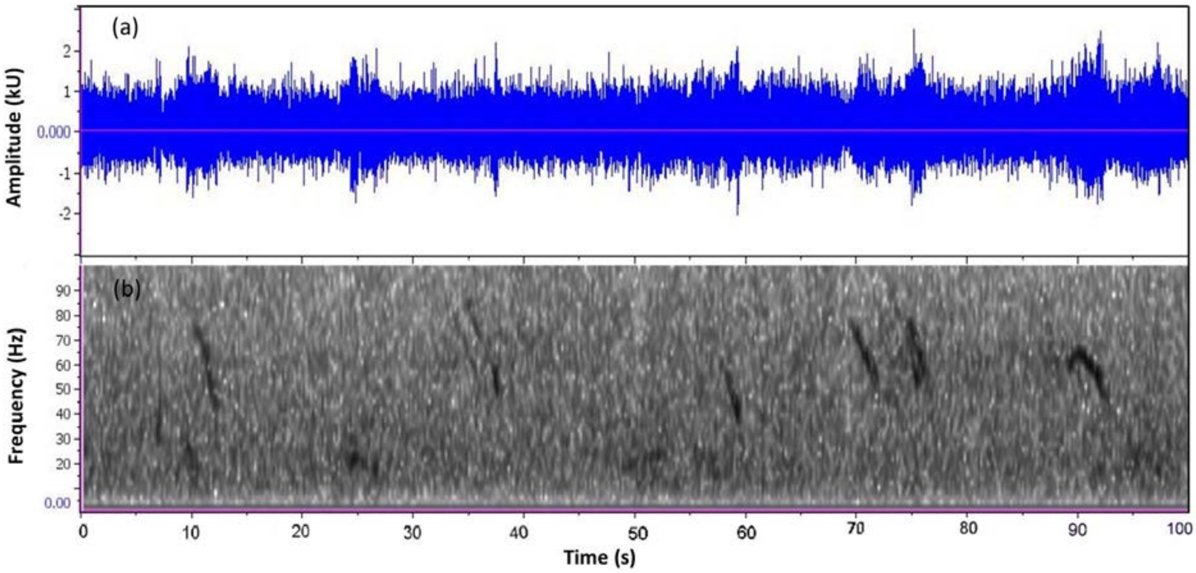


Figure 2.3. A spectrogram of the Antarctic blue whale's high-frequency modulated D-calls showing the waveform amplitude modulations (a) and frequency modulations (b) over time during the 2001/02 IWC SOWER cruise.

For Z-calls, both the frequency sweeps within a call and the several call harmonics improve long-distance communication by making the call stand out from the ambient noise (Edds-Walton, 1997). McDonald *et al.* (2009) and Gavrilov *et al.* (2011) reported a worldwide decrease in the frequency and source levels of blue whales. The reasons for this are not well understood, but factors like depleted/recovering populations, mate selection, animal size, cultural behaviour and ocean ambient noise have been associated with the change. Comparisons of the regional call patterns of blue whales can provide biologists with an understanding and knowledge of the population structure, seasonal relative abundance patterns, migrations and distribution (McDonald *et al.* 2006a) of the species or populations. Thus, the determination of species identification techniques is important for the effective recognition of a sound producer at a particular location (Tyack, 1998).

2.3.5 Passive acoustic monitoring research on large baleen whales in South Africa – the South African Blue Whale Project

South African cetacean scientists are actively involved in the Southern Ocean Research Partnership (SORP), which is an IWC initiative to enhance cetacean conservation and deliver methods of non-lethal whale research using techniques such as PAM in the Southern Ocean. Prior to the initiation of the SORP, the IWC’s IDCR and SOWER cruises were conducted between 1979 and 2010. These cruises utilised PAM stations (1995-2009) that deployed sonobuoys. The timing and distribution of the sounds recorded are shown in Figure 2.4 and Figure 2.5. However, the main aim of the IWC’s IDCR and SOWER circumpolar surveys was to estimate the abundance and distribution of whales using sighting surveys. The acoustic data collected during these surveys is currently being analysed in South Africa to investigate the spatio-temporal distribution patterns of vocalising Antarctic blue whales and to determine the call rates of the observed whale groups. Demultiplexed bearings of vocalising Antarctic blue whales can be estimated from directional DIFAR sonobuoy PAM data to differentiate between vocalising whale groups.

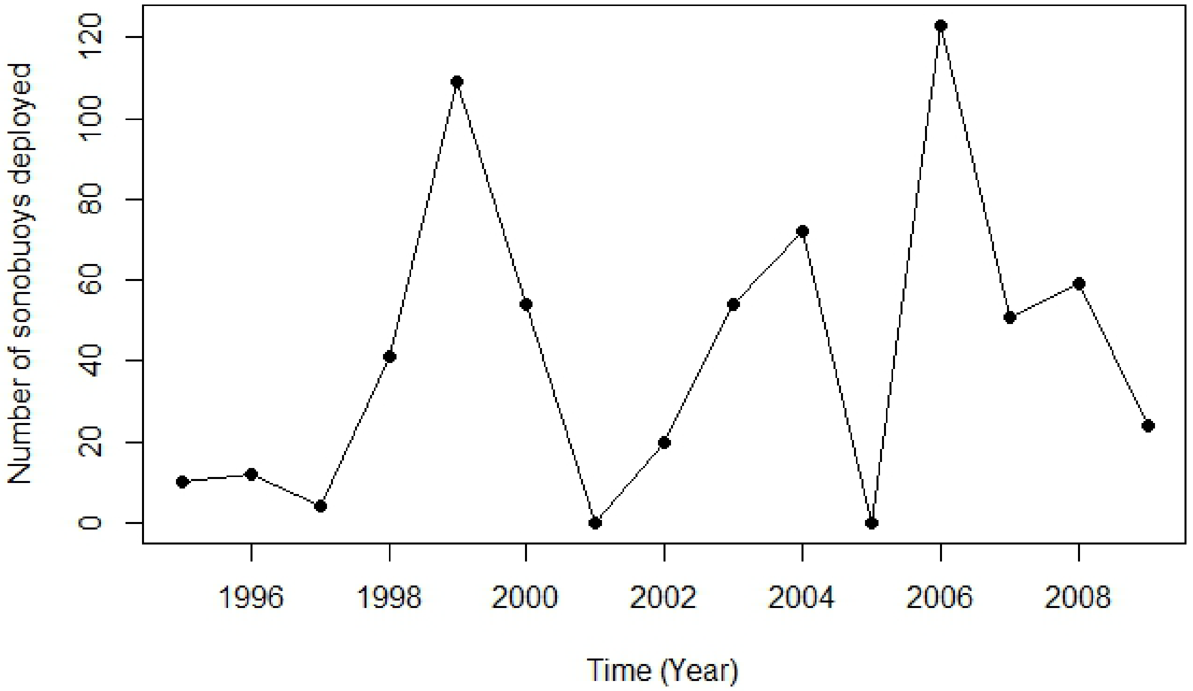


Figure 2.4. The IWC's sonobuoy acoustic research effort over time in the Southern Ocean during the IDCR and SOWER cruises, including the 1995 Australia, 1996 Madagascar and 1998 Chile cruises. A total of 633 sonobuoys were deployed over 15 years, which recorded sounds for 1,505 hours. The database that is currently being analysed comprises 93% of the IDCR and SOWER sonobuoy data.

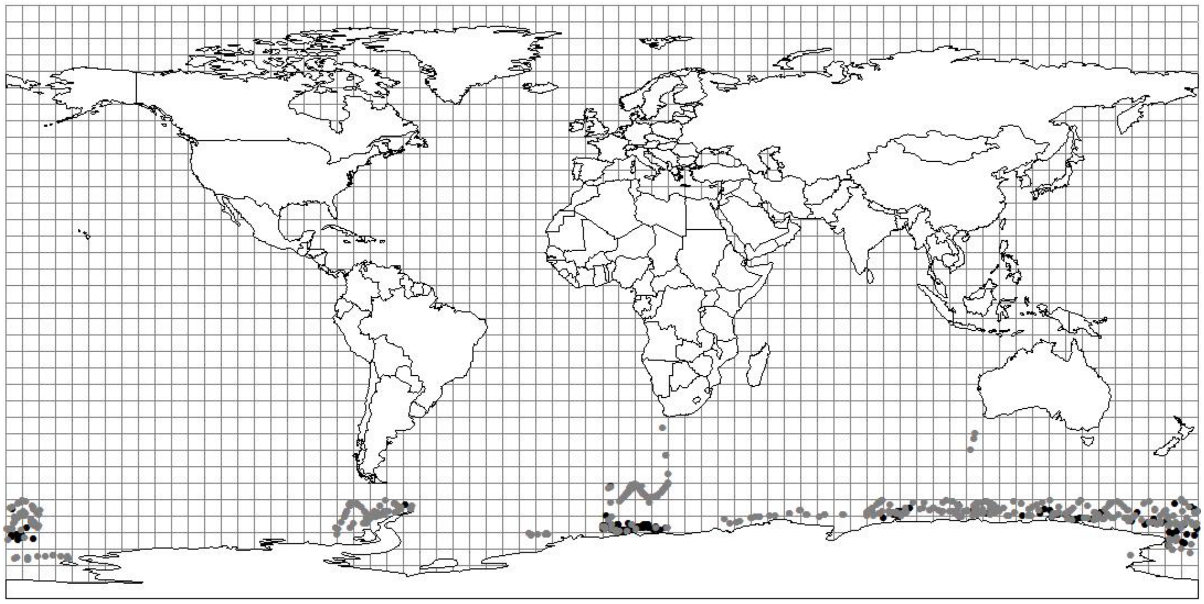


Figure 2.5. Detections of blue whales from sonobuoys deployed during the IWC's SOWER voyages, 1999 to 2009. Sonobuoy deployment sites are shown on the map as grey points, while black points show locations at which Antarctic blue whales were heard by acoustic researchers. Each block is 5° of latitude and longitude. The data is courtesy of the IWC.

The SABWP started a long-term passive acoustic programme in 2014 to monitor Antarctic blue whales in the Antarctic sector south of South Africa (0°-20°E); one of the areas with the highest abundance of the species in terms of calls recorded (Figure 2.5). An aural M2 autonomous acoustic recorder (AAR) deployed on the Maud Rise (65°S; 2.5°E) in water depths of 1,200 m will monitor low-frequency whale calls until February 2015 when the mooring (and the archived acoustic data) will be recovered and most probably redeployed for a further year (Findlay *et al.* 2014). The recorded PAM data is archived on the recording instrument's hard drive for later analyses once the hydrophone is retrieved. The AAR is operated on batteries for the duration of the deployment and the duty cycle is determined by both battery life and hard drive space.

Such passive acoustic technology is being combined with the conventional sighting survey and mark-recapture methods to study the distribution, abundance and migration of Antarctic blue whales in the South-East Atlantic. The SABWP also deploys AAR moorings off the coast of South Africa and Namibia to monitor and track the abundance, movement and distribution of Antarctic blue whales during their migrations. The seasonal occurrence of other large baleen whales, such as the humpback *Megaptera novaeangliae*, fin and southern right whale *Eubalaena australis* may also be monitored from this passive acoustic system, depending on the target frequencies being recorded (which are obviously a trade-off on battery duration).

The research done by the SABWP contributes important knowledge towards estimating the current population status of Antarctic blue whales, in conjunction with genetic and photographic data collected to help understand the stock structure of the species. The SABWP is also conducting investigations of predator-prey relationships by using active acoustic echo sounders to determine the abundance and distribution of Antarctic krill relative to whales.

2.4 Challenges and the way forward

A number of challenges in PAM methodology need to be addressed in the future.

PAM only detects and records sounds from marine mammals that vocalise, so acoustic studies need to be conducted at times when animals are known to vocalise or throughout the year to determine the times when the animals are vocally active. Thus, sighting surveys combined with PAM using DIFAR sonobuoys can assist in discriminating vocally active whales from non-vocal ones. However, such sonobuoys are not easily accessible in South Africa. The presence or absence of a species in a particular area can be derived independently of the acoustic recording instrument from visual sighting surveys and from historic whale catches, assuming those mammals currently utilise the same areas as during whaling (although this can be biased by catch selectivity). The acoustic research effort from the previous IWC programmes is low (Figure 2.4), varies over the years, and is non-randomly distributed as research was focused in areas with high densities of whales (Figure 2.5). Consequently, a greater acoustic research effort is required in all the other IWC management areas.

The determination of marine mammal call rates and their variation with age, sex and season are still problematic. The detection range and source levels of many species are unknown and may include considerable variability. Thus, density estimation is difficult to determine from source levels, as they vary considerably between the three currently available Antarctic blue whale studies. Research to determine the vocal behaviour of Antarctic blue whales will answer questions about the diel, seasonal and annual variability of these marine mammals' calls and songs (Chapters 4-6).

Once call rates are determined, the relative amount of calling animals at a given time and location can be determined, as calling animals will be identified to an individual level through concurrent visual observations. The maximum ranges at which a marine mammal call can be detected are estimated based on factors that affect sound propagation, i.e. environmental factors (such as temperature and salinity) and bathymetric data. Therefore, the lack of such data limits such estimations. Oceanographic mooring, as well as conductivity/

temperature/depth (CTD) instruments and model data, can be used effectively to provide such environmental data around the South African coast for the duration of acoustic recordings (Chapter 5). Positional identification of individual marine mammals requires both source levels and transmission loss to be known to accurately determine the relative density of animals in a given area, as illustrated by the equations in Section 2.3.2.

The use of DIFAR hydrophones and arrays of hydrophones can enable the estimation of detection range, bearing and source levels of the sounds of marine mammals, although hydrophones must be calibrated regularly. The calibration of hydrophones used for collecting acoustic data is challenging and complicated, as this process cannot be conducted at sea easily, but needs laboratory conditions to produce reliable or robust outcomes. Miller *et al.* (2014c) present a relatively smooth method of calibrating the magnetic compass of the sonobuoy used for the real-time tracking of Antarctic blue whales *in situ*. The Institute for Maritime Technology (IMT) in South Africa has laboratory facilities for *ex situ* calibrations, and access to such facilities could facilitate an effective calibration process.

Acoustic instruments are expensive in South Africa as these are usually manufactured overseas, and greater capital investment is required in South Africa to purchase the equipment to conduct this kind of research. Despite the expenses of deployment, the relative cost-effectiveness of AAR systems' long-term monitoring means that such acoustic monitoring is a highly cost-beneficial technique. The use of existing infrastructure may reduce the cost of deployment (Van Opzeeland *et al.* 2014). For instance, hydrophones can be installed on existing South African oceanographic moorings (Chapter 5), and the acoustic data from the South African Navy's underwater acoustic surveillance hydrophone 'waterbug' can be used effectively for PAM of marine mammals. The deployment of more hydrophones in arrays around the coast of South Africa is recommended, and such deployments need to be aligned with the further development of human capacity in acoustic research in the South African region.

The seas of the world are becoming increasingly noisy as anthropogenic noise at sea is increasing dramatically (National Research Council, 2003; Hildebrand, 2009). For example, McDonald *et al.* (2006b) estimated an average increase rate of 2.5–3 dB per decade in ocean noise between 1965 and 2003 for the Northeast Pacific Ocean. Seismic surveys and other anthropogenic activities can result in the masking of sounds from marine mammals (Finneran *et al.* 2002). In turn, marine mammals may change their behaviour in response to the prevailing noise levels (McDonald *et al.* 2006b). Stricter marine laws are to be devised and implemented by the United Nations Convention on the Law of the Sea (UNCLOS) to combat the increasing noise levels in the ocean (Reeve, 2012). As AARs record ambient and anthropogenic noise across the frequencies of interest, monitoring such noise levels can provide up-to-date knowledge about the status of background and anthropogenic noise levels around the coast of South Africa.

Collaboration among researchers is fundamental and key to the future success in this field, as exemplified by the SORP Antarctic blue and fin whale Acoustic Trends Working Group (ATWG). The ATWG aims to establish simultaneous circum-Antarctic acoustic monitoring coverage through a Southern Ocean Hydrophone Network (SOHN) in the next decade, thus effectively reducing acoustic research costs to permit the density estimation of Antarctic blue and fin whales (Van Opzeeland *et al.* 2014). The PAM component of the SABWP forms an integral regional component of the SOHN.

2.5 Conclusion

The use of bioacoustics to study marine mammals is still in its infancy in South Africa, granting South African researchers an ideal opportunity to develop and apply established methods in South African coastal waters. This acoustic technique has great potential to study vocal marine animals that are difficult to observe or survey visually. More acoustic research on marine mammals is required in South Africa to fully understand the behaviour, distribution and migration of the region’s marine mammals. There are opportunities to extend passive acoustic research to other marine taxa to obtain useful data about these animals without disturbing the marine environment and ecosystem.

2.6 Acknowledgements

We would like to thank the IWC for providing us with the IWC's IDCR and SOWER cruise acoustic data. We thank the South African National Research Foundation and the South African National Antarctic Programme for funding the SABWP. Meredith Thornton and the 2013/14 Blue Whale Team are thanked for their outstanding technical assistance with the deployment of the Maud Rise AAR hydrophone. The authors thank Dr Ilse van Opzeeland, Karolin Thomisch and anonymous reviewers for their invaluable comments and suggestions for improvements to this chapter. Other members of the SORP ATWG are thanked for their support and encouragement towards the SABWP. Our sincere gratitude goes to Prof Peter Best for fruitful discussions and valuable suggestions to the SABWP.

2.7 References

André, M., Van der Schaar, M., Zaugg, S., Hoúegnigan, L., Sánchez, A. and Castell, J. 2011. Listening to the deep: live monitoring of ocean noise and cetacean acoustic signals. Marine Pollution Bulletin 63: 18–26.

Au, W.W.L. and Hastings, M.C. 2008. Principles of marine bioacoustics. New York: Springer.

Ballance, L.T. 2002. Cetacean ecology. In: Perrin, W.F., Wursig, B. and Thewissen, J.G.M. (eds) Encyclopedia of marine mammals. p. 208–214. California: Academic Press.

Bannister, J.L. 2002. Baleen whales, mysticetes. In: Perrin, W.F., Wursig, B. and Thewissen, J.G.M. (eds) Encyclopedia of marine mammals. p. 62–72. California: Academic Press.

Baumgartner, M.F., Fratantoni, D.M., Hurst, T.P., Brown, M.W., Cole, T.M., Van Parijis, S.M. and Johnson, M. 2013. Real-time reporting of baleen whale passive acoustic detections from ocean gliders. Journal of the Acoustical Society of America 134(3): 1814–1823.

Beamish, P. 1979. Behavior and significance of entrapped baleen whales. In: Winn, H.E. and Olla, B.L. (eds) Behavior of marine animals: current perspective in research. p. 291–309. New York: Plenum.

Best, P.B. 1993. Increase rates in severely depleted stocks of baleen whales. ICES Journal of Marine Science 50: 169–186.

Best, P.B. 1994. A review of the catch statistics for modern whaling in southern Africa, 1908−1930. Paper SC/44/O 16 (Revised). Report of the International Whaling Commission, 44: 467–85.

Best, P.B. 2007. Whales and dolphins of the Southern African subregion. Cape Town: Cambridge University Press.

Best, P.B. and Ross, G.J.B. 1989. Whales and whaling. In: Payne, A.I.L. and Crawford, R.J.M. (eds) Oceans of life of southern Africa. p. 315–338. Cape Town: Vlaeberg.

Blyth, E. 1859. On the great rorqual of the Indian Ocean, with notices of other cetals, and of the Syrenia or marine pachyderms. Journal of the Asiatic Society of Bengal 28: 481–498.

Bobbitt, A.M., Dziak, R.P., Stafford, K.M. and Fox, C.G., 1997. GIS analysis of oceanographic remotely-sensed and field observation data. Marine Geodesy, Special Issue: Marine and Coastal Geographic Information Systems 20(2): 153–161.

Boisseau, O., Gillespie, D., Leaper, R. and 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: 23–30.

Branch, T.A., Matsuoka, K. and Miyashita, T. 2004. Evidence for increases in Antarctic blue whales based on Bayesian modelling. Marine Mammal Science 20(4): 726–754.

Branch, T.A., Stafford, K.M., Palacios, D.M., Allison, C., Bannister, J.L., Burton, C.L.K., Cabrera, E., Carlson, C.A., Vernazzani, B.G., Gill, P.C., Hucke-Gaete, R., Jenner, K.C.S., Jenner, M.N.M., Matsuoka, K., Mikhalev, Y.A., Miyashita, T., Morrice, M.G., Nishiwaki, S., Sturrock, V.J., Tormosov, D., Anderson, R.C., Baker, A.N., Best, P.B., Borsa, P., Brownell, R.L., Childerhouse, S., Findlay, K.P., Gerrodette, T., Ilangakoon, A.D., Joergensen, M., Kahn, B., Ljungblad, D.K., Maughan, B., McCauley, R.D., McKay, S., Norris, T.F., Whale, O., Rankin, S., Samaran, F., Thiele, D., Van Waerebeek, K. and Warneke, R.M. 2007. Past and present distribution, densities and movements of blue whales (*Balaenoptera musculus*) in the Southern Hemisphere and northern Indian Ocean. Mammal Review 37(2): 116–175.

Buckland, S.T. and York, A.E. 2002. Abundance estimation. In: Perrin, W.F., Wursig, B. and Thewissen, J.G.M. (eds) Encyclopedia of marine mammals. p. 1–6. California: Academic Press.

Burmeister, H. 1871. Del Año 1871 (In Spanish). Boletin del Museo Publico de Buenos Aires 1871: 11–20.

Clapham, P.J., Young, S.B. and Brownell Jr, R.L. 1999. Baleen whales: conservation issues and the status of the most endangered populations. Mammal Review 29:35–60.

Clapham, P.J. and Baker, C.S. 2002. Modern whaling. In: Perrin, W.F., Wursig, B. and Thewissen, J.G.M. (eds) Encyclopedia of marine mammals. p. 1328–1332. California: Academic Press.

Cummings, W.C. and Thompson, P.O. 1971. Underwater sounds from the blue whale, *Balaenoptera musculus*. Journal of Acoustical Society of America 50(4): 1193–1198.

Double, M.C., Andrews-Goff, V., Jenner, K.C.S., Jenner, M-N., Laverick, S.M., Branch, T.A. and Gales, N.J. 2014. Migratory movements of pygmy blue whales (*Balaenoptera musculus brevicauda)* between Australia and Indonesia as revealed by satellite telemetry. PLoS ONE 9(4): e93578.

Dudzinski, K.M., Thomas, J.A. and Douaze, E. 2002. Communication. In: Perrin, W.F., Wursig, B. and Thewissen, J.G.M. (eds) Encyclopedia of marine mammals. p. 248–267. California: Academic Press.

Edds-Walton, P.L. 1997. Acoustic communication signals of mysticete whales. The International Journal of Animal Sound and its Recording. p. 8: 47–60.

Findlay, K., Thornton, M., Shabangu, F., Venter, K., Thompson, I. and Fabriciussen, O. 2014. Report of the 2013/14 South African Antarctic blue whale survey, 000° – 020° E. Paper presented to the Scientific Committee of the International Whaling Commission, Bled, Slovenia, SC/65b/SH01.

Finneran, J.J., Schlundt, C.E., Dear, R., Carder, D.A. and Ridgway, S.H. 2002. Temporary shift in masked hearing thresholds in odontocetes after exposure to single underwater impulses from a seismic watergun. Journal of the Acoustical Society of America 111: 2929–2940.

Frankel, A.S. 2002. Sound production. In: Perrin, W.F., Wursig, B. and Thewissen, J.G.M. (eds) Encyclopedia of marine mammals. p. 1126−1138. California: Academic Press.

Gavrilov, A.N., McCauley, R.D., Salgado-Kent, C., Tripovich, J. and Burton, C. 2011. Vocal characteristics of pygmy blue whales and their change over time. Journal of the Acoustical Society of America 130: 3651–3660.

Hildebrand, J.A. 2009. Anthropogenic and natural sources of ambient noise in the ocean. Marine Ecological Progress Series 395: 5–20.

Huang, T., Sun, L., Stark, J., Wang, Y., Cheng, Z., Yang, Q. and Sun, S. 2011. Relative changes in krill abundance inferred from Antarctic fur seal. PLoS ONE 6(11): e27331.

Ichihara, T. 1966. The pygmy blue whale, Balaenoptera musculus brevicauda, a new subspecies from the Antarctic. In: Norris, K.S. (ed) Whales, dolphins, and porpoises. p. 79–111. Berkeley-Los Angeles, CA: University of California Press.

Jefferson, T.A., Leatherwood, S. and Webber, M.A. 1993. FAO species identification guide. Marine mammals of the world. Rome: FAO.

Kelly, N., Miller, B., Peel, D., Double, M.C., De la Mare, W. and Gales, N. 2012. Strategies to obtain a new circumpolar abundance estimate for Antarctic blue whales: survey design and sampling protocols. Paper presented to the Scientific Committee of the International Whaling Commission, Panama City, Panama, SC/64/SH10.

Kenshalo, D.R. 1967. Sound orientation as seen by a psychologist. In: Busnel, R.G. (ed) Animal sonar systems: biology and bionics. p. 497–521. Jouy-en-Josas, 78. France: Laboratoire de Physiologie Acoustique.

Ketten, D.R. 1992. The marine mammal ear: specializations for aquatic audition and echolocation. In: Webster, D.B., Fay, R.R. and Popper, A.N. (eds) The evolutionary biology of hearing. p. 717–750. New York, NY: Springer-Verlag.

Ketten, D.R. 1994. Functional analyses of whale ears: adaptations for underwater hearing. I.E.E.E. Proceedings in Underwater Acoustics 1: 264–270.

Klinowska, M. 1991. Dolphins, porpoises and whales of the world: the IUCN red data book. Gland: IUCN – The World Conservation Union.

Kusel, E.T., Mellinger, D.K., Thomas, L., Marques, T.A., Moretti, D. and Ward, J. 2011. Cetacean population density estimation from single fixed sensors using passive acoustics. Journal of the Acoustical Society of America 129: 3610–3622.

Leaper, R. and Miller, C. 2011. Review management of Antarctic baleen whales amid past exploitation, current threats and complex marine ecosystems. Antarctic Science 1–27.

Leatherwood, S., Caldwell, D.K. and Winn, H.E. 1976. Whales, dolphins, and porpoises of the western North Atlantic: a guide to their identification. U.S. Department of Commerce, NOAA Technical Report NMFS, 396.

Linnaeus, C. 1758. System nature, 10th Edition (In Latin). Laurentii Salvii: Holmiae.

Ljungblad, D.K., Clark, C.W. and Shimada, H. 1998. A comparison of sounds attributed to pygmy blue whales (*Balaenoptera musculus brevicauda*) recorded south of the Madagascar Plateau and those attributed to 'true' blue whales (*Balaenoptera musculus*) recorded of Antarctica. Report of International Whaling Commission 48:439–442.

Lurton, X. 2002. An introduction to underwater acoustics: principles and applications. London: Springer.

Mackintosh, N.A. and Wheeler, J.F.G. 1929. Southern blue and fin whales. Discovery Reports I: 259–540.

Marques, T.A., Thomas, L., Ward, J., DiMarzio, N. and Tyack, P.L. 2009. Estimating cetacean population density using fixed passive acoustics sensors: an example with beaked whales. Journal of the Acoustical Society of America 125(4): 1982–1994.

Marques, T.A., Thomas, L., Martin, S., Mellinger, D., Ward, J., Moretti, D., Harris D. and Tyack, P. 2013. Estimating animal population density using passive acoustics. Biological Reviews 8:287–309.

McDonald, M.A. 2004. DIFAR hydrophones applied to whale research. Canadian Acoustics 32(2): 155–160.

McDonald, M.A., Calambokidis, J., Teranishi, A.M. and Hildebrand, J.A. 2001. The acoustic calls of blue whales off California with gender data. Journal of Acoustical Society of America 109(4): 1728–1735.

McDonald, M.A., Hildebrand, J.A. and Mesnick, S.L. 2006a. Biogeographic characterization of blue whale song worldwide: using song to identify populations. Journal of Cetacean Research and Management 8: 55–65.

McDonald, M.A., Hildebrand, J.A. and Wiggins, S.M. 2006b. Increases in deep ocean ambient noise in the Northeast Pacific west of San Nicolas Island, California. Journal of the Acoustical Society of America 120: 711–718.

McDonald, M.A., Hildebrand, J.A. and Mesnick, S.L. 2009. Worldwide decline in tonal frequencies of blue whale songs. Endangered Species Research 9: 13–21.

Medwin, H. and Clay, C.S. 1998. Fundamentals of acoustical oceanography. San Diego: Academic Press.

Mellinger, D.K. and Barlow, J. 2003. Future directions for marine mammal acoustic surveys: stock assessment and habitat use. Workshop held in La Jolla, California, 20−22 November 2002. Technical report, NOAA/PMEL, 2557. Seattle: NOAA/PMEL.

Mellinger, D.K. and Clark, C.W. 2003. Blue whale (*Balaenoptera musculus*) sounds from the North Atlantic. Journal of the Acoustical Society of America 114(2): 1108–1119.

Mellinger, D.K., Thode, A.M. and Martinez, A. 2003. Passive acoustic monitoring of sperm whales in the Gulf of Mexico, with a model of acoustic detection distance. p. 493–501. In: McKay, M. and Nides, J. (eds.) Proceedings of the Twenty-first Annual Gulf of Mexico Information Transfer Meeting, January 2002. U.S. Department of the Interior, Minerals Management Service, Gulf of Mexico OCS Region, New Orleans, Los Angeles.

Mellinger, D.K., Stafford, K.M., Moore, S.E., Dziak, R.P. and Matsumoto, H. 2007. An overview of fixed passive acoustic observation methods for cetaceans. Oceanography 20(4): 36–45.

Miller, B.S., Kelly, N., Double, M.C., Childerhouse, S.J., Laverick, S. and Gales, N. 2012. Cruise report on SORP 2012 blue whale voyages: development of acoustic methods. Paper presented to the Scientific Committee of the International Whaling Commission, Panama City, Panama, SC/64/SH11.

Miller, B.S., Leaper, R., Calderan, S., Collins, K. and Double, M. 2014a. Source levels of Antarctic blue whale calls measured during the 2013 Antarctic blue whale voyage: preliminary results. Paper presented to the Scientific Committee of the International Whaling Commission, Bled, Slovenia, SC/65b/SH11.

Miller, B.S., Collins, K., Barlow, J., Calderan, S., Leaper, R., McDonald, M., Ensor, P., Oleson, P., Olavarria, C. and Double, M.C. 2014b. Blue whale vocalizations recorded around New Zealand: 1964–2013. Paper presented to the Scientific Committee of the International Whaling Commission, Bled, Slovenia, SC/65b/Forinfo26.

Miller, B.S., Gedamske, J., Calderan, S., Collins, K., Johnson, C., Miller, E., Samaran, F., Smith, J. and Double, M.C. 2014c. Accuracy and precision of DIFAR localisation systems: calibrations and comparative measurements from three SORP voyages. Paper presented to the Scientific Committee of the International Whaling Commission, Bled, Slovenia, SC/65b/SH08.

Mobley, C.D. 1994. Light and water: radiative transfer in natural waters. San Diego: Academic Press.

National Research Council, 2003. Ocean noise and marine mammals. Washington, DC: National Academies Press.

Nicol, S., Worby, A. and Leaper, R. 2008. Changes in the Antarctic sea ice ecosystem: potential effects on krill and baleen whales. Marine and Freshwater Research 59: 361–382.

Oleson, E.M., Calambokidis, J., Barlow, J. and Hildebrand, J.A. 2007. Blue whales visual and acoustic encounter rates in the Southern California Bight. Marine Mammal Science 23(3): 574–597.

Peel, D., Miller, B.S., Kelly, N., Dawson, S., Slooten, E. and Double, M. 2014. A simulation study of acoustic-assisted tracking of whales for mark-recapture surveys. PLoS ONE 9(5): e95602.

Purves, P.E. 1967. Anatomical and experimental observations on the cetacean sonar system. In: Busnel, R.G. (ed) Animal sonar systems: biology and bionics. p. 197–270. Jouy-en-Josas, 78. France: Laboratoire de Physiologie Acoustique.

Rankin, S., Ljungblad, D., Clark, C. and 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, Antarctica. Journal of Cetacean Research and Management 7: 13–20.

Reeve, L.L.N. 2012. Of whales and ships: impacts on the great whales of underwater noise pollution from commercial shipping and proposals for regulation under international law. Ocean and Coastal Law Journal 18: 127–166.

Reeves, R.R., Clapham, P.J. Brownell, R.L. Jr. and Silber, G.K. 1998. Recovery plan for the blue whale (*Balaenoptera musculus*). Silver Spring, MD: National Marine Fisheries Service.

Rice, D.W. 1998. Marine mammals of the world: systematics and distribution. Society for Marine Mammalogy Special Publication No. 4. Lawrence, KS: Allen Press.

Rossing, T.D. 2007. Springer handbook of acoustics. New York, NY: Springer Science and Business Media.

Samaran, F., Guinet, C., Adam, O., Motsch, J-F. and Cansi, Y. 2010a. Source level estimation of two blue whale subspecies in southwestern Indian Ocean. Journal of Acoustical Society of America 127: 3800–3808.

Samaran, F., Adam, O. and Guinet, C. 2010b. Detection range modelling of blue whale calls in South Western Indian Ocean. Applied Acoustics 71: 1099–1106.

Samaran, F., Stafford, K.M., Branch, T.A., Gedamke, J., Royer, J-Y., Dziak, R.P. and Guinet, C. 2013. Seasonal and geographic variation of southern blue whale subspecies in the Indian Ocean. PLoS ONE 8(8):e71561.

Sears, R. 2002. Blue whale *Balaenoptera musculus*. In: Perrin, W.F., Wursig, B. and Thewissen, J.G.M. (eds) Encyclopedia of marine mammals. p. 112–116. California, CA: Academic Press.

Shabangu, F.W., Ona, E. and Yemane, D. 2014. Measurements of acoustic attenuation at 38 kHz by wind-induced air bubbles with suggested correction factors for hull-mounted transducers. Fisheries Research 151: 47–56.

Simmonds, E.J. and MacLennan, D.N. 2005. Fisheries acoustics: theory and practice, 2nd edition. Oxford: Blackwell.

Širovic, A., Hildebrand, J.A. and Wiggins, S.M. 2007. Blue and fin whale call source levels and propagation range in the Southern Ocean. Journal of Acoustical Society of America 122: 1208–1215.

Širovic, A., Hildebrand, J.A., Wiggins, S.M. and Thiele, D. 2009. Blue and fin whale acoustic presence around Antarctica during 2003 and 2004. Marine Mammal Science 25: 125–136.

Stafford, K.M., Bohnenstiehl, D.R., Tolstoy, M., Chapp, E., Mellinger, D.K. and Moore, S.E. 2004. Antarctic-type blue whale calls recorded at low latitudes in the Indian and eastern Pacific Oceans. Deep Sea Research Part 1: Oceanographic Research Papers 51: 1337–1346.

Swift, R. 2004. The physics of underwater sound. In: Simmonds, M., Dolman, S. and Weilgart, L. (eds) Oceans of noise: a whale and dolphin conservation society (WDCS) science report. p. 11–24. Wiltshire: WDCS.

Thode, A., Mellinger, D.K., Stienessen, S., Martinez, A. and Mullin, K. 2002. Depth-dependent acoustic features of diving sperm whales (*Physeter macrocephalus*) in the Gulf of Mexico. Journal of the Acoustical Society of America 112(1): 308–321.

Thomas, L. and Marques, T.A. 2012. Passive acoustic monitoring for estimating animal density. Acoustics Today l8(3): 35–44.

Thompson, P.O., Findley, L.T., Vidal, O. and Cummings, W.C. 1996. Underwater sounds of blue whales, *Balaenoptera musculus*, in the Gulf of California, Mexico. Marine Mammal Science 12(2): 288–92.

Tyack, P.L. 1981. Interactions between singing Hawaiian humpback whales and conspecifics nearby. Behavioral Ecology and Sociobiology 8: 105–116.

Tyack, P.L. 1998. Acoustic communication under the sea. In: Hopp, S.L., Owren, M.J. and Evans, C.S. (eds) Animal acoustic communication: sound analysis and research methods. p. 163–214. New York, NY: Springer-Verlag.

Tyack, P.L. 1999. Communication and cognition. In: Reynolds J.E. III and Rommel, S.A. (eds). Biology of marine mammals. p. 287–323. Washington, DC: Smithsonian Institution.

Tyack, P.L. 2011. Using digital acoustic recording tags to detect marine mammals on navy ranges and study their responses to naval sonar. SERDP Project RC-1539.

Tyack, P.L. and Miller, H.M. 2002. Vocal anatomy, acoustic communication and echolocation. In: Hoelzel, A.R. (ed) Marine mammal biology: an evolutionary approach. p. 142–184. Oxford: Blackwell Science.

Urick, R.J. 1963. Low-frequency sound attenuation in the deep ocean. Journal of the Acoustical Society of America 35(9):1413–1422.

Urick, R.J. 1983. Principles of underwater sound, 3rd edition. New York, NY: McGraw Hill.

Van Opzeeland, I.C., Samaran, F., Stafford, K.M., Findlay, K., Gedamke, J., Harris, D. and Miller, B.S. 2014. The Southern Ocean Hydrophone Network (SOHN): circum-Antarctic passive acoustic monitoring of Antarctic blue and fin whales. Paper presented to the Scientific Committee of the International Whaling Commission, Bled, Slovenia, SC/65b/Forinfo10.

Van Parijs, S.M., Clark, C.W., Sousa-Lima, R.S., Parks, S.E., Rankin, S., Risch, D. and Van Opzeeland, I.C. 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.

Xiaohong, S., Haiyan, W., Yuzhi, Z. and Ruiqin, Z. 2012. Adaptive technique for underwater acoustic communication. In: Bourennane, S. (ed) Underwater acoustics 59–74. Rijeka: InTech.

Zimmer, W.M.X. 2011. Passive acoustic monitoring of cetaceans. Cambridge: Cambridge University Press.

Chapter 3: Overview of the IWC SOWER cruise circumpolar acoustic survey data and analyses of Antarctic blue whale calls within the dataset

Accepted at the Journal of Cetacean Research and Management: Shabangu, F.W., Stafford, K.M., Findlay, K.P., Rankin, S., Ljungblad, D., Tsuda, Y., Morse, L., Clark, C.W., Kato, H., and Ensor, P.

This Chapter describes the extensive database archival process required prior to the analyses of the data in the following Chapter.

Abstract

The International Whaling Commission (IWC) carried out blue whale research components within its annual austral summer Southern Ocean Whale and Ecosystem Research (SOWER) cruises between 1996 and 2010. Over 700 sonobuoys were deployed to record blue whale vocalizations during 11 Antarctic and three low latitude blue whale cruises off Australia, Madagascar and Chile. The recorded acoustic files from these deployments were collated and reviewed to develop a database of both the digital acoustic files and the associated deployment station metadata of 7,486 acoustic files from 484 stations. Acoustic files were analysed using the automated detection template and visual verification methods. We found a significant difference between the total number of acoustic recording hours (2,481) reported for these cruises (in the associated cruise reports) and the currently available number of acoustic recording hours (1,541). Antarctic blue whale vocalizations (9,315 and 24,902 D- and Z-calls) were detected on 4,183 of the 7,486 acoustic files. December had the lowest call rates whilst January and February yielded high call rates. Although the majority (63%) of the sonobuoys were deployed between 18h00 and 06h00 the following day, most calls (62%) were detected during observation periods between 06h00 and 18h00. The recently described southeastern Pacific 2 song of the Chilean pygmy blue whale was also found from Chilean blue whale cruise acoustic data. The difference between the available and reported data are of

concern and a reconciliation of these and any future IWC acoustic data is strongly recommended.

3.1 Introduction

There are two recognized subspecies of Southern Hemisphere blue whale: the ‘Antarctic’ blue whale (*Balaenoptera musculus intermedia,* Burmeister, 1871) and the ‘pygmy’ blue whale (*B m brevicauda,* Ichihara, 1966). The Indian Ocean blue whale *B. m. indica* (Blyth, 1859) is considered an approximate synonym of *B. m. brevicauda* (Reeves *et al.* 1998; Rice, 1998). Differentiation of the sub-species at sea is difficult and the IWC therefore initiated a programme of passive acoustic monitoring and recording in the presence of blue whales to determine whether the different subspecies might produce distinctly different sounds.

Blue whales whaled to near extinction by the modern whaling (1904-1973); with catches of 360,000 individuals from the Southern Hemisphere. The 1996 estimate of their population size 1,700 (860–2,900) remains at less than 1% of their pre-exploitation abundance of 239,000 (Branch *et al.* 2004). The recovery and population status after protection from whaling in 1964 has remained challenging to estimate from visual sighting surveys due to the current low abundance (Branch *et al.* 2007) and wide winter dispersal of the species. However, the population is increasing at an average rate of 8.2% per annum (Branch *et al.* 2004; Thomas *et al.* 2015). The recovery statuses of pygmy blue whale populations are unknown. Population assessment must consider sub-species to allow for different rates in recovery (IWC, 1995); however, field identification of sub-species based on visual observation is considered unreliable (Kato *et al.* 1995). Within the SOWER programme, the IWC considered alternative methodologies for blue whale sub-species identification, including surface expression of dive, relative body proportion, and blow-hole morphology (Ichihara, 1996; Donovan, 1984; Kato *et al.* 2002) and passive acoustic monitoring (Ljungblad *et al.* 1998).

Some of the earliest acoustic studies of blue whales suggested that blue whale sounds, in particular their various songs as recorded in different regions and ocean basins, were distinctly different from each other (Cummings and Thompson, 1977; Thompson *et al.* 1996; McDonald *et al.* 2006). Acoustic monitoring of blue whale sounds might provide a means of determining sub-species in the field (Ljungblad *et al.* 1997; Ljungblad *et al.* 1998; Stafford *et al.* 1999, 2001) in much the same way that humpback whale songs can be used to identify and distinguish between populations (Payne and Guinee, 1983).

Sounds recorded in the presence of blue whales are basically of two forms: calls and songs. Blue whale D-calls typically occur as single or short sequences of frequency-modulated (FM) sounds in the 22-106 Hz frequency band, last ca 2-6 s, and are always downswept but sometimes start with an up-down frequency inflection (Thompson *et al.* 1996; Mellinger and Clark, 2003; Rankin *et al.* 2005; Ljungblad and Stafford, 2005; Oleson *et al.* 2007). In contrast, songs are composed of ca. 1-4 stereotyped sounds (i.e. notes), that have been reported as 1-2 s amplitude-modulated (AM), 1-2 s pulses; or long-duration (5-25 s), FMs, with and without harmonics. Song notes are organized into phrases that are repeated in a patterned sequence lasting ca. 10-20 mins (i.e. a song), which is sung repeatedly (i.e. song bout) over periods of hours to many days (Cummings and Thompson, 1971; Edds, 1982; Thompson and Friedl, 1982; Thompson *et al.* 1996; Alling *et al.* 1991; Stafford *et al.* 1999; Stafford *et al.* 2001; Clark and Gagnon, 2002; Mellinger and Clark, 2003; Rankin *et al.* 2005; McDonald *et al.* 2006). D-calls have been reported for both males and females, while to date all identified singers have been males (McDonald *et al.* 2001; Oleson *et al.* 2007).

Antarctic blue whales and pygmy blue whales in the Southern Hemisphere exhibit geographic variation in their songs (Ljungblad *et al.* 1997; Clark and Fowler, 2001; McDonald *et al.* 2006; Samaran *et al.* 2010a; Stafford *et al.* 2011). The songs recorded from Antarctic blue whales consist of patterned sequences of tonal sounds composed of three distinct parts; an 8 – 12s tone centered at 28 Hz (28-Hz component), a 2 s FM downsweep, and a 3-6 s tone centered at 18 Hz (Ljungblad *et al.* 1998). Subsequent to IWC SOWER studies, there has been a documented decrease in the tonal frequency of the first part of the song to between 26 and 27 Hz (Gavrilov *et al.* 2012; Ward *et al.* 2017). This contrasts with the song of Southern Hemisphere pygmy blue whales, which at least 6 different songs have been described to date that consist of 2-4 units including frequency- and amplitude-modulated notes (Ljungblad *et al.* 1998; McCauley *et al.* 2000; Samaran *et al.* 2010a; Stafford *et al.* 1999, 2011; Buchan *et al.* 2014; Miller *et al.* 2014).

Dedicated research effort directed at Antarctic blue whales in the Southern Ocean was carried out by the IWC SOWER programme conducted from 1996 to 2010. The IWC SOWER was preceded by the IWC's International Decade of Cetacean Research (IWC IDCR) programme that ran from 1978 to 1995. The IWC SOWER programme included a blue whale research component that centred on both the evaluation of acoustic techniques for their assessment, and identifying criteria for distinguishing the Antarctic and pygmy blue whales in the field (Donovan *et al.* 1996). Although the IWC SOWER programme was conducted within all of the six IWC Management Areas in the Southern Ocean (Donovan, 1991): Area I (120°W-60°W), Area II (60°W-0°), Area III (0°-70°E), Area IV (70°E-130°E), Area V (130°E-170°W) and Area VI (170°W-120°W) much of the blue whale research centred on Area III.

The blue whale component of the IWC SOWER cruises included video, behavioural notes, photographs, biopsy samples, and acoustic recordings of blue whales that can be integrated to learn more about the behavioural ecology of blue whales. This included, but was not limited to, determining the sex of vocal whales (by combining biopsy results with recordings of localized whales), estimating the proportion of calling whales in a region (by comparing the number of whales seen with the number heard) and comparing the types of sounds recorded in association with observed behaviours. Finally, although blue whales were the primary targets of acoustic monitoring, the data collected included acoustic detections from other species, including other baleen whales, killer whales (*Orcinus orca*), sperm whales (*Physeter* *macrocephalus*) and crabeater (*Lobodon carcinophaga*) and leopard (*Hydrurga leptonyx*) seals.

The South African Blue Whale Project (SABWP) was aimed at estimating the relative abundance, distribution and seasonal movements of Antarctic blue whales within the South Eastern Atlantic Ocean including through investigation of seasonal call rates (Findlay *et al.* 2012; Shabangu and Findlay, 2014- Chapter 2). The SABWP applied for and received permission to analyse the IWC SOWER Antarctic and low latitude blue whale cruise acoustic data from 1996/1997 through 2008/2009 in 2013. This paper summarises the acoustic data collection during the circumpolar IWC SOWER Antarctic cruises and compilation of a database of the resultant data from these cruises.

3.2 Materials and methods

3.2.1 Field recordings

Acoustic data were collected on board the research vessels *Shonan Maru*, (SM) and *Shonan Maru* No. 2, (SM2) during 9 IWC SOWER cruises in the austral summers between 1996 and 2009, with opportunistic recordings obtained during an additional 3 cruises in the Southern Ocean in 1996/1997, 1997/1998 and 2000/2001 (Table 3.1, Figure 3.1). These cruises in both the Antarctic and in low latitude regions have been fully described by Branch *et al.* (2007) and Kelly *et al.* (2012) whilst detailed descriptions of survey methodology are provided in the annual cruise reports (Ensor *et al.* 1997, 1998, 1999, 2000, 2001, 2002, 2003, 2004, 2005, 2006 2007, 2008, 2009; Kato *et al.* 1996; Ljungblad *et al*,. 1998; Findlay *et al.* 1998; Sekiguchi *et al.* 2010). Sonobuoys were deployed on acoustic stations in close proximity to sighted blue whales and fin whales during directed research on these species, but were otherwise deployed while drifting at night.

Table 3.1. Summary and comparison of available and reported acoustic data associated with Antarctic blue whale vocalization from the IWC SOWER cruises. Values in brackets refer to those reported in the cruise reports. RVs used: *Shonan Maru* (SM), *Shonan Maru No. 2* (SM2) and *Kaiko Maru* (KM). Only the acoustic recording data are presented here. The species detected include BL = blue whales (*Balaenoptera musculus*), PBL = pygmy blue whales (*Balaenoptera musculus brevicauda*), FW = fin whales (*Balaenoptera physalus*), RW = southern right whale (*Eubalaena australis*), HW = humpback whales (*Megaptera novaeangliae*), KW = killer whale (*Orcinus orca*), SW = sperm whale (*Physeter macrocephalus*), and SE = seals (Pinniped). There was no acoustic component during the 2000/2001, 2004/2005, and the 2009/2010 cruises.

Cruise Year	RV	Recording dates	Total hours recorded	Number of sonobuoys	Hydro-phones	IWC Area	Species reported	Reference
1996/1997	SM	15 Jan- 04 Feb 1997	42.85 (59.73)	3 (6)	9 (10)	II	BL, PBL	Ensor *et al.* (1997)
	SM2	08-12 Feb 1997	12.42 (12.00)	4 (3)	0 (0)	II		
1997/1998	SM	-	0 (17.32)	0 (2)	0 (13)	II	BL	Ensor *et al.* (1998)
	SM2	29 Jan 1998	5.00 (26.40)	2 (12)	0 (1)	II		
1998/1999	SM	08 Jan-23 Feb 1999	190.10 (241.96)	98 (50)	0 (7)	III and IV	BL, SP, KW, FW, HW, SE, BN, HG	Ensor *et al.* (1999)
	SM2	13 Jan-21 Feb 1999	30.53 (235.84)	11 (35)	0 (11)	III and IV		
1999/2000	SM	14 Jan-12 Feb 2000	33.62 (151.5)	10 (30)	0 (0)	I and II	BL, SP, KW, FW, HW, SE, UN	Ensor *et al.* (2000)
	SM2	14 Jan-13 Feb 2000	164.70 (177.8)	50 (51)	0 (0)	I and II		
2000/2001	SM	12 Jan 2001	0 (2.63)	0 (0)	0 (1)	V, VI and I	none	Ensor *et al.* (2001)
	SM2	-	0 (0)	0 (0)	0 (0)	V, VI and I		
2001/2002	SM	31 Dec 2001-23 Jan 2002	64.30 (117)	17 (26)	3 (8)	V	BL, SP, KW, HW, SE	Ensor *et al.* (2002)
	SM2	-	0 (118.5)	0 (7)	0 (20)	V		
2002/2003	SM	23 Dec 2002-24 Feb 2003	120.17 (271.1)	26 (39)	7 (16)	V	BL, SP, KW, FW, HW, SE, UN	Ensor *et al.* (2003)
	SM2	22 Dec 2002-24 Feb 2003	44.95 (162.25)	23 (42)	0 (2)	V		
2003/2004	SM	26 Dec 2003-26 Feb 2004	68.00 (106)	18 (26)	5 (18)	V	BL, SP, KW, HW, SE	Ensor *et al.* (2004)
	SM2	26 Dec 2003-28 Feb 2004	142.23 (136)	28 (28)	12 (12)	V		
2004/2005	SM & SM2	-	0 (0)	0 (0)	0 (0)	III	none	Ensor *et al.* (2005)
2005/2006	SM2	23 Dec-15 Feb 2006	231.40 (264)	127 (127)	0 (0)	III	BL, SP, KW, FW, SE, UN	Ensor *et al.* (2006)
2006/2007	SM2	29 Dec 2006-08 Feb 2007	76.32 (87)	51 (55)	0 (0)	III	BL, SP, FW, SE	Ensor *et al.* (2007)
2007/2008	SM2	26 Dec 2007-13 Feb 2008	251.77 (251)	59 (71)	0 (0)	IV	BL, SP, FW, RW, KW, SE, UN	Ensor *et al,* (2008)
2008/2009	SM2	21 Jan-09 Feb 2009	40.00 (43.38)	23 (25)	0 (0)	IV	BL, SP, FW	Ensor *et al.* (2009)
2009/2010	KM	-	0 (0)	0 (0)	0 (0)	IV	none	Sekiguchi *et al.* (2010)
Total			**1,518 (2,481)**	**550 (635)**	**36 (119)**			

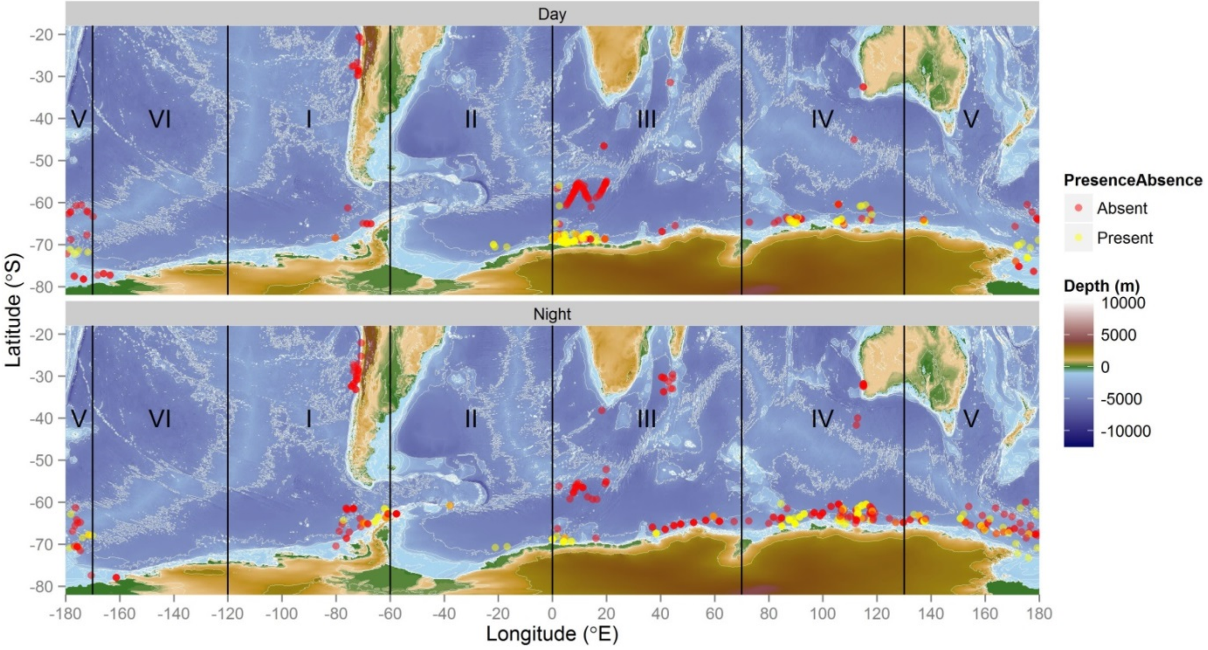


Figure 3.1. Distribution of IWC SOWER sonobuoy deployments showing the presence/absence Antarctic blue whale calls over various depths of the Antarctic Peninsula and the low latitudes. The six "outlying" sonobuoys in Area VI are from three stations of the 2003/2004 *SM*2 cruise supposedly deployed in Area V.

The primary acoustic recording method used expendable DiFAR (Direction Finding and Ranging) sonobuoys (Spartan Electronics Model AN/SSQ53D DIFAR). A modified reusable AN/SSQ 57A Sonobuoy (fixed 27.4 m (90 ft) hydrophone cable) and a fixed hydrophone with a preamp and 305 m (1000 ft) of cable were also available for recordings while the ship was drifting. These "Donobuoys" could be retrieved and recharged for redeployment. No intercalibrations were conducted between different listening systems used nor were individual unit calibrated before surveys.

The sonobuoy radio signal was received via the ship antenna, which was coupled to an ICOM IC-R100 single channel receiver that had been modified to extend its audio bandwidth. This output was connected to a Sony DAT TCD-D7 recorder (flat frequency response from 5 Hz to 24 kHz) or a Sony mini-disk MZ-R700 recorder (frequency response 20 Hz - 20 kHz ± 3 dB). Recordings were later digitized to a Sony PCG-FX120 computer (sample rate 48 kHz) using the software program Ishmael (Mellinger, 2001). As opportunity allowed, recordings were monitored visually using a scrolling spectrographic display in Ishmael or Raven

(Bioacoustics Research Program, 2008) and often aurally using headphones. The spectrographic display characteristics varied by user, but in general were selected to allow for detection of very low frequency sounds associated with blue or fin whales (< 200 Hz). Not all recordings were monitored to detect sounds from other species (e.g., sounds > 200 Hz). There may therefore be additional acoustic recordings of other species in the existing, but unreviewed, data.

When possible, DiFAR processing provided bearings to sounds. DiFAR signal processing was performed using an automatic Matlab function within Ishmael that executes a series of commands for de-multiplexing the DiFAR signal (software developed by Greeneridge Sciences, Inc) and determines the bearing to a sound source. DiFAR was not always available in real-time for surveys although on occasion it was used to obtain bearings to animals in real-time, and extensive post-cruise analysis was performed on a subset of these DiFAR data (see Rankin *et al.* 2005). During the 2001/2002 cruise, the paucity of recording media necessitated recording at the lowest possible sampling rate to maximize the recording time (with a sample rate of 32 kHz, the frequency response of the Sony TCD-D7 was 20 – 14,500 Hz ± 1 dB). This eliminated the multiplexed DiFAR signal, so bearings could not be obtained for these data.

Acoustic monitoring and recording durations at stations ranged between 5 minutes and 17 hours. For the purposes here, acoustic monitoring is defined here as when the underwater environment was acoustically monitored (listened to using headphones or viewed on a spectrogram without recording in ISHMAEL (Mellinger, 2002) or Raven (Bioacoustics Research Program, 2013). Acoustic recording, on the other hand, is defined as when encountered blue whale sounds were recorded and archived for future use.

All acoustic stations were described by an acoustic record form which included the monitoring and/or recording times. Acoustic recordings were made over short intervals although animal calls were monitored for a longer time period (Ensor *et al.* 1997, 1998, 1999, 2000, 2001, 2002, 2003, 2004, 2005, 2006 2007, 2008, 2009; Kato *et al.* 1996; Findlay *et al.* 1998; Ljungblad *et al.* 1998). In some few cases, marine mammal vocalizations were recorded but not documented on the acoustic record form. Prior to 2005, recorded acoustic files were logged at hourly intervals and were saved in an Audio Interchange File Format (AIFF) at a 16-bit encoding with the majority of the files having two channels. From 2005 and onwards, the sampling interval was decreased to 10 minutes and sound file type was changed from AIFF to Waveform Audio File format (WAV) at a 16-bit signed encoding.

3.2.2 Database compilation

All the currently available IWC SOWER acoustic recording files (including duplicates) amounting to 286 gigabytes were sourced from archives held by the Cornell University Laboratory of Ornithology or from individual cruise participants. The acoustic recording files from the low latitudes; i.e. the Australia, Madagascar and Chile blue whale cruises, amounted to only 3.31 GB, whilst the remainder were largely from south of 40°S. Spatial and temporal metadata of the observed stations were extracted from the cruise reports (Ensor *et al.* 1997, 1998, 1999, 2000, 2001, 2002, 2003, 2004, 2005, 2006 2007, 2008, 2009; Kato *et al.* 1996; Findlay *et al.* 1998; Ljungblad *et al.* 1998; Sekiguchi *et al.* 2010). Acoustic data forms and the associated sightings forms were sourced from the IWC Secretariat. The reconciled acoustic database and all metadata are currently held at Mammal Research Institute Whale Unit of the University of Pretoria.

Received acoustic data files were archived in the following file and folder format. Folder (Cruise Year and Region), sub-folder (Vessel), sub-folder (Tape or Hard-drive) and File (acoustic file). A corresponding Microsoft Excel database was designed to include these fields for each acoustic file. For example, the database entries for these fields for an acoustic file from the 2000 Antarctic *Shonan Maru* cruise included: 2000 Antarctic (Cruise Year and Region), SM1 (Vessel), Tape 01 (Tape or Hard Drive number), and SM1_000114-000000.aif (acoustic file). Once these data had been captured, duplicates and empty folders were identified and deleted from the working database. Thereafter the date, time and the location (latitude and longitude) data of each station were derived from the cruise reports and the acoustic record forms and were merged with the acoustic file database to complete the properties of each acoustic station. File duration, the visual presence or absence of blue whales and the determined total recording time (which comprised a number of files at each station) were thereafter entered into the database.

Records were categorized to daytime/night time based on their recording times depicted on the file names with daytime designated as 06h00-18h00 and night time designated as 18h00-06h00 (although not daylight schedules in the Antarctic means that this in reality reflects whether the vessel was engaged in sighting survey operations between 06h00 and 18h00 rather than natural light regimes). The visual survey operations during the daylight hours (06h00 to 18h00) meant that acoustic stations were biased towards the night period, and daytime acoustic stations were biased towards deployments in association with whale groups. Acoustic data were further grouped by IWC Management Area. Data fields were later added to the dataset to include numbers and rates of D- and Z-calls detected at each station once the data analyses had been completed. The final spreadsheet dataset contained: cruise year, IWC Management Area, research vessel, date (year, month and day), tape/sonobuoy number, station number, file name, acoustic file type, time of the day, file duration, blue whale presence/absence, station total recording duration, station position (latitude, longitude) and a comments field (Table 3.2).

Table 3.2. Example of the final database content.

Field	Example
Cruise (Year and Region)	2007/2008 Antarctic Cruise
Research vessel	SM2
Date	12 February 2008
Tape/sonobuoy number	SB 59
IWC Management Area	IV
Station number	46
File name	SOWERD-080212-000000
Acoustic file type	WAV
Time of the day	Night
File duration (hr)	8.08
Blue whale presence/absence	Present
Station total recording duration (hr)	8.08
Station position (latitude, longitude)	-64.27, 105.59
Comments	Faint calls

3.2.3 Database analyses

Acoustic data were investigated and characterised using the Raven Pro software (Bioacoustics Research Program, 2013). Antarctic blue whale call detection templates (Figure 3.2) were created and applied to all acoustic files in eXtensible Bio-Acoustic Tool (XBAT) software (Figueroa, 2006) operated on the MATLAB R2014a platform (MathWorks Inc, 2014). The non-decimated acoustic files from 2003/2004 through 2008/2009 sampled at 48 kHz were decimated to 1 kHz using custom-written MATLAB script to improve the frequency resolution and the fast Fourier transform (FFT) length. All call detections were verified by manual visual verification method (more details about the detector performance are given in Shabangu et al. (2017- Chapter 4), and visually scrutinised for pygmy blue whale calls (Figure 3.3). Sonobuoy deployments from Australia, Chile and Madagascar are not considered in our analyses as they do not contain Antarctic blue whale calls.

Statistical data analyses and plotting of the call data were performed in the R statistical software package (R Development Core Team, 2015), using script editor RStudio version 0.99.473 (RStudio Team, 2015). The call data were standardised by survey effort (recording duration) to calls per hour, which defines call rates. Pearson’s correlation coefficients (r) were estimated to measure the linear correlation (dependence) between variables, while a two-sample Kolmogorov-Smirnov test (KS test) was used to determine if datasets differed significantly.

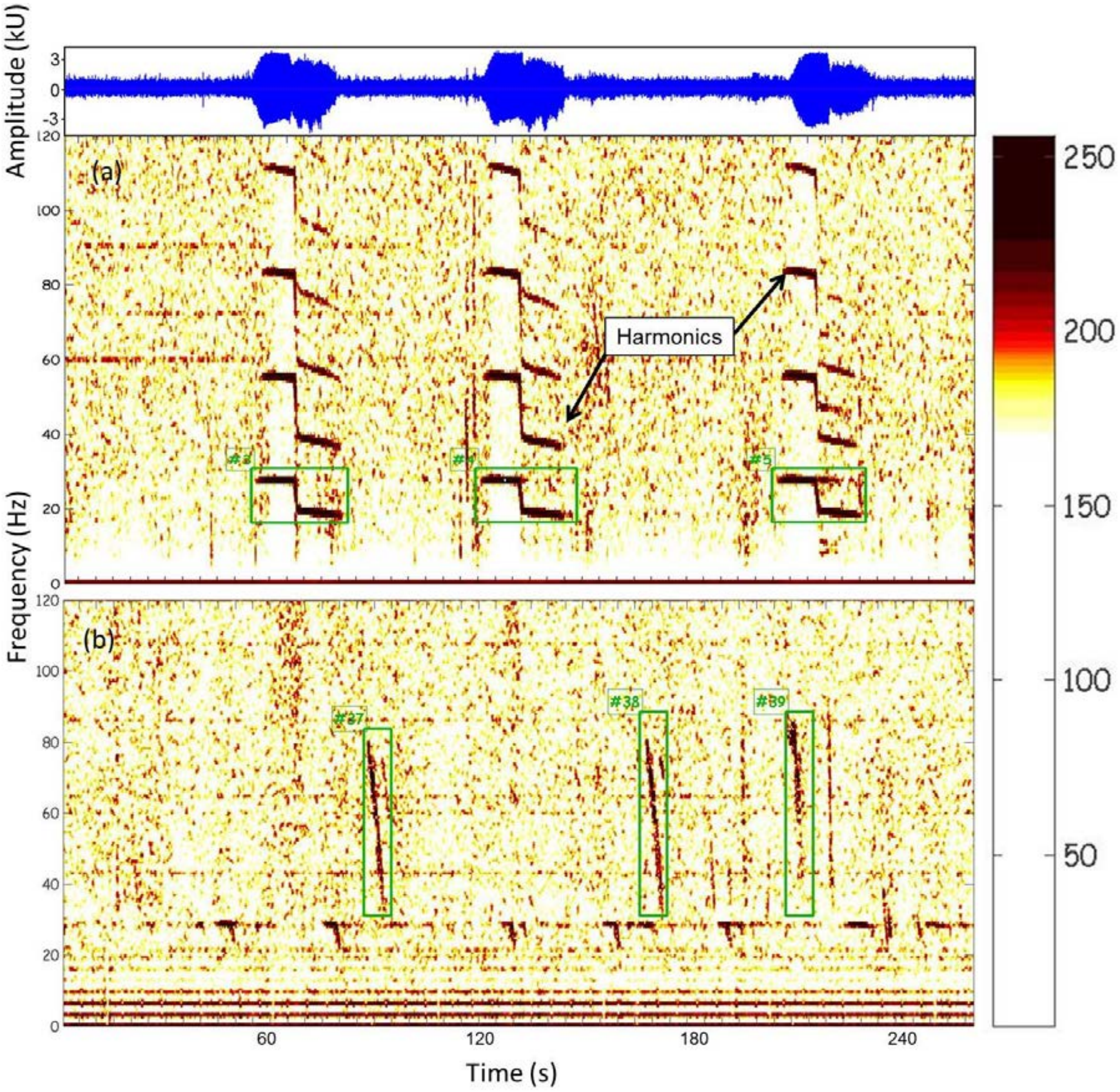


Figure 3.2. Spectrograms of three auto-detected Antarctic blue whale (a) Z- and (b) D-calls (in green boxes). Z-calls and their amplitudes (top panel, kU is kilo unit) were recorded during the 2001/02 IWC SOWER cruise at -64.57°S and 137.68°E, and D-calls were recorded during the 1996/97 IWC SOWER cruise at 68°48’S and 00°06’E. The hash (#) number on the top left corner of each box refers to the call-type auto count number for that particular acoustic file. Spectrogram parameters: frame size 1.28 s, 50% overlap, FFT size 1650 points, Hanning window.

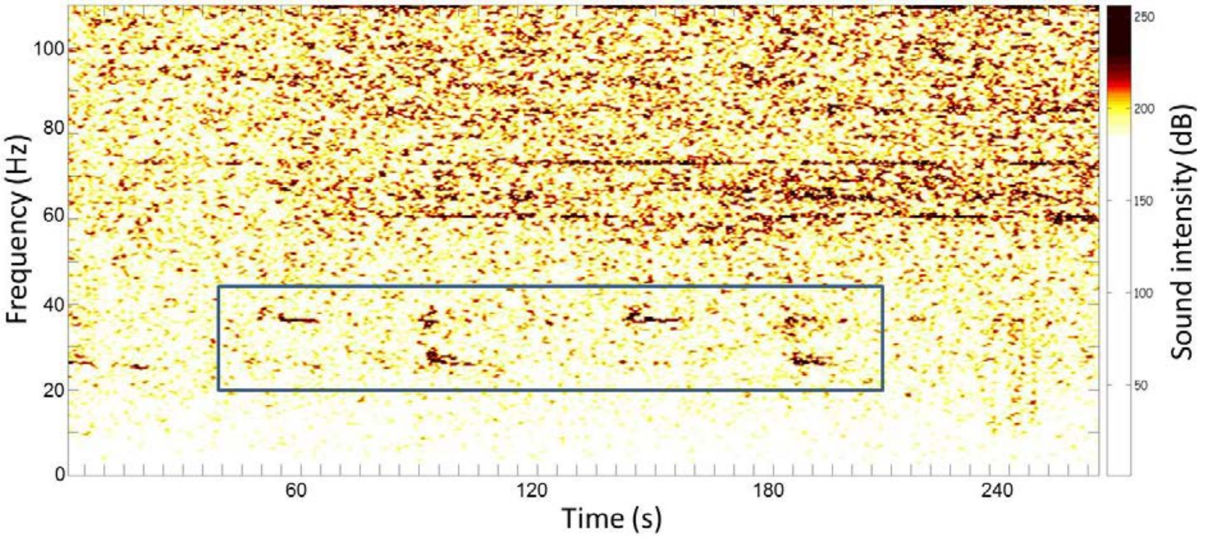


Figure 3.3. Spectrogram showing calls of pygmy blue whales (rectangle) recorded in Madagascar during the 1996/1997 IWC SOWER cruise. Spectrogram parameters: frame size 1.28 s, 50% overlap, FFT size 1650 points, Hanning window.

3.3 Results

Based on the information extracted from the cruise reports, acoustic data were collected at a total of 716 acoustics stations during the IWC SOWER cruises between the 1996/1997 and the 2009/2010 seasons (Figure 3.1). Sampling at acoustic stations was conducted in all IWC Areas except Area VI, and most effort occurred in Areas III, IV, and V. A total of 525 sonobuoys were deployed during 11 cruises (Table 3.1). Not all sonobuoys were functional; the overall failure rate of sonobuoys ranged from 0 to 40% of deployed sonobouys per cruise. Overall, over 2,794 hours of acoustic monitoring were conducted in real-time during the cruises where acousticians listened to sounds and monitored spectrograms in real time (Table 3.1). Recording acoustic data to media occurred for 24 hours of the day. Detections included Antarctic blue whales (Figure 3.2), Madagascan pygmy blue whales (Figure 3.3), fin whales, humpback whales, killer whales, southern right whales, sperm whales, small odontocetes and seals (Table 3.1, Figures 3.4-3.8). Assignment of a species to recorded call types was based on a combination of: 1) acoustician experience with visual spectrogram and real-time listening; 2) comparison of signals with the literature; 3) post-processing attribution (as was the case for leopard seal sounds previously attributed to humpback whales based on presence of humpback whales and humpback whale –like low-frequency vocalisations reported in the literature).

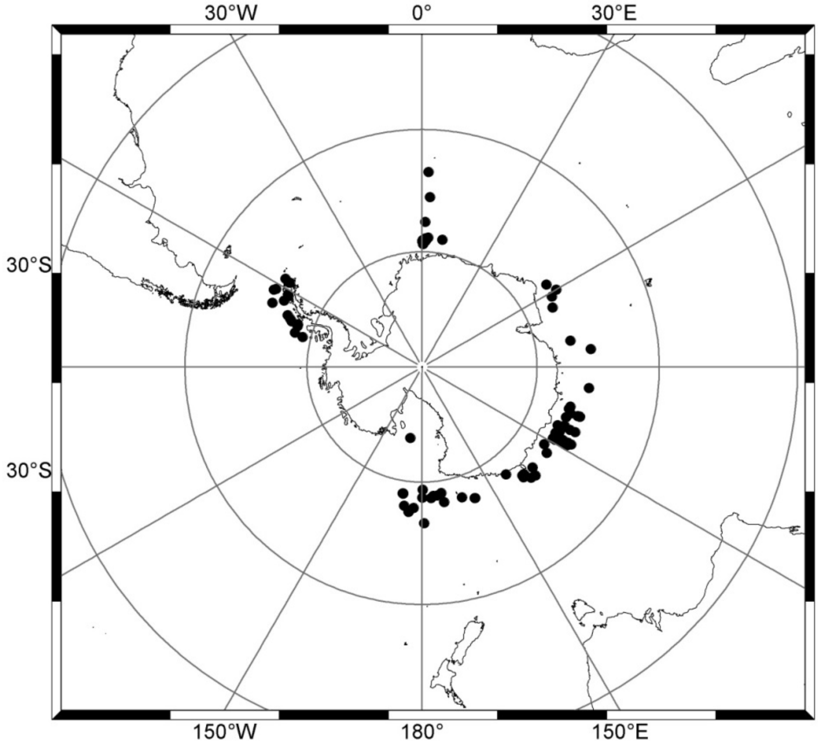


Figure 3.4. Locations of all sonobuoy recordings with identified acoustic detections of humpback whales (●) from 1996 to 2009.

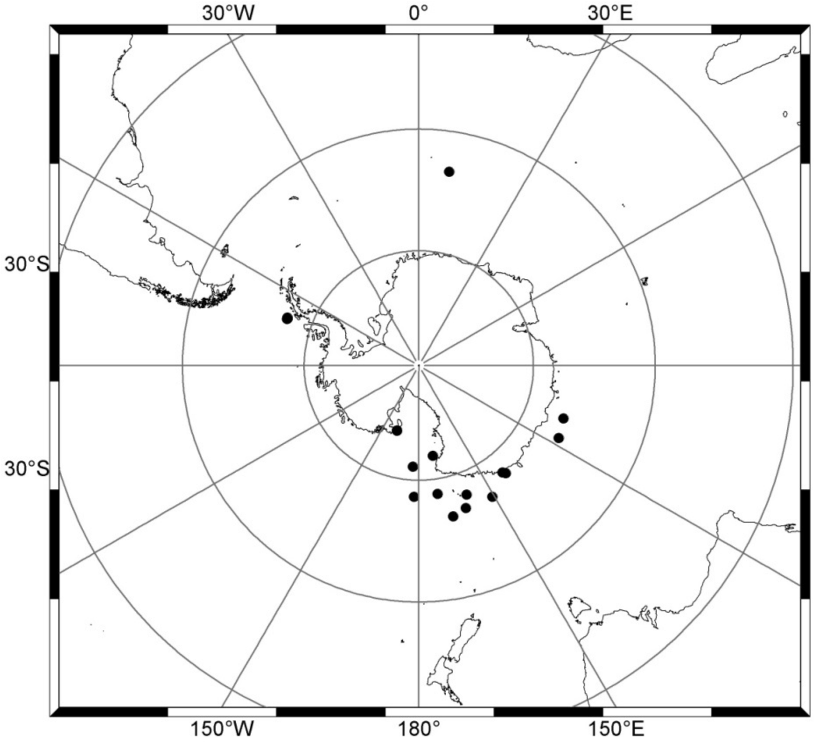


Figure 3.5. Locations of all sonobuoy recordings with identified acoustic detections of killer whales (●) from 1996 to 2009.

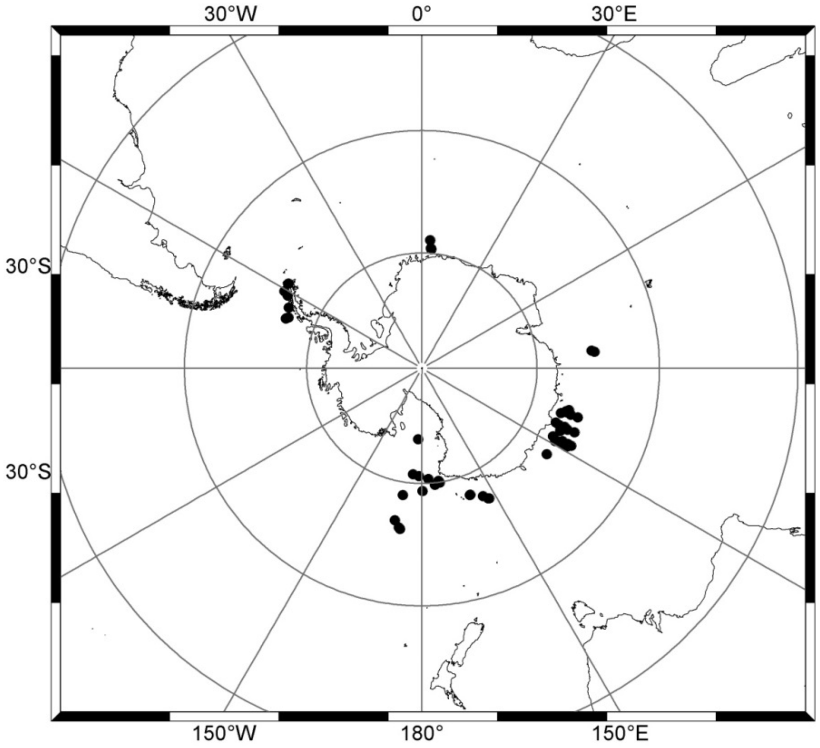


Figure 3.6. Locations of all sonobuoy recordings with identified acoustic detections of unidentified and other marine mammal species including southern right whales (●) from 1996 to 2009.

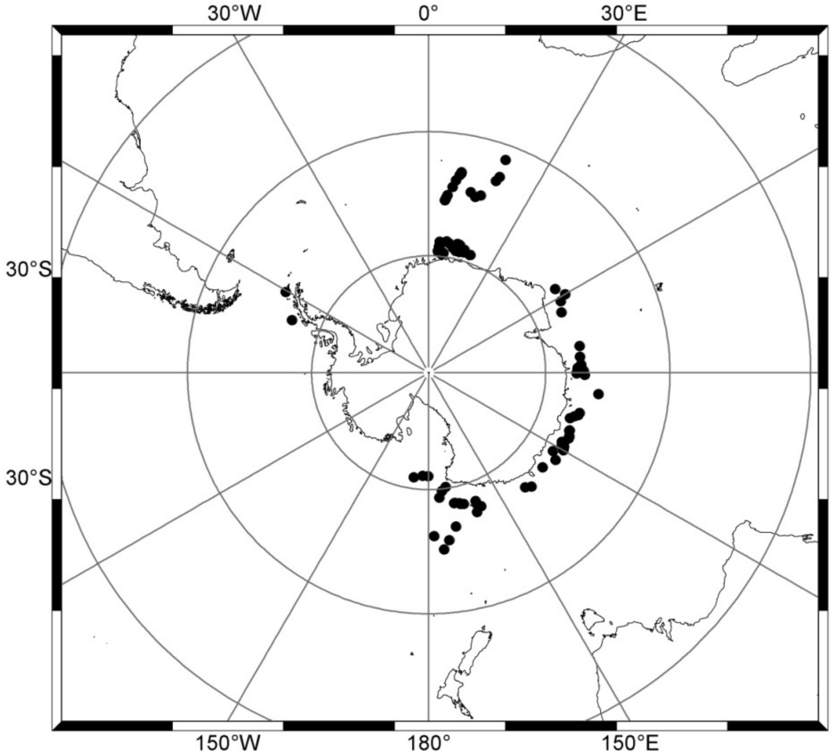


Figure 3.7. Locations of all sonobuoy recordings with identified acoustic detections of sperm whales (●) from 1996 to 2009.

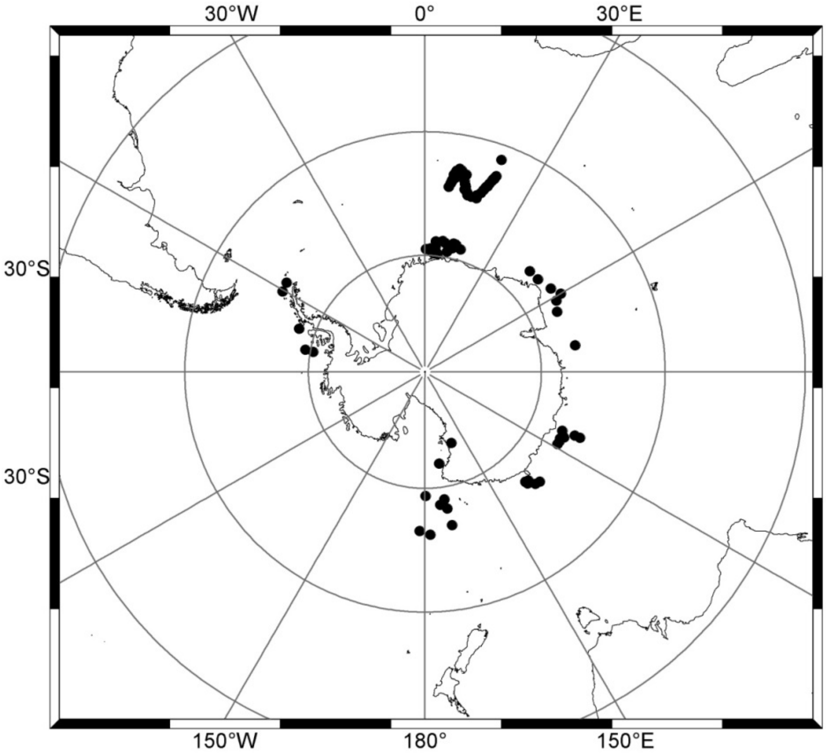


Figure 3.8. Locations of all sonobuoy recordings with identified acoustic detections of all seal species (Leopard, crabeater, Weddell) from 1996 to 2009.

Distinct Antarctic blue whale sounds were detected at 179 stations (Table 3.1, Figure 3.1). With the exception of the 1996/1997 cruise, all blue whale songs detected were D-calls or 28 Hz tonals attributed to Antarctic blue whales (Figure 3.2), while songs associated with other Southern Hemisphere blue whales were recorded near Madagascar and off Chile (Ljungblad *et al.* 1998, Clark and Fowler 2001) and not during the Antarctic cruises. Not all Antarctic blue whale songs comprised all three note types; however, the songs always contained the first 28-Hz component (see Rankin *et al.* 2005 for a full description). In addition to these stereotyped long-duration songs, shorter duration, FM D-calls were also detected at some stations. Ljungblad *et al.* (1998) compared data from recordings made south of 60°S with those made off the Madagascar Plateau (25°-35°S and 40°-45°E) and described differences in the sounds produced by blue whales in these areas. These recordings amounted to the first descriptions of each of these two song types and supported the idea that acoustic monitoring was a robust means of distinguishing between Antarctic and pygmy blue whales.

3.3.1 Available recordings – new analyses of the compiled database

After database compilation, approximately 7,485 recorded acoustic files were available from 484 stations of the Antarctic cruises comprising a total of 1,518 hours of acoustic recordings from the analysed 586 deployed acoustic recorders (i.e. 550 sonobuoys and 36 towed or deployed hydrophones). Antarctic blue whale calls were detected on 4,183 of the 7,485 recorded files. The available hours of recordings and number of sonobuoys represent only 63% and 80% respectively of the effort documented in the cruise reports as significant numbers of the acoustic data files from the IWC SOWER cruises could not be sourced (Table 3.1). The 2003/2004 and 2005/2006 cruises were the only two years where the available data are equivalent to the documented data in the cruise reports. It is also apparent that some of the acoustic data collected using cabled hydrophones from earlier years are missing (Table 3.1). The longitudinal acoustic survey coverage of the Southern Ocean is fairly sporadic between IWC Management Areas (Figure 3.1) during the IWC SOWER programme. Areas III, IV and V had the highest acoustic survey coverage (Tables 3.1 and 3.3). Most sonobuoy deployments were conducted between the ice edge and 60°S but most blue whale call detections were close to the ice edge (Figure 3.1) within this region.

Table 3.3. The total number of available acoustic stations recorded on IWC SOWER cruises grouped by IWC management Area.

Area	Total number of stations
Area I	31
Area II	19
Area III	193
Area IV	119
Area V	122
Area VI	0
Total	484

The acoustic survey effort in terms of the number of acoustic stations and duration of the recordings varied significantly (Two-sample KS test, $p < 0.05$) between years and Areas (Tables 3.1 and 3.3). Furthermore, the duration of the recordings at each station varied considerably as some acoustic stations had two or more sonobuoy deployments whereas others had just one deployment. Acoustic recordings were made in 11 years out of 14 years of the IWC SOWER programme. Only one acoustic recording was listed for Area VI from *Shonan Maru* for 2.38 hours on 12 January 2001 in the presence of four blue whales (Ensor *et al.* 2001), although this acoustic recording file, however, could not be sourced for analyses. Details of the available acoustic data from the IWC SOWER blue whale cruises conducted in the low latitudes are given in Table 3.4. Acoustic data files from the 1997/1998 Antarctic cruise have not yet been sourced, although the data files from the preceding Chile blue whale cruise (the cruises ran back to back) have been reviewed, including the identification of files grouped with the Chile cruise data but dated within the Antarctic cruise time period.

Table 3.4. Details of the available acoustic data recorded from other IWC blue whale cruises conducted in the low latitudes. Values in brackets refer to records in the cruise reports.

Cruise Year	RV	Recording dates	Total hours recorded	Number of sonobuoys	Cruise Area	Positions (longitude)	Reference
1995/1996	SM	-	0 (18.06)	0 (12)	Australia	114°-115°E	Kato *et al.* (1996)
	SM2	07-26 Dec 1995	17.60 (78.04)	10 (43)	Australia	114°-115°E	Kato *et al.* (1996)
1996/1997	SM	10-24 Dec 1996	39.93 (182.12)	12 (52)	Madagascar	40°-44°E	Ljungblad *et al.* (1998)
	SM2	-	0 (81.18)	0 (45)	Madagascar	40°-44°E	Ljungblad *et al.* (1998)
1997/1998	SM	09 Dec 1997- 02 Jan 1998	43.32 (72.50)	16 (29)	Chile	72°-74°W	Findlay *et al.* (1998)
	SM2	17 Dec 1997-02 Jan 1998	100.97 (106.21)	23 (30)	Chile	70°-74°W	Findlay *et al.* (1998)
Total			201.82 (538)	61 (211)			

3.3.2 Antarctic blue whale call detections

The characteristic Antarctic blue whale Z-calls (Figure 3.2a) were successfully detected using the template method in that a total of 24,902 calls were counted across the region surveyed. The blue whale feeding call, D-call (Figure 3.2b), was also detected using the template method and a total of 9,315 calls were counted. The acoustic presence of Antarctic blue whales from the sonobuoy deployments shows a patchy distribution over the surveyed area

(Figure 3.1). Not all sonobuoys deployed yielded blue whale vocalisations (Figures 3.1 and 3.9) but there was a good correlation between blue whale Z-call detections and number of sonobuoys deployed (r= 0.66, n= 586, p> 0.05). A weak correlation was found between D-calls and number of sonobuoys deployed (r= 0.49, n= 586, p> 0.05). Only 241 of the 586 available sonobuoy deployments contained either or both types of the Antarctic blue whale calls. Area III had the highest call rates of both the D- and Z-calls (Figures 3.10 and 3.11). No call detections were made in Area VI due to lack of acoustic survey effort.

A total of 214 sonobuoys were deployed during daytime and 372 deployed during the night time. More Z-calls were detected during daytime (14,724) than at night time (10,178; Two-sample KS test, p < 0.05). This was also the case for D-calls with more calls being detected in the daytime (6,492) than at night time (2,823; Two-sample KS test, p<0.05). Weak correlations were found between acoustic station duration and the number of calls detected for both call types (r= 0.33 and 0.49 for D- and Z-calls respectively).

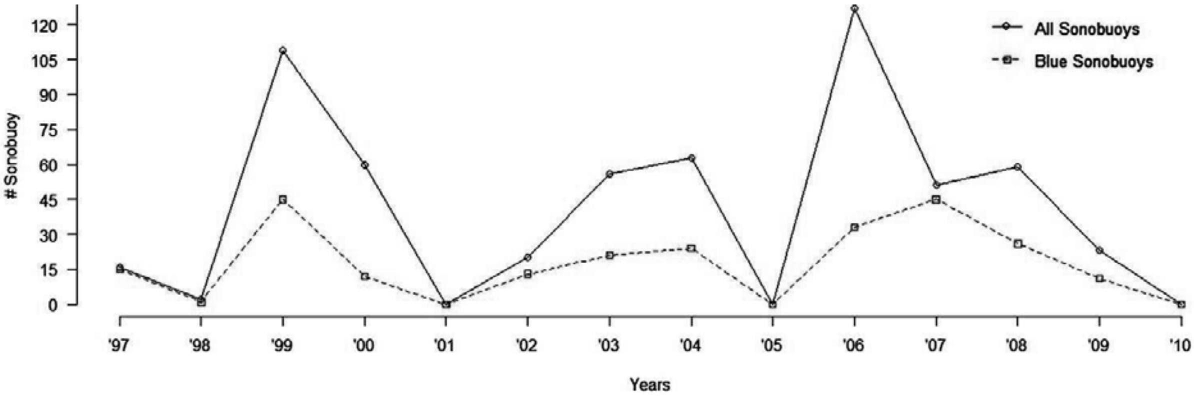


Figure 3.9. Total number of sonobuoys deployed per year (All sonobuoys) and the resultant sonobuoys containing Antarctic blue whale calls (Blue sonobuoys) from all IWC SOWER cruises.

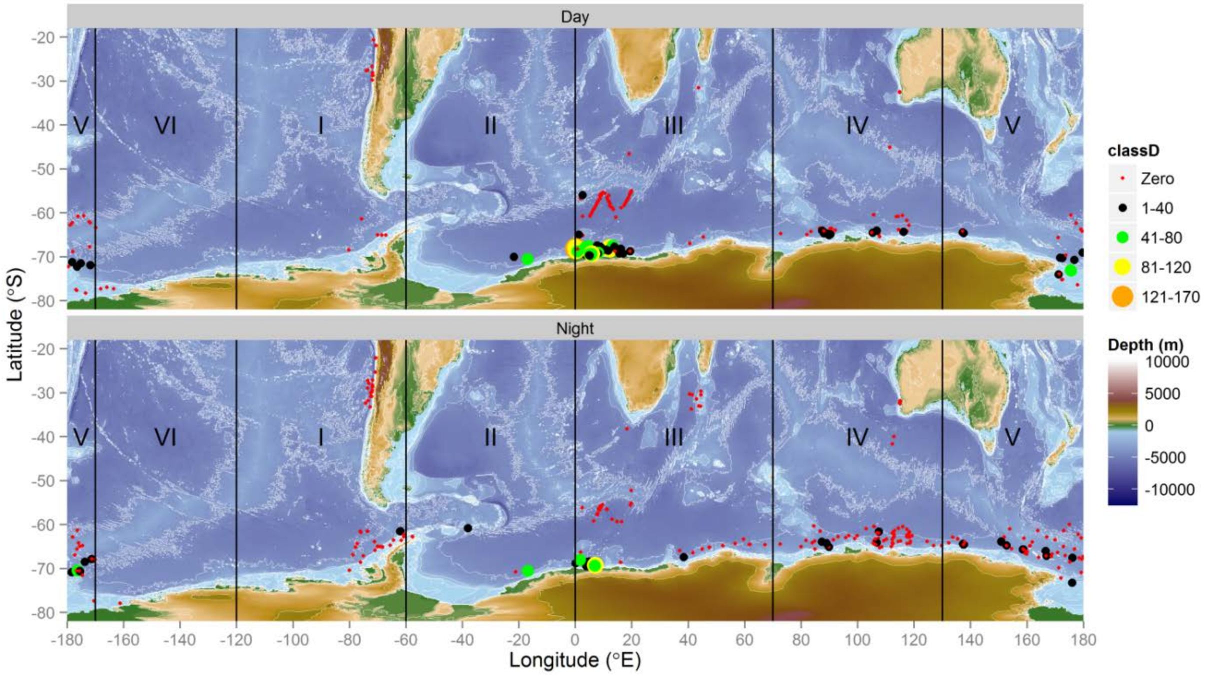


Figure 3.10. Day and night distribution of D-call numbers in the Southern Ocean. ClassD is the class of D-call rates.

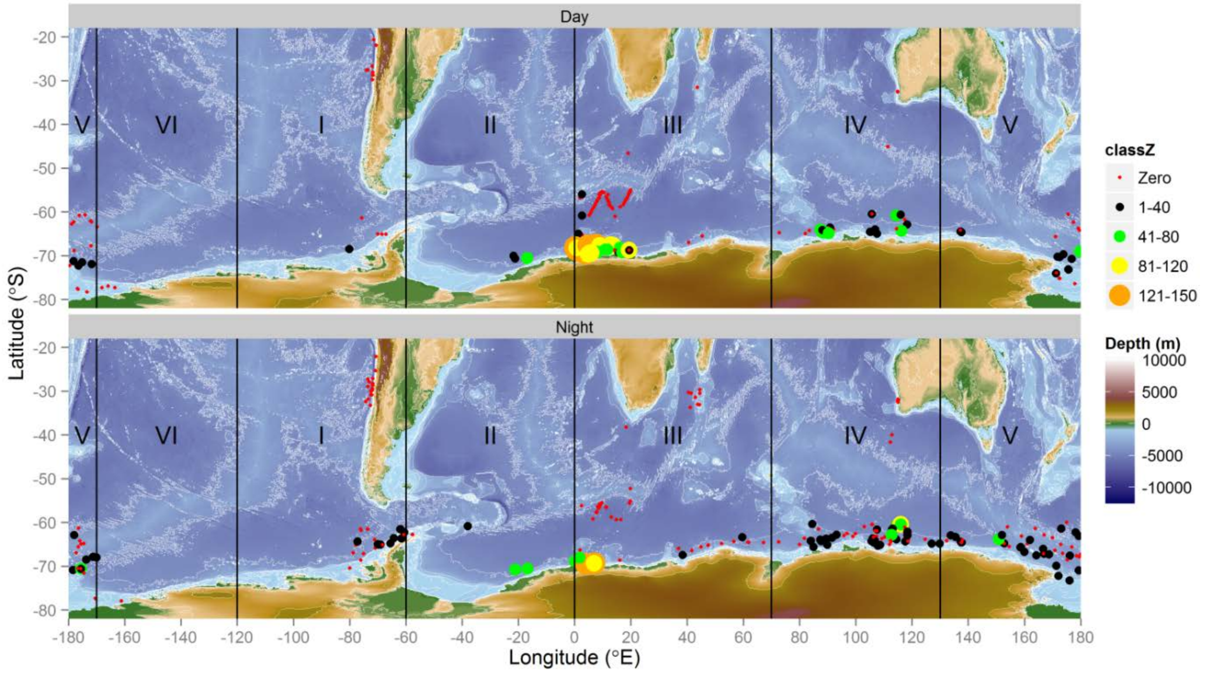


Figure 3.11. Day and night distribution of Z-call rates in the Southern Ocean. ClassZ is the groups of Z-call rates.

3.3.3 Data comparison

Comparisons of mean number of hours recorded in all cruises indicated that there was a significant difference between the available recorded hours from the dataset and documented recorded hours from cruise reports (Two-sample KS test, $p < 0.05$). A significant difference was observed between the number of sonobuoys available in the dataset and the sonobuoy numbers documented in cruise reports (Two-sample KS test, p= 0.05). There was a good agreement between our analysed blue whale call detection results and blue whale calls observed and documented in cruise reports (r= 0.62).

3.3.4 Other sounds and vocalisations detected

No calls of either Antarctic or pygmy blue whales were detected from the 1995/1996 Australia low latitude cruise but calls of pygmy blue whales (Figure 3.3) and fin whales were found from the 1996/1997 Madagascar acoustic data (Ljungblad *et al.* 1998). No Z-calls were found in the 1997/1998 Chile cruise although D-calls and numerous southeastern Pacific 2 (SEP2) calls of the Chilean pygmy blue whale were found (Figure 3.12). These call detections confirm the observation by previous studies in the southeastern Pacific Ocean (Cummings and Thompson, 1971; Stafford *et al.* 1999; Buchan *et al.* 2010, 2014). The SEP2 call has a C2 unit which is 5 s long (Figure 3.12) followed by an inter-unit gap of 3 s and then a 9 s long D2 unit, and the overall duration of the call is approximately 17 s (Buchan *et al.* 2014). The D-calls observed from the southeastern Pacific Ocean were not considered for analyses in this study since we concentrated mainly on the Southern Hemisphere Antarctic blue whale population.

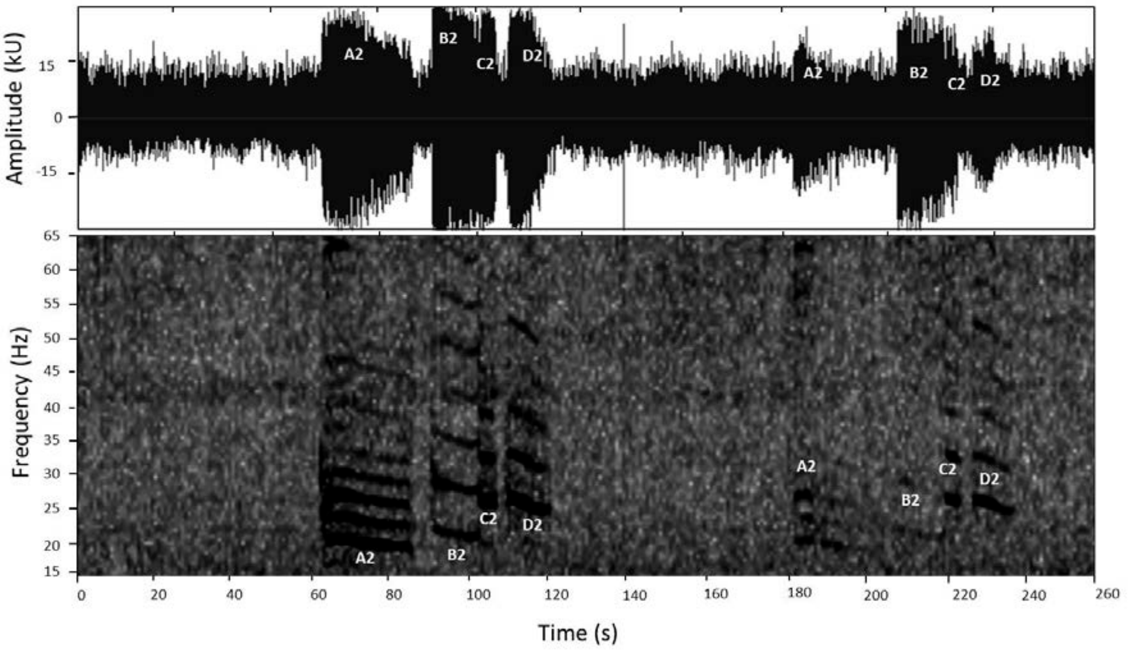


Figure 3.12. Pressure waveform (top panel) and spectrogram (bottom pannel) of the Chilean blue whale SEP2 song phrases (A2, B2, C2 and D2). This sonobouoy was deployed on 31 December 1997 off the southeastern Pacific Ocean at 28°39'N, 71°47'W during the 1997/1998 SOWER cruise, Chile. kU is kilo unit. Spectrogram parameters: frame size 1.39 s, 50% overlap, FFT size 2048 s, Hanning window.

Detections of other marine mammal species included fin whales, humpback whales, killer whales, southern right whales, sperm whales, small odontocetes and seals (Table 3.1, Figures 3.4-3.8). In addition, ice noise, seismic air guns and other unidentified sounds were detected on numerous occasions.

3.4 Discussion

The original goal of the acoustics component of the IWC SOWER cruises was to determine if passive acoustics could be used as a tool to help identify sighted blue whales to sub-species level. In 2006/2007 and 2007/2008, the passive acoustic method was also assessed for their utility in monitoring fin whales. Unfortunately, numerous limitations prevented the realization of this potential during the IWC cruises, including limited resources (sonobuoys and recording tapes) available for field personnel. Most of the sonobuoys used were surplus instruments whose expiration dates had long passed, which resulted in sometimes very high failure rates. Nevertheless, the collective electronics expertise of the ships' radiomen and one of the co-authors (DL), allowed the acousticians to modify some of the sonobuoys while at sea.

These cruises were moderately successful, despite numerous limitations, and they served to lay the foundation for future work using acoustics to study blue whales in the Southern Ocean. For instance, Ljungblad *et al.* (1998) compared data from recordings made south of 60°S with those made off the Madagascar Plateau (25°-35°S and 40°-45°E) and described differences in the sounds produced by blue whales in these areas. These recordings amounted to the first descriptions of each of these two song types and supported the idea that acoustic monitoring was a robust means of distinguishing between Antarctic and pygmy blue whales. The acoustic data collected on both Antarctic and pygmy blue whale vocalizations (Ljungblad *et al.* 1998; Clark and Fowler, 2001; Rankin *et al.* 2005) paved the way for numerous studies delineating occurrence and habitat usage of blue whales based on PAM and further strengthened the concept of “acoustic populations” of blue whales (Stafford *et al.* 2004, 2011; McDonald *et al.* 2006; Samaran *et al.* 2010a, 2010b, 2013). Further, recent surveys that actively used passive acoustics to detect, identify, track, and approach blue whales in the Southern Ocean for photo-identification and biopsy referred to IWC SOWER reports and publications (Clark and Fowler, 2001; Rankin *et al.* 2005; Gedamke and Robinson, 2010) to select a target research area, develop methods and train field personnel (B. Miller, pers. comm.) The success of the Australian Antarctic Division, Southern Ocean Research Partnership (SORP) 2013 blue whale survey was based on the foundation built by the IWC SOWER cruises (Double *et al.* 2013; Miller *et al.* 2013a).

3.4.1 Distribution and occurrence of Antarctic blue whale call types

The higher number of Antarctic blue whale calls (31% and 56% more Z- and D-calls respectively) found during daytime, despite more sonobuoys being deployed at night time might be an indication that Antarctic blue whales are vocally active mostly during daytime and less vocal at night time. A similar observation has been made from autonomous acoustic recorders off the Maud Rise and Benguela ecosystem off South Africa (Shabangu *et al.* Unpublished- Chapters 5 and 6). Alternatively, this higher daytime call numbers might arise because daytime acoustic recordings were often conducted in the presence of visually sighted blue whales whereas nighttime acoustic recordings were conducted blindly without knowledge of the blue whale presence or absence. Low numbers and rates of Antarctic blue whale calls observed in December could be due to fact that most of the IWC SOWER cruises usually started in late December when the majority of the Antarctic blue whales may still have been in transit from the low latitude overwintering grounds to the Southern Ocean feeding grounds (Mackintosh and Wheeler, 1929).

Sea ice extent in December could also have affected the number of vocal active Antarctic blue whales as suggested by Širovic *et al.* (2004) since recordings from stationary autonomous Acoustic Recording Packages (ARPs) in Area II also found low call numbers in December. This IWC SOWER data showed that Antarctic blue whale call rates peaked in February (Shabangu *et al.* 2017- Chapter 4), which is closer to the blue whale call peak period of March and April observed by Širovic *et al.* (2004) from their ARPs. Despite most acoustic recordings being conducted earlier than mid-February, a considerable number of calls were detected in this month showing the availability of Antarctic blue whales in high numbers in the Southern Ocean at this time of the year when sea ice retreat is maximal. The increased call rates of Antarctic blue whales observed in the later years of the IWC SOWER programme (Shabangu *et al.* 2017- Chapter 4) may be indicative of the initial population recovery of 8.2% estimated by Branch *et al.* (2004). The increase in blue whale call rates in later years is not due to more dedicated ship time to record blue whale calls as there was no increase in the number of hours dedicated to acoustic research in those years (Table 3.1). The observed good correlation between blue whale call detections and number of sonobuoys deployed demonstrate that the more coverage effort in particular Areas of interest improved the precision of the distribution and occurrence estimates (Aglen, 1989). However, it is worth noting that a special effort was dedicated to certain IWC Areas with suspected high blue whale prevalence.

Antarctic blue whale calls have previously been detected in the South Pacific Ocean as far north as 08°S (Stafford *et al.* 2004) and as far north as 08°S in the Indian Ocean (Samaran *et al.* 2013). Nevertheless, during these analyses no Antarctic blue whale calls were found off Australia, in the southeastern Pacific and south of Madagascar in the low-latitude cruises, presumably reflecting the summer periods during which they were carried out. The IWC SOWER low latitude acoustic data were collected within a single summer month each year when the majority of Antarctic blue whales would be expected to be further south than the region surveyed whereas the data analysed by Stafford *et al.* (2004) were collected over 24 months. Calls of pygmy blue and fin whales were found during our analyses of the incomplete acoustic data from Madagascar, confirming Ljungblad *et al.* (1998) observation. Field results of the 1995/1996 Australia blue whale cruise reported pygmy blue whale calls (Kato *et al.* 1996), however, such calls were not found from the incomplete acoustic dataset analysed here.

Ljungblad *et al.* (1998) and Rankin *et al.* (2005) analysed a subset of the IWC SOWER acoustic data from 1996/1997; 2001/2002 and 2002/2003 respectively. This study is a first of its kind to review and analyse a more complete IWC SOWER acoustic dataset for Antarctic blue whale vocalizations. However, the difference between the available and reported acoustic datasets from the cruise reports is of concern and a fuller reconciliation of the IWC SOWER cruises acoustic dataset is recommended if possible. This IWC SOWER acoustic dataset is a valuable acoustic time series of Antarctic blue whale vocalizations. It is further recommended that the archiving and management of these data be centralised to ensure that these circum-Antarctic data are readily available to future studies. The Acoustic Trends Working Group (ATWG) of the Southern Ocean Research Partnership (SORP) is adopting a similar approach for its ongoing acoustic data collection (see van Opzeeland *et al.* 2014).

Although the reconciliation of the full circumpolar IWC SOWER acoustic dataset could not be completed, the compilation of this dataset has allowed for the merging of both acoustic data from the recordings and associated metadata (including both spatial and temporal data) from the station and acoustic record forms. Further analyses of these data (and particularly call rates) by locations (position, depth and distance from the ice edge), and timing (both across the summer season and by time of day) and in association with both observed groups of blue whales and broader blue whale densities obtained from line-transect visual observations will provide important information on Antarctic blue whale calling behaviour, migrations and distribution. For instance, Shabangu *et al.* (2017- Chapter 4) used the IWC SOWER blue whale recordings to examine the occurrence of Antarctic blue whale call types in the context of oceanographic variability in the region and over the 14-year span of data collection. They found that the number of D-calls recorded was positively related to the number of animals seen during visual observations but the call rate of Z-calls was not. Call rates for both types were dictated by region and the location of the southern boundary of the Antarctic Circumpolar Current (ACC). Such knowledge about blue whale acoustic behaviour is important to the analyses and understanding of autonomous acoustic recordings and other long-term acoustic recordings from the Southern Ocean region.

3.4.2 IWC SOWER data mining potential

Compiling most of the IWC SOWER acoustic dataset and analysing it for the presence and different types of blue whale calls recorded over more than a decade of survey effort was a first step towards expanding the utility of these data. With a more coherent understanding of the available data, in-depth studies can be undertaken that will improve an understanding of the role sound production plays in blue whale ecology. There are numerous further studies using these IWC SOWER recordings that would be valuable and deserve serious consideration. Although the acoustic equipment were not calibrated, these recordings could provide important baseline data regarding ambient noise, and vocal repertoire and seasonal calling behaviours of species other than blue whales. The combination of photo-identification, biopsy, and behavioural data with the acoustic data can provide valuable insights that are otherwise difficult and expensive to obtain.

Presently, there are no data on what proportion of blue whales produce downsweeps, nor what proportion of males sings. Analysis of IWC SOWER acoustic data in conjunction with sighting survey and behavioural data (for which there were at least 120 instances over the years, Table 3.1) may be used to develop distribution curves for acoustically active blue whales. That is, when blue whales that appeared to be feeding were sighted, what types of sounds were recorded, which of those could be attributed to the observed animal, and what was the behavioural context under which those sounds were produced? What was the whale doing when no sounds were recorded? Was acoustic behaviour different when females with calves were present? Resultant understandings of Antarctic blue whale variability in acoustic behaviour and the associated behavioural context will lead to better understandings of acoustic functions. Vocal rates under different contexts will inform efforts to determine absolute or relative population sizes from remote passive acoustic monitoring as has been suggested by the IWC-sponsored SORP blue and fin whale acoustics working group (Samaran *et al.* 2012).

In cases when two DiFAR sonobuoys were deployed at the same time, processing of the same blue whale sound on each buoy can be used to localize calling whales. Although these opportunities were not taken advantage during IWC SOWER cruises, this type of post-cruise analyses is readily feasible (Rankin *et al.* 2005). For whales from which a biopsy was obtained, acoustic localization can be used to compare vocal behaviours between females and males (see for example Rankin *et al.* 2005 for data that could be used). This information is critical for the application of passive acoustic monitoring for population estimation. Based on data from the eastern North Pacific population of blue whales, there is evidence that only male blue whales sing (McDonald *et al.* 2006; Oleson *et al.* 2007), while both males and females appear to produce D-calls (Oleson *et al.* 2007). If this is the case, then the use of 28-Hz song notes to determine acoustic occurrence only accounts for males in a population. Assuming the present-day sex ratio for blue whales is similar to that during commercial whaling (47:53 female: male, Branch *et al.* 2004), then correction factors could be made to account for non-singing females.

One of the requirements of estimating abundance from passive acoustic monitoring is knowledge of the range at which sounds of interest can be detected. The source level of a signal (i.e. how loud it is) is needed to estimate detection range and therefore detection probability. Presently there are few source level estimates for Antarctic blue whales (Širović *et al.* 2007, Samaran *et al.* 2010b). For Antarctic blue whales there are estimates of detection range based on known sighting locations and calls attributed to those sightings based on DiFAR processing. Although our hydrophones were uncalibrated, these data can be used to calculate relatively robust measures of received level by which to estimate source levels, which, when combined with estimating distances of whales from a hydrophone can be used to estimate source levels. Data from the IWC SOWER cruises might be used to obtain statistical data, including detection ranges, from Antarctic blue whale source levels, particularly where the animals are a known distance from a sonobuoy. Whereupon factors such as call detection range, probability of call detection, cue rate per individual, and group sizes may be evaluated. These parameters are crucial to the successful estimation of animal densities and relative abundance of vocalising whales in an area (see Marques *et al.* 2013). What complicates this analysis is that the frequency response of the recording systems and the gain settings used over the years were not generally reported and the age of the sonobuoys may have influenced the received levels of signals. Our observed good agreement between sightings and acoustic detections is encouraging for whale abundance estimation using passive acoustic monitoring as it indicates that passive acoustic monitoring can successful capture the amount of animals in an area.

There is recent evidence that the fundamental frequency of the Antarctic blue whale 28-Hz song note is changing both within a season and over years on a wintering ground (Gavrilov *et al.* 2012; Ward *et al.* 2017). The IWC SOWER acoustic database has data from over the span of a decade that could be used to determine if this decrease exists on the feeding grounds. These data could also be used to examine variability in individual tonal frequencies and if/how these change within a season and across regions and years. In addition, analysis of some very low frequency sounds (9-11 Hz) in relation to behaviour could be examined to identify any vocal response to directed vessel approach (see Ljungblad *et al.* 2001).

3.4.3 Other species

There are ways by which these data might be useful. For example, since the initiation of the IWC SOWER programme, four distinct morpho-types of killer whale (A, B, C and D) have been identified from Antarctic waters (Pitman and Ensor, 2003; Pitman *et al.* 2010). Each form is readily distinguishable in the field, and each is thought to occupy different ecological niches based on prey and habitat preferences (Pitman and Ensor, 2003). The IWC SOWER dataset contains at least 18 instances of recordings of killer whale vocalizations. A database of call types from each of these forms (based on photo-identification) could contribute to acoustic identification as has been done for killer whales in other parts of the world (Ford, 1989; Deecke *et al.* 2011; Riesch and Deecke, 2011).

For at least one Southern Hemisphere sperm whale population there is no evidence for recovery following the cessation of whaling (Carroll *et al.* 2014). It may be feasible to investigate the IWC SOWER recordings to see if there has been a change in relative occurrence of sperm whale sounds on a circumpolar basis, or conversely if there has been low recruitment and therefore a change in age structure which might be investigated by looking at inter-click interval to determine animal size (e.g. Adler-Fenchel, 1980; Miller *et al.* 2013b). Finally, seal vocalizations recorded around the Antarctic could be used to determine if individuals might be identified or if pan-Antarctic geographic variation exists (i.e. Rogers and Cato, 2002; Van Parijs and Clark, 2006; Terhune *et al.* 2008).

3.5 Acknowledgements

We are extremely grateful to the International Whaling Commission for granting permission to use the IWC SOWER acoustic data together with the cruise reports, acoustic data records and visual survey data. We are indebted to the IWC SOWER cruise participants, ships' captains and crew who spent long hours at sea collecting the data used in this study. George Murphy and the Naval Surface Warfare Center Crane Indiana Division; and Nick Gales and the Australian Antarctic Division provided surplus sonobuoys for this project. When there was no dedicated acoustician on board Sharon Hedley, Hiroyuki Shimada and Hiroto Murase undertook the acoustic recordings. Special thanks to Jay Barlow, Robert Brownell, Paul Ensor, Keiko Sekiguchi, Koji Matsuoka, and Southwest Fisheries Science Center for their support. Stimulating discussions and communications with other SORP members improved and smoothed our data analyses. We are sincerely grateful to Brendan Boulle, Stellenbosch University, for his help with the MATLAB script for decimating acoustic files. We thank the South African National Antarctic Programme and the National Research Foundation for funding of the South African Blue Whale Project.

3.6 References

Adler-Fenchel, H.S., 1980. Acoustically derived estimate of the size distribution for a sample of sperm whales (*Physeter catodon*) in the Western North Atlantic. Canadian Journal of Fisheries and Aquatic Sciences 37: 2358–2361.

Aglen, A. 1989. Empirical results on precision- effort relationships for acoustic surveys. International Council for the Exploration of the Sea C.M.1989/B:30.

Alling, A., Dorsey, E.M. and Gordon, J.C.D. 1991. Blue whales (*Balaenoptera musculus*) off the northeast coast of Sri Lanka: Distribution, feeding, and individual identification.

In: Leatherwood, S. and Donovan, G.P. (eds.). Cetaceans and Cetacean Research in the Indian Ocean Sanctuary. Nairobi, Kenya: UNEP Marine Mammal Technical Report No. 3, pp. 247–258.

Attard, C.R.M., Beheregaray, L.B. and Möller, L.M. 2016. Towards population-level conservation in the critically endangered Antarctic blue whale: the number and distribution of their populations. Scientific Reports 6: 22291.

Bannister, J.L. 2009. Baleen whales, mysticetes. In: Perrin, W.F., Wursig, B. and Thewissen, J.G.M. (eds) Encyclopedia of marine mammals. 2nd Edition. Academic Press, California. i-xxxiv+1316pp.

Best, P.B. 2007. Whales and dolphins of the Southern African subregion. Cambridge University Press, Cape Town. i-xiii+338 pp.

Bioacoustics Research Program. 2013. 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.

Blyth, E. 1859. On the great rorqual of the Indian Ocean, with notices of other cetals, and of the Syrenia or marine pachyderms. Journal of the Asiatic Society of Bengal 28: 481–498.

Branch, T.A., Matsuoka, K. and Miyashita, T. 2004. Evidence for increases in Antarctic blue whales based on Bayesian modelling. Marine Mammal Science 20: 726–754.

Branch, T.A., Stafford, K.M., Palacios, D.M., Allison, C., Bannister, J.L., Burton, C.L.K., Cabrera, E., Carlson, C.A., Vernazzani, B.G., Gill, P.C., Hucke-Gaete, R., Jenner, K.C.S., Jenner, M.N.M., Matsuoka, K., Mikhalev, Y.A., Miyashita, T., Morrice, M.G., Nishiwaki, S., Sturrock, V.J., Tormosov, D., Anderson, R.C., Baker, A.N., Best, P.B., Borsa, P., Brownell, R.L., Childerhouse, S., Findlay, K.P., Gerrodette, T., Ilangakoon, A.D., Joergensen, M., Kahn, B., Ljungblad, D.K., Maughan, B., McCauley, R.D., McKay, S., Norris, T.F., Whale, O., Rankin, S., Samaran, F., Thiele, D., Van Waerebeek, K. and Warneke, R.M. 2007. Past and present distribution, densities and movements of blue whales *Balaenoptera musculus* in the Southern Hemisphere and northern Indian Ocean. Mammal Review 37(2): 116–175.

Brownell Jr., R.L., Galletti-Vernazzi, B., de Vos, A., Olson, P.A., Findlay, K., Bannister, J.L. and Lang, A.R. 2015. Assessment of pygmy type blue whales in the Southern Hemisphere. Paper SC/66a/SH/21 presented to the IWC Scientific Committee, May 2015. 25 pp.

Buchan, S.J., Rendell, L. and Hucke-Gaete, R. 2010. Preliminary recordings of blue whale (*Balaenoptera musculus*) vocalizations in the Gulf of Corcovado, northern Patagonia, Chile. Marine Mammal Science 26(2): 451–459.

Buchan, S.J., Hucke-Gaete, R., Rendell, L. and Stafford, K. 2014. A new song recorded from blue whales in the Corcovado Gulf, Southern Chile, and an acoustic link to the Eastern Tropical Pacific. Endangered Species Research 23: 241–252.

Burmeister, H. 1871. Del año 1871. Boletin del Museo Publico de Buenos Aires 1871: 11–20. [In Spanish].

Carroll, G., Hedley, S., Bannister, J., Ensor, P., and Harcourt, R. 2014. No evidence for recovery in the population of sperm whale bulls off Western Australia, 30 years post-whaling. Endangered Species Research 24: 33–43.

Clark, C.W. and Fowler, M. 2001. Status of archival and analysis effort of acoustic recordings during SOWER and IWC cruises 1996-2000. Reports of the International Whaling Commission SC/53/IA28.

Clark, C.W. and Gagnon, G.C. 2002. Low-frequency vocal behaviors of baleen whales in the North Atlantic: Insights from IUSS detections, locations and tracking from 1992 to 1996. U.S. Navy Journal of Underwater Acoustics 52 (3): 609–640.

Cummings, W.C. and Thompson, P.O. 1971. Underwater sounds from the blue whale, Balaenoptera musculus. Journal of the Acoustical Society of America 50(4): 1193–1198.

Deecke, V.B., Nykaenen, M., Foote, A.D., and Janik, V.M. 2011. Vocal behaviour and feeding ecology of killer whales *Orcinus orca* around Shetland, UK. Aquatic Biology 13(1): 79–186.

Donovan, G.P. 1991. A review of IWC stock boundaries. Reports of the International Whaling Commission (special issue 13): 39–68.

Donovan, G.P., Hammond, P.S., Larsen, F., Reilly, S.B., Kato, H., Clark. C.W. and Brownell, R.L. 1996. Report of the Scientific Committee, Annex E. Report of the sub-committee on Southern Hemisphere baleen whales. Appendix 2. An approach for responding to the Commission's resolution. Reports of the International Whaling Commission 46: 126-127.

Double, M.C., Barlow, J., Miller, B.S., Olson, P., Andrews-Goff, V., Leaper, R., Ensor, P., Kelly, N., Lindsay, M., Peel, D., Calderan, S., Collins, K., Davidson, M., Deacon, C., Donnelly, D., Olavarria, C., Owen, K., Rekdahl, M., Schmitt, N., Wadley, V., and Gales, N. 2013. Cruise report of the 2013 Antarctic blue whale voyage of the Southern Ocean Research Partnership. Paper SC/65a/SH21 presented to the IWC Scientific Committee, May 2013. 16 pp.

Edds, P.L. 1982. Vocalisations of the blue whale, *Balaenoptera musculus,* in the St. Lawrence River. Journal of Mammalogy 63: 345–347.

Edds-Walton, P.L. 1997. Acoustic communication signals of mysticete whales. The International Journal of Animal Sound and its Recording 8: 47–60.

Ensor, P., Findlay, K., Hara, T., Hedley, S., Pitman, R., Sekiguchi, K., Tsurui, T. and Yamagiwa, D. 1997. 1996-97 IWC-Southern Ocean Whale and Ecosystem Research (IWC SOWER) Antarctic cruise, Area II. Paper SC/49/SH7 presented to the IWC Scientific Committee, September 1997. 47 pp.

Ensor, P., Pastene, L.A., Cawthorn, M., Findlay, K., Hedley, S., Iwakami, H., Kleivane, L., Pitman, R., Tsurui, T. and Sakai, K. 1998. 1997-98 IWC Southern Ocean Whale and

Ecosystem Research (IWC SOWER) Antarctic cruise, Area II. Paper SC/50/Rep1 presented to the IWC Scientific Committee, April 1998. 45 pp.

Ensor, P., Sekiguchi, K., Doherty, J., Kleivane, L., Ljungblad, D., Marques, F., Matsuoka, K., Narita, H., Pitman, R. and Sakai, K. 1999. 1998-99 IWC-Southern Ocean Whale and Ecosystem Research (IWC SOWER) Antarctic cruise, Areas III and IV. Paper SC/51/Caws6 presented to the IWC Scientific Committee, May 1999. 61 pp.

Ensor, P., Findlay, K.P., Hucke-Gaete, R., Kleivane, L., Komiya, H., Ljungblad, D., Marques, F., Muira, T., Sekiguchi, K. and Shimade, H. 2000. 1999-2000 IWC-Southern Ocean Whale and Ecosystem research (IWC SOWER) Antarctic cruise, Areas I and II. Paper SC/52/IA1 presented to the IWC Scientific Committee, June 2000. 51 pp.

Ensor, P., Matsuoka, K., Marques, F., Miura, T., Murase, H., Pitman, R., Sakai, K. and Van Waerebeek, K. 2001. 2000-2001 International Whaling Commission - Southern Ocean Whale and Ecosystem Research (IWC SOWER) circumpolar cruise, Area V, VI and I. Paper SC/53/IA5 presented to the IWC Scientific Committee, July 2001. 56 pp.

Ensor, P., Sekiguchi, K., Cotton, J., Hucke-Gaete, R., Kariya, T., Komiya, H., Ljungblad, D., Narita, H., Olson, P. and Rankin, S. 2002. 2001-2002 International Whaling Commission-Southern Ocean Whale and Ecosystem Research (IWC SOWER) circumpolar cruise, Area V. Paper SC/54/IA2 presented to the IWC Scientific Committee, April 2002. 51 pp.

Ensor, P., Matsuoka, K., Hirose, K., Ljungblad, D., Minami, K., Olson, P., Rankin, S., Stevick, P., Tsunekawa, M. and Ugarte, F. 2003. 2002-2003 International Whaling Commission-Southern Ocean Whale and Ecosystem Research (IWC SOWER) circumpolar cruise, Area V. Paper SC/55/IA1 presented to the IWC Scientific Committee, May 2003. 65 pp.

Ensor, P., Matsuoka, K., Komiya, H., Ljungblad, D., Miura, T., Morse, L., Olson, P., Olavarria, C., Mori, M. and Sekiguchi, K. 2004. 2003- 2004 International Whaling Commission-Southern Ocean Whale and Ecosystem Research (IWC SOWER) circumpolar cruise, Area V. Paper SC/56/IA13 presented to the IWC Scientific Committee, July 2004. 68 pp.

Ensor, P., Findlay, K., Friedrichsen, G., Hirose, K., Komiya, H., Morse, L., Olson, P., Sekiguchi, K., Van Waerebeek, K., and Yoshimura, I. 2005. 2004-2005 International Whaling Commission- Southern Ocean Whale and Ecosystem Research (IWC SOWER) cruise, Area III. Paper SC/57/IA1 presented to the IWC Scientific Committee, June 2005. 90 pp.

Ensor, P., Komiya, H., Olson, P., Sekiguchi, K. and Stafford, K. 2006. 2005-2006 International Whaling Commission- Southern Ocean Whale and Ecosystem Research (IWC SOWER) cruise. Paper SC/58/IA1 presented to the IWC Scientific Committee, June 2006. 58 pp.

Ensor, P., Komiya, H., Beasley, I., Fukutome, K., Olson, P. and Tsuda, Y. 2007. 2006-2007 International Whaling Commission—Southern Ocean Whale and Ecosystem Research (IWC- SOWER) cruise. Paper SC/59/IA1 presented to the IWC Scientific Committee, June 2007. 58 pp.

Ensor, P., Minami, K., Morse, L., Olson, P. and Sekiguchi K. 2008. 2007–2008 International Whaling Commission-Southern Ocean Whale and Ecosystem Research (IWC SOWER) cruise. Paper SC/60/IA1 presented to the IWC Scientific Committee, June 2008. 51 pp.

Ensor, P., Komiya, H., Kumagai, S., Kuningas, S., Olson, P. and Tsuda, Y. 2009. 2008-2009 International Whaling Commission-Southern Ocean Whale and Ecosystem Research (IWC- SOWER) cruise. Paper SC/61/IA19 presented to the IWC Scientific Committee, June 2009. 54 pp.

Figueroa, H.K. 2006. XBAT: Extensible BioAcoustic Tool. Available from http://xbat.org.

Findlay, K., Pitman, R., Tsurui, T., Sakai, K., Ensor, P., Iwakami, H., Ljungblad, D., Shimada, H., Thiele, D., Van Waerebeek, K., Hucke-Gaete, R. and Sanino-Vattier, G.P. 1998. 1997/1998 IWC-Southern Ocean Whale and Ecosystem Research (IWC SOWER) blue whale cruise, Chile. Paper SC/50/Rep2 presented to the IWC Scientific Committee, April 1998. 40 pp.

Findlay, K., Thornton, M., Stafford, K. and Best, P.B. 2012. The South African Blue Whale Project (SABWP) - An introduction and objectives for the forthcoming year. Paper SC/64/O16 presented to the IWC Scientific Committee, June 2012. 7 pp.

Ford, J.K.B. 1989. Acoustic behaviour of resident killer whales (*Orcinus orca*) off Vancouver Island, British Columbia. Canadian Journal of Zoology 67(3): 727–745.

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

Gedamke, J., and Robinson, S.M. 2010. Acoustic survey for marine mammal occurrence and distribution off East Antarctica (30-80°E) in January-February 2006. Deep-Sea Research Part II 57: 968–981.

Ichihara, T. 1966. The pygmy blue whale, *Balaenoptera musculus brevicauda*, a new subspecies from the Antarctic. In: Norris, K.S. (ed) Whales, dolphins, and porpoises. pp. 79–111. University of California Press, Berkeley- Los Angeles, CA. i- xv+789 pp.

Jefferson, T.A., Leatherwood, S. and Webber, M.A. 1993. FAO species identification guide. Marine mammals of the world. Rome: FAO. i-viii+320 pp.

Kato, H., Bannister, J., Burton, C., Ljungblad, D., Matsuoka, K., and Shimada, H. 1996. Report on the Japan/IWC blue whale cruise 1995-96 off the southern coast of Australia. Paper SC/48/SH9 presented to the IWC Scientific Committee, June 1996. 35 pp.

Kelly, N., Miller, B., Peel, D., Double, M.C., De la Mare, W. and Gales, N. 2012. Strategies to obtain a new circumpolar abundance estimate for Antarctic blue whales: survey design and sampling protocols. Paper SC/64/SH10 presented to the Scientific Committee of the International Whaling Commission, June 2012. 34 pp.

LeDuc, R.G., Dizon, M.G., Pastene, L.A., Kato, H., Nishiwaki, S., Leduc, C.A. and Brownell Jr, R.L. 2007. Patterns of genetic variation in Southern Hemisphere blue whales and the use of assignment test to detect mixing on the feeding grounds. Journal of Cetacean Research and Management 9(1): 73–80.

Ljungblad, D.K. and Stafford, K.M. 2005. Circumpolar cruise, Area V. 2005. Abstract presented at the 16th Biennial conference on the Biology of Marine Mammals, San Diego CA. p 171.

Ljungblad, D. K., Stafford, K. M., Shimada, H., and Matsuoka, K. 1997. Sounds attributed to blue whales recorded off the southwest coast of Australia in December 1995. Reports of the International Whaling Commission 47: 435-439.

Ljungblad, D.K., Clark, C.W. and Shimada, H. 1998. A comparison of sounds attributed to pygmy blue whales (*Balaenoptera musculus brevicauda*) recorded south of the Madagascar Plateau and those attributed to 'true' blue whales (*Balaenoptera musculus*) recorded of Antarctica. Reports of the International Whaling Commission 48: 439–442.

Mackintosh, N.A. and Wheeler, J.F.G. 1929. Southern blue and fin whales. Discovery Reports I: 259–540.

Marques, T.A., Thomas, L., Martin, S., Mellinger, D., Ward, J., Moretti, D., Harris, D., and Tyack, P. 2013. Estimating animal population density using passive acoustics. Biological Reviews 8: 287–309.

Matworks Inc, 2014. MATLAB R2014a version 8.3.0.532. The MathWorks, Inc., Natick, Massachusetts, United States.

McDonald, M.A. 2004. DIFAR hydrophones applied to whale research. Canadian Acoustics 32(2): 155–160.

McDonald, M.A., Hildebrand, J.A. and Mesnick, S.L. 2006. Biogeographic characterization of blue whale song worldwide: using song to identify populations. Journal of Cetacean Research and Management 8: 55–65.

McDonald, M.A., Hildebrand, J.A., and Mesnick, S.L. 2009. Worldwide decline in tonal frequencies of blue whale songs. Endangered Species Research 9: 13–21.

Mellinger, D.K., 2001. Ishmael 1.0 User’s Guide. NOAA Technical Memorandum OAR PMEL-120, available from NOAA/PMEL/OERD, 2115 SE OSU Drive, Newport, OR 97365–5258.

Mellinger, D.K. and Clark, C.W. 2003. Blue Whale (*Balaenoptera musculus*) sounds from the North Atlantic. Journal of the Acoustical Society of America 114: 1108–1119.

Miller, B.S., Barlow, J., Calderan, S., Collins, K., Leaper, R., Kelly, N., Peel, D., Olson, P., Ensor, P., and Double, M.C. 2013a. Long-range acoustic tracking of Antarctic blue whales. Paper SC/65a/SH18 presented to the Scientific Committee of the International Whaling Commission, May 2013. 17 pp.

Miller, B.S., A. Growcott, E. Slooten, and Dawson, S.M. 2013b. Acoustically derived growth rates of sperm whales (*Physeter macrocephalus*) in Kaikoura, New Zealand. Journal of the Acoustical Society of America 134: 2438-2445.

Miller, B.S., Collins, K., Barlow, J., Calderan, S., Leaper, R., McDonald, M., Ensor, P., Olson, P.A., Olavarria, C., and Double, M.C. 2014. Blue whale vocalizations recorded around New Zealand: 1964-2013. Journal of the Acoustical Society of America 135: 1616–1623.

Miller, B.S., Barlow, J., Calderan, S., Collins, K., Leaper, R., Olson, P., Ensor, P., Peel, D., Donnelly, D., Andrews-Goff, V., Olavarria, C., Owen, K., Rekdahl, M., Schmitt, N., Wadley, V., Gedamke, J., Gales, N., and Double, M.C. 2015. Validating the reliability of passive acoustic localisation: a novel method for encountering rare and remote Antarctic blue whales. Endangered Species Research 26: 257–269.

Oleson, E.M., Calambokidis, J., Barlow, J. and Hildebrand, J.A. 2007. Blue whales visual and acoustic encounter rates in the Southern California Bight. Marine Mammal Science 23(3): 574–597.

Payne, R.S. and Guinee, L.N. 1983. Humpback whale (*Megaptera novaeangliae*) songs as an indicator of “stocks”. Pp 333-358. In: Payne, R. (ed) Communication and behavior of whales. Westview Press, Boulder CO. 643 pp.

Pitman, R.L. and Ensor, P. 2003. Three forms of killer whales (*Orcinus orca*) in Antarctic waters. Journal of Cetacean Research and Management 5: 131–139.

Pitman, R.L., Durban, J.W., Greenfelder, M., Guinet, C., Jorgensen, M., Olson, P.A., Plana, J., Tixier, P., and J.R. Towers. 2010. Observations of a distinctive morphotype of killer whale (*Orcinus orca*), type D, from sub-Antarctic waters. Polar Biology 34: 303–306.

R Development Core Team, 2015. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. URL http://www.R-project.org/

Rankin, S., Ljungblad, D., Clark, C., and Kato, H., 2005. Vocalizations of Antarctic blue whales, *Balaenoptera musculus intermedia*, recorded during the 2001/2002 and 2002/2003 IWC/SOWER circumpolar cruises, Area V, Antarctica. Journal of Cetacean Research and Management 7: 13–20.

Reeves R.R., Clapham, P.J., Brownell, Jr., R.L. and Silber, G.K. 1998. Recovery plan for the blue whale (*Balaenoptera musculus*). National Marine Fisheries Service, Silver Spring, MD. 42 pp.

Rice, D.W. 1998. Marine mammals of the world: systematics and distribution. Society for Marine Mammalogy Special Publication No. 4. Lawrence, KS: Allen Press.

Riesch, R. and Deecke, V.B. 2011. Whistle communication in mammal-eating killer whales (*Orcinus orca*): further evidence for acoustic divergence between ecotypes. Behavioral Ecology and Sociobiology 65(7): 1377–1387.

Rogers, T.L., and Cato, D.H. 2002. Individual variation in the acoustic behaviour of the adult male leopard seal, *Hydrurga leptonyx*. Behaviour 139(10): 1267–1286.

RStudio Team. 2015. RStudio: Integrated Development for R. RStudio, Inc., Boston, MA. URL http://www.rstudio.com/.

Samaran, F., Adam, O. and Guinet, C. 2010a. Discovery of a mid-latitude sympatric area for two Southern Hemisphere blue whale subspecies. Endangered Species Research 12(2): 157–165.

Samaran, F., Guinet, C., Adam, O., Motsch, J.-F., and Cansi, Y. 2010b. Source level estimation of two blue whale subspecies in southwestern Indian Ocean. Journal of the Acoustical Society of America 127(6): 3800–3808.

Samaran, F., Stafford, K., Gedamke, J., Van Opzeeland, I., Miller, B.S., Adam, O., Baumgartner, M., Mussoline, S., and Pressiat, G. 2012. Acoustic trends in abundance, distribution, and seasonal presence of Antarctic blue whales and fin whales in the Southern Ocean. In: Annual Report of the Southern Ocean Research Partnership (SORP) 2011/12. Compiled by: E. Bell. Paper presented to the Scientific Committee of the International Whaling Commission, Panama City, Panama. SC/64/O13.

Samaran, F., Stafford, K.M., Branch, T.A., Gedamke, J., Royer, J-Y., Dziak, R.P. and Guinet, C. 2013. Seasonal and geographic variation of southern blue whale subspecies in the Indian Ocean. PLos ONE 8(8): e71561.

Sekiguchi, K., Fukotome, K., Morse, L., Shinyashiki, Y. and Oedekoven, C. 2010. 2009-2010 International Whaling Commission-Southern Ocean Whale and Ecosystem Research (IWC SOWER) cruise. Paper SC/62/IA1 presented to the IWC Scientific Committee, June 2010. 56 pp.

Shabangu, F.W. and Findlay, K. 2014. Passive acoustic monitoring of marine mammals in South Africa, with special reference to Antarctic blue whales. pp. 153-73. In: Funke, N., Claassen, M., Meissner, R. and Nortje, K. (eds) Reflections on the state of research and development in the marine and maritime sectors in South Africa. Council for Scientific and Industrial Research, Pretoria. i-ii+316pp.

Shabangu, F.W., Yemane, D., Stafford, K.M., Ensor, P. and Findlay, K.P. 2017. Modelling the effects of environmental conditions of the acoustic occurrence and behavior of Antarctic blue whales. PLoS ONE 12(2): e0172705.

Širovic, A., Hildebrand, J.A., Wiggins, S.M., McDonald, M.A., Moore, S.E. and Thiele, D. 2004. Seasonality of blue and fin whale calls and the influence of sea ice in the Western Antarctic Peninsula. Deep-Sea Research II 51: 2327–2344.

Širovic, A., Hildebrand, J.A. and Wiggins, S.M. 2007. Blue and fin whale call source levels and propagation range in the Southern Ocean. Journal of the Acoustical Society of America 122: 1208–1215.

Sremba, A.L., Hancock-Hanser, B., Branch, T.A., LeDuc, R.L. and Baker, C.S. 2012. Circumpolar diversity and geographic differentiation of mtDNA in the critically endangered Antarctic blue whale (*Balaenoptera musculus intermedia*). PLos ONE 7(3): e32579.

Stafford, K.M., Nieukirk, S.L. and Fox, C.G. 1999. Low-frequency whale sounds recorded on hydrophones moored in the eastern tropical Pacific. Journal of the Acoustical Society of America 106: 3687–3698.

Stafford, K.M., Bohnenstiehl, D.W.R., Tolstoy, M., Chapp, E., Mellinger, D.K. and Moore, S.E. 2004. Antarctic-type blue whale calls recorded at low latitudes in the Indian and eastern Pacific Oceans. Deep-Sea Research I 51: 1337–1346.

Terhune, J.M., Quin, D., Dell’Apa, A., Mirhaj, M., Plötz, J., Kindermann, L., and Bornemann, H. 2008. Geographic variations in underwater male Weddell seal Trills suggest breeding area fidelity. Polar Biology 31(6): 671–680.

Thomas, P.O., Reeves, R.R. and Brownell Jr., R.L. 2015. Status of the world’s baleen whales. Marine Mammal Science 32(2): 682–734.

Thompson, P.O., Findley, L.T., Vidal, O. and Cummings, W.C. 1996. Underwater sounds of blue whales, Balaenoptera musculus, in the Gulf of California, Mexico. Marine Mammal Science 12(2): 288–292.

Van Opzeeland, I., Samaran, F., Stafford, K.M., Findlay, K., Gedamke, J. Harris, D. and Miller, B.S. 2014. Towards collective circum-Antarctic passive acoustic monitoring: The Southern Ocean Hydrophone Network (SOHN). Polarforschung 83(2): 47–61.

Van Parijs, S. and Clark, C.W. 2006. Long term mating tactics in an aquatic mating pinniped – the bearded seal, *Erignathus barbatus*. Animal Behavior 72: 1269–1277.

Ward, R., Gavrilov, A.N., and McCauley, R.D. 2017. “Spot” call: A common sound from an unidentified great whale in Australian temperate waters. Journal of the Acoustical Society of America 142(2): EL231– EL236.

Chapter 4: Modelling the effects of environmental conditions on the acoustic occurrence and behaviour of Antarctic blue whales

---

Published as: Shabangu, F.W., Yemane, D., Stafford, K.M., Ensor, P. and Findlay, K.P. 2017. Modelling the effects of environmental conditions of the acoustic occurrence and behavior of Antarctic blue whales. PLoS ONE 12(2): e0172705. doi:10.1371/journal.pone.0172705.

Abstract

Harvested to perilously low numbers by commercial whaling during the past century, the large-scale response of Antarctic blue whales *Balaenoptera musculus intermedia* to environmental variability is poorly understood. This study uses acoustic data collected from 586 sonobuoys deployed in the austral summers of 1997 through 2009, south of 38^{o}S, coupled with visual observations of blue whales during the IWC SOWER line-transect surveys. The characteristic Z-call and D-call of Antarctic blue whales were detected using an automated detection template and visual verification method. Using a random forest model, we showed the environmental preferences pattern, spatial occurrence and acoustic behaviour of Antarctic blue whales. Distance to the southern boundary of the Antarctic Circumpolar Current (SBACC), latitude and distance from the nearest Antarctic shores were the main geographic predictors of blue whale call occurrence. Satellite-derived sea surface height, sea surface temperature, and productivity (chlorophyll-a) were the most important environmental predictors of blue whale call occurrence. Call rates of D-calls were strongly predicted by the location of the SBACC, latitude and visually detected number of whales in an area while call rates of Z-call were predicted by the SBACC, latitude and longitude. Satellite-derived sea surface height, wind stress, wind direction, water depth, sea surface temperatures, chlorophyll-a and wind speed were important environmental predictors of blue whale call rates in the Southern Ocean. Blue whale call occurrence and call rates varied significantly in

response to inter-annual and long term variability of those environmental predictors. Our results identify the response of Antarctic blue whales to inter-annual variability in environmental conditions and highlighted potential suitable habitats for this population. Such emerging knowledge about the acoustic behaviour, environmental and habitat preferences of Antarctic blue whales is important in improving the management and conservation of this highly depleted species.

4.1 Introduction

Antarctic blue whales *Balaenoptera musculus intermedia* were widely distributed in the Southern Ocean prior to commercial whaling (Rice, 1998; Best, 2007; Branch *et al.* 2007). The current population status of Antarctic blue whale remains critically low five decades after the end of whaling; however, there are recent signs of population increase (Branch *et al.* 2004; Thomas *et al.* 2016). These whales feed predominantly in the euphausiid-rich waters of the Southern Ocean during the austral summer through autumn; and they have been presumed to fast during their over-wintering periods in low latitudes (Mackintosh and Wheeler, 1929; Branch *et al.* 2007). Acoustic monitoring efforts have detected their calls as far north as 8° S in the eastern Pacific and 8°S in the Indian Oceans respectively (Stafford *et al.* 2004; Samaran *et al.* 2013).

The very loud (up to ~188 dB re 1uPa @1m) sounds produced by Antarctic blue whales enable passive acoustic survey instruments to detect Antarctic blue whales over considerable distances (Samaran *et al.* 2010; Miller *et al.* 2013) and thereby investigate the behaviour, ecology, and habitat preferences of these critically endangered whales *in situ* (Thompson *et al.* 1996; Širović *et al.* 2007). Antarctic blue whales produce both characteristic three part sounds, known as Z-calls that are frequency modulated from 28 to 17 Hz lasting up to 18 s (Rankin *et al.* 2005), and D-calls which are variable frequency modulated signals over 106-25 Hz. The Z-calls are produced in long bouts (Rankin *et al.* 2005) and are thought to be a male reproductive display while D-calls are produced during feeding behaviour by both sexes

(Oleson *et al.* 2007). Recent detections of blue whale D-calls indicate that part of the population are feeding and resident at low latitudes in the Indian Ocean year-round (Samaran *et al.* 2013). Little is known about the relationship of call rates of Antarctic blue whales and environmental parameters or the effects on environmental variability on blue whale occurrence in the Southern Ocean.

The Southern Ocean is the only ocean basin that is circumpolar; it contains the strong eastward flowing Antarctic Circumpolar Current (ACC) and is the connecting link at all depths for water mass exchanges between the earth's major ocean basins (White and Peterson, 1996; Rintoul, 2011). The southern boundary of the ACC is a region of upwelling (i.e. the Antarctic Divergence) that occurs at the Southern Front (Nowlin and Klinck, 1986). Inter-annual variations in the atmospheric pressure at sea level, wind stress, sea surface temperature, cloud cover, and sea-ice extent over the Southern Ocean are important drivers of the ocean circulation in the region (White and Peterson, 1996; Behrenfeld *et al.* 2006; Moore, 2009; Rahmstorf, 2011). Annual change in sea ice extent is the major oceanographic/climatic feature of the Southern Ocean and controls the morphological and physiological adaptations of whales, seals, and penguins to life in these frigid waters both through its presence as a physical barrier and as critical habitat for Antarctic krill, *Euphausia superba* (Elliott and Simmonds, 2007; Riffenburgh, 2007; Nicol *et al.* 2008).

Satellite measurements of ocean colour are the principal remote-sensing tool for measuring ocean productivity and its response to climate change/variability (e.g., Behrenfeld *et al.* 2006; Kahru and Mitchell, 2010), consequently sea surface chlorophyll-a concentrations (measured as ocean colour) are often used as proxy for primary productivity (e.g., Swart *et al.* 2014). Remotely sensed environmental parameters have the potential to identify biological hotspots for cetaceans and to therefore establish areas of marine conservation priority (e.g., Etnoyer *et al.* 2006; Elliott and Simmonds, 2007; Ballance, 2009).

Here we present the results of analyses on the call type distribution (as call occurrence) and acoustic behaviour (as call rates) of Antarctic blue whales as a function of satellite-derived environmental parameters using the circumpolar passive acoustic measurements during the Southern Ocean Whale and Ecosystem Research (SOWER) program of the International Whaling Commission (IWC), hereafter IWC SOWER. The IWC SOWER program was a long series (1978-2009) of line-transect survey cruises directed primarily at obtaining abundance estimates for Antarctic minke whales (Matsuoka *et al.* 2003a) and for a period of 14 years (1997-2009) also incorporated a blue whale research component which included collection of acoustics recordings. This paper contains the interpretation of an applied modelling exercise fitting one model to the sets of environmental variables to the observed call occurrence and acoustic behaviour of Antarctic blue whales. Random forest (RF) model reveals the response of Antarctic blue whales to environmental variability and also highlight the importance of environmental variability in monitoring the status of Antarctic blue whales.

4.2 Materials and Methods

4.2.1 Developing and testing detectors

We analysed passive acoustic data collected using both sonobuoys and towed hydrophones during the IWC SOWER cruises conducted south of 55°S to the ice edge from December to February of 1996/97 to 2008/09. Some acoustic observations extended as far north as 38°S during transits to and from the Antarctic (Figure 4.1). Acoustic data analyses were performed in the eXtensible Bio-Acoustic Tool (XBAT) software (Figueroa, 2006) implemented as a MATLAB routine (MathWorks Inc, 2014) with automatic detection templates for Z- and D-calls developed and applied in XBAT. A complete Z-call with all the three-units (Figure 4.2a) and the D-call downsweeping from 90-30 Hz (Figure 4.2b) were used as templates because they both contained most of the energy of the calls. The first unit (8-12 s) of the Z-call is at 28 Hz (Figure 4.2a1), the second unit is relatively short (2-5 s) and downsweeps from 28 to 19 Hz (Figure 4.2a2), and the third unit (8-12 s) is a slightly frequency-modulated between

19 and 17 Hz (Figure 4.2a3). Multi-harmonics of Z-calls (Figure 4.2a) reflect the strong sound energy level at the receiver usually associated with that sounds produced by animals closer to the recorder whilst faint Z-calls with weak energy levels are those produced by animals farther from the recorder (Figure 4.2b).

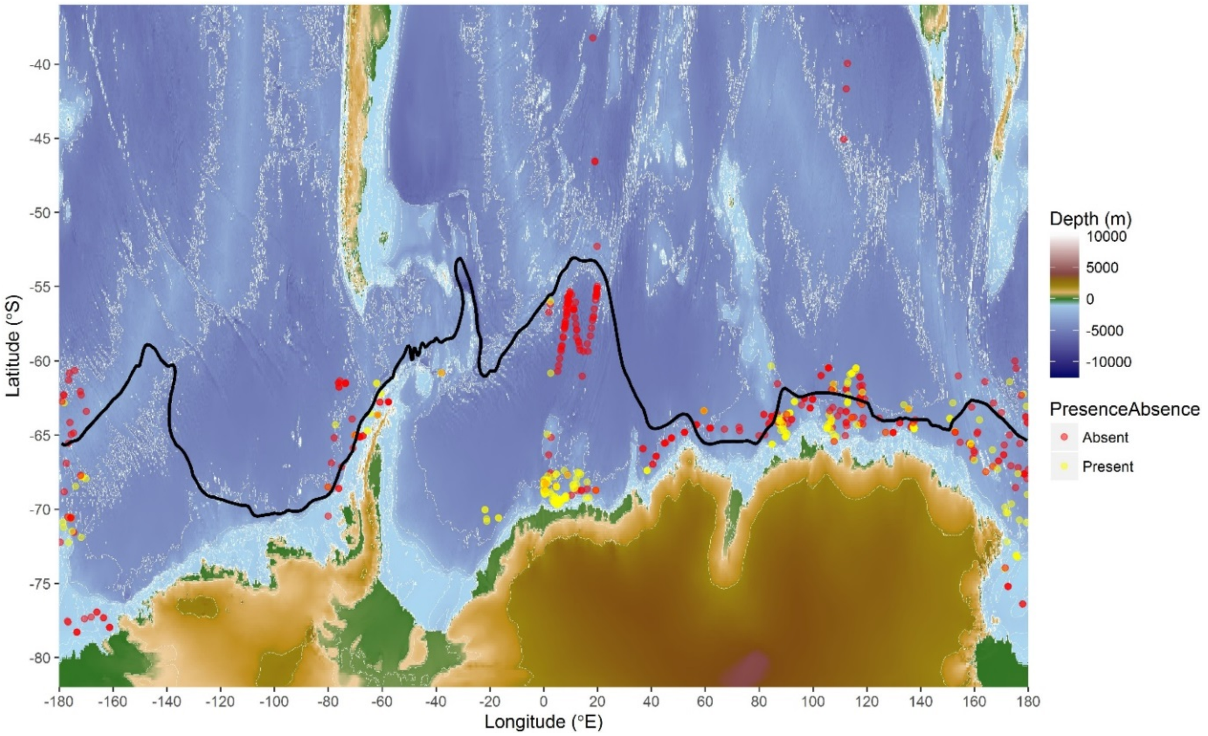


Figure 4.1. Map showing the location of sonobuoy deployments. Those with acoustic detections of Antarctic blue whales are shown as yellow dots. Locations with no blue whale detections are shown as red dots. The black line represents the positions of SBACC based on Orsi *et al.* (1995).

The template detector method operates on an acoustic time series of spectrograms by constructing a correlation kernel for the vocalization (Mellinger and Clark, 2000). Calls were recognized from spectrograms by cross-correlating with the template kernel based on a similarity level above a set threshold. We used effective detection templates from 1997 to automatically detect Z- and D-calls from 1997 to 2004 acoustic data, and then templates from 2009 were used for 2006 to 2009 data to account for changes in fundamental frequency of the Z-call (Gavrillov *et al.* 2012). In order to assess the performance of the automated detectors, the entire acoustic dataset (1,518 hours) was assessed visually to estimate the number of false positive (detections that were not blue whale calls) and false negative (missed blue whale calls) calls. The visually identified false positive detections were manually excluded from further acoustic analyses. Visually identified false negatives were manually incorporated into the final total call number calculations.

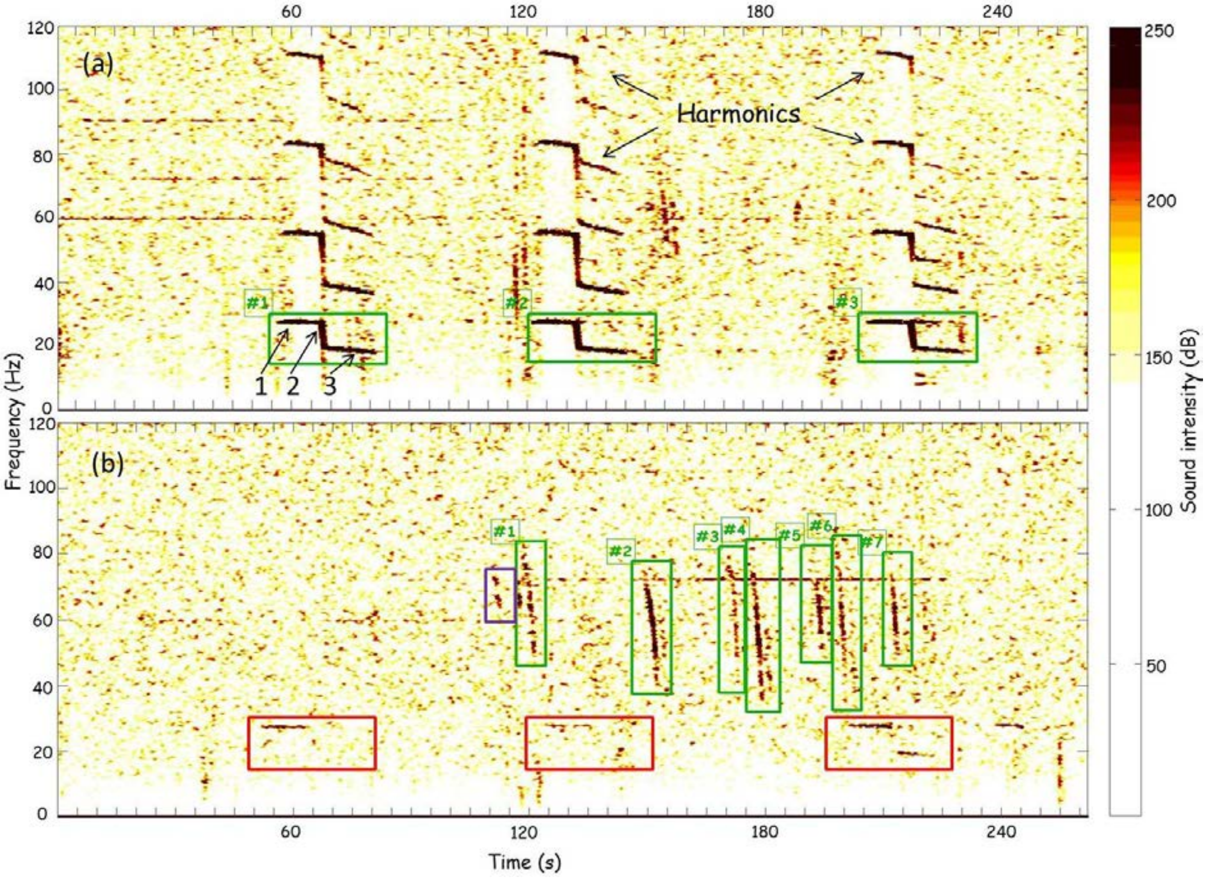


Figure 4.2. Spectrograms showing the two types of Antarctic blue calls; a) the three-unit (1, 2, and 3) frequency modulated 28 to 17 Hz blue whale Z-calls (green rectangles), and b) high frequency 90-30 Hz downsweeping D-calls (green rectangles). Each green rectangle represents calls detected by the detector and the hash (#) represents the count of each call detected. Also presented are one-unit faint Z-calls (red rectangles) and faint D-call (purple rectangle). Spectrogram parameters: frame size 1.28 s, 25% overlap, FFT size 4,096 points, Hanning window.

4.2.2 Outcomes of detectors

We tested six different thresholds from 20% to 70% by increments of 10% to determine optimal thresholds for our analyses (Figure 4.3). The 20% detection threshold was best suited to our study as it produced the fewest missed calls compared to other thresholds, although the number of false positives was much higher. Low thresholds are generally known to be effective at scanning through large data set such as the one used here (Mellinger and Clark, 2000). False negative error rate refers to the percentage of false negative calls. Detection templates from 1997 produced false negative error rates of 58% for Z-calls and 79% for D-calls; and accuracy rates of 42% for Z-calls and 21% for D-calls (Figure 4.3). On the other hand, templates from 2009 produced false negative error rates of 17% for Z-calls and 29% for D-calls; and accuracy rates of 83% for Z-calls and 71% for D-calls (Figure 4.3).

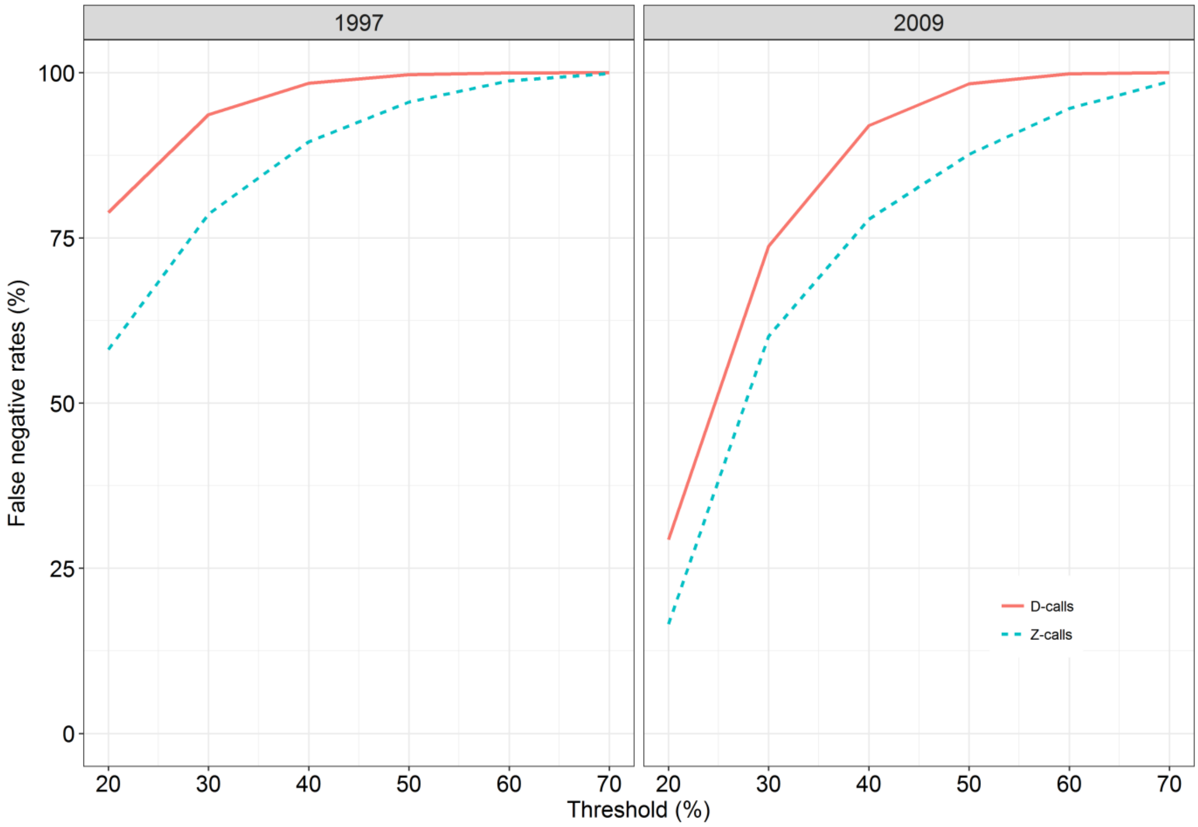


Figure 4.3. False negatives percentage at different thresholds for Z- and D-calls using the 1997 (left) and 2009 (right) detection templates.

4.2.3 Detector caveats

Automated detection of animal vocalizations is effective at accelerating acoustic data analyses and producing more robust results than human visual sound detections (Mellinger and Clark, 2000; Širović, 2016). The very high false negative error rates and low accuracy rates of the automatic detector produced by the 1997 templates could indicate the identified change of blue whale call frequency shift over time (Gavrillov *et al*. 2012; Širović, 2016). In contrast, the 2009 templates analysed data within relatively comparable time periods, hence produced relatively better detection performances. The fact that not all recorded Z-calls contained the three-units of the complete call used in the template and also that not all recorded D-calls contained frequency downsweep range (Figure 4.2) of the detector could have induced challenges to this automatic cross-correlation detection method. Noise, possibly from airguns and other unknown sources, contributed false positive error rates for both call types. Overall, the XBAT template detector algorithm was useful at detecting highly stereotyped blue whale calls even though it yielded higher false negative rates and lower accuracy rates than other studies (e.g., Mellinger and Clark, 2000; Gavrillov *et al.* 2012; Širović, 2016). Nonetheless, the method could be improved by an allowance to simultaneously use of more than one call template. For example, the simultaneous use of 3 templates for the Z-calls, i.e. one complete three-unit call template, plus a two-unit call template and one unit call template (Figure 4.2) and/or the use of templates from different years simultaneously. Such multi-template will permit the use of high thresholds without inducing high false negative error rates.

Širović (2016) observed that intra- and inter-annual changes of call frequency affected the automatic detection of Northeast Pacific blue whale *B. m. musculus* calls, and recommended a new detection template for each year. More detailed estimates of the changes of start and end frequency of Antarctic blue whale calls over time from this IWC SOWER acoustic dataset and the most recently recorded blue whale calls both in the Southern Ocean and low latitudes will inform on the long term behavioural changes in blue whale vocalizations and whether such templates for each year should be used to reduce false detections.

4.2.4 Whale numbers and groups

Acoustic stations (484 total) were differentiated into two types: type 1 stations were sonobuoy deployments in association with a visual sighting of blue whales (107 stations); type 2 stations were deployments without blue whales visually detected (377 stations). Estimates of numbers of individual blue whales and of blue whale groups observed in type 1 acoustic stations were sourced from the acoustic data forms completed during the IWC

SOWER cruises as provided by the IWC Secretariat and from the line transect visual survey sighting forms, if whales were seen during the normal line transect visual surveys. The date, time of the day, and station number of each acoustic recording were used to link blue whale sightings to the acoustic results. In instances where blue whale calls were detected from the analyses but not heard during the *in situ* monitoring, the whale numbers and number of groups seen were assumed to be zero unless a matching time and position with a whale was found in the visual sighting forms.

4.2.5 Call rate calculation

The number of calls recorded from each sonobuoy and/or hydrophone deployment were allocated to each station as documented in the IWC SOWER cruise reports and acoustic forms. The recording duration of each deployment was determined during acoustic data analyses, and the station duration was calculated as the sum of durations of recordings from that station. Call rates of both the Z- and D-calls were calculated for each station as the total number of calls divided by the station duration to give calls per hour at each station. Call rates were not determined as calls per hour per individual, however, but as call rates per group(s) per hour due to the difficulty in determining the precise number of vocally active animals within any groups. Results of call rates were thereafter assigned into day (06:00 to 18:00 local time) and night (18:00 to 06:00) depending on their recoding time before fitting to the models, although such day/night differentiation reflected the survey mode of the vessel rather than Antarctic summer light regimes as visual monitoring only took place from 06:00-18:00 each day.

4.2.6 Environmental data used

Satellite chlorophyll-a (chl-a) measurements were obtained from the globally blended and binned high resolution level-3, case 1 water GlobColour project (Maritorena *et al.* 2010) that merges the remotely sensed ocean colour measurements from three satellite data sources: MERIS (Medium Resolution Imaging Spectrometer), MODIS-Aqua (Moderate-resolution Imaging Spectroradiometer) and SeaWiFS (Sea-viewing Wide Field-of-View Sensor). Thus, only the SeaWiFS measured global chlorophyll-a data were available for December 1997 through February 2002. The GlobColour chlorophyll-a data were extracted at a monthly temporal resolution and 0.05° (approximately 4 km) spatial resolution in the regions of the South Ocean surveyed during the IWC SOWER cruises. Three month chl-a averages were calculated for each surveyed resolution point where chl-a values were not available due to cloud cover. All three months used in this study fell within the same summer season associated with sustained phytoplankton blooms (e.g., Swart *et al.* 2014). However, the December 1997 average chl-a concentrations were used for January and February 1997 because there were no chl-a data for those months as the GlobColour chl-a time series only began in September 1997. Data were processed in R statistical software package (R Core Team, 2015) using the following packages: Matrix (Bates and Maechler, 2015), stringr (Wickham, 2015a), and ncdf4 (Pierce, 2014). The isin.convert.R function from www.menugget.blogspot.com was used to convert the binned GlobColour chl-a data to a grid format.

Satellite-derived sea surface temperatures (SST) were obtained from the Group for High Resolution Sea Surface Temperature (GHRSST) global Level 4 sea surface temperature analysis produced daily on a 0.25° grid spatial resolution at the NOAA National Climatic Data Center (Donlon *et al.* 2007). GHRSST product uses optimal interpolation (OI) boosted by data from the 4 km Advanced Very High Resolution Radiometer (AVHRR) Pathfinder Version 5 time series (when available, otherwise operational NOAA AVHRR data are used) and *in situ* ship and buoy observations. The OI analysis is a daily average SST that is bias adjusted using a spatially smoothed 7-day *in situ* SST average and is therefore tuned to about 0.3 meter (National Climatic Data Center, 2007). The Open-source Project for a Network Data Access Protocol (OPeNDAP) facility was used to get SST data via the Environmental Research Division's Data Access Program (ERDDAP) data server using the rerddap (Chamberlain, 2016) and xtractomatic (Mendelssohn, 2015) packages in R as a simple, consistent method to download subsets of data from a gridded dataset via a specially formed Uniform Resource Locator (URL). The daily SST products were subsequently averaged into monthly SST products to standardise with other variables that were available only in monthly resolutions.

Sea surface height (SSH) daily measurements were obtained from the Archiving, Validation and Interpretation of Satellite Oceanographic (AVISO) data program using the erdTAssh1day function in R. AVISO SSH product combines data from up to six multiple satellites, including Jason-1, TOPEX/Poseidon, the European Remote Sensing (ERS) Satellites 1 and 2 and their successor, the Environmental Satellite (ENVISAT), and the Geodetic Satellite (GEOSAT) (Ducet *et al.* 2000). The monthly SSH was subsequently computed from the daily product to standardise with other variables that were available only in monthly resolutions. The Southern Ocean bathymetry data (Figure 4.1) were obtained from the ETOPO1 global relief model that integrates land topography and ocean bathymetry using the Earth's surface 1 arc-minute global relief model (Amante and Eakins, 2009).

Monthly blended vector sea surface wind speed and direction (at 10 m above sea level) and sea surface wind stresses were downloaded from ftp://eclipse.ncdc.noaa.gov/pub/seawinds/SI/ and processed in R using custom built functions. These wind speeds and directions are blended from multiple satellites (up to six, including the DMSP Special Sensor Microwave/Imager (SSM/I), the Tropical Rainfall Measuring Mission (TRMM), Microwave Imager (TMI), the Quick Scatterometer (QuikSCAT) and the Advanced Microwave Scanning

Radiometer-EOS (AMSR-E)) observations, on a global 0.25 degree spatial grid and a 6-hourly temporal resolution (see Zhang *et al.* 2006). The sea surface wind stress, tau (τ), was used for our modelling since it is the wind stress amplitude as a scalar mean given in N m^{-2}. Distance in kilometres (km) to the nearest Antarctic coastline was calculated using the custom developed function defined as the shortest distance to the Antarctic coastline for each of the acoustic stations.

Monthly sea ice extents were downloaded from the G02135 dataset (Fetterer *et al.* 2016) at the National Snow and Ice Data Centre (NSIDC) data pool repository: ftp://sidads.colorado.edu/DATASETS/NOAA/G02135/shapefiles/. Sea ice index version 2 uses V1.1 of the sea ice concentrations from Nimbus-7 SMMR and DMSP SSM/I-SSMIS Passive Microwave Data (also known as GSFC product) as the input data source for the final portion of the Sea Ice Index record. The data are a level-3 gridded product, mapped to a polar stereographic grid at a spatial resolution of 25 km. Data were processed using the rgdal mapping package (Bivand *et al.* 2015) in R. Distances (km) of acoustic stations to the ice edge were calculated.

We used positions of the southern boundary of ACC (Figure 4.1) defined by Orsi *et al.* (1995) using historical hydrographic data from the Southern Ocean. The data with the positions were downloaded from http://gcmd.nasa.gov/records/AADC_southern_ocean_fronts.html. The distance (km) of acoustic stations to the closest southern boundary of ACC calculated using a custom design R function.

4.2.7 Model choice

Before modelling the data, we determined the effects of multi-collinearity between predictor variables using the generalised variance inflation factors (GVIF; Fox and Monette, 1992) implemented through the car library (Fox and Weisberg, 2011) in R. GVIF is used to describe how much multicollinearity (correlation between predictors) exists in regression analyses such as Random Forest (RF). Low GVIF values (around one) indicate weak or no correlations, GVIF values around five indicate moderate correlations; and values of 10 or more indicate strong correlations (O’Brien, 2007; Hair *et al.* 2009). Our GVIF values ranged from 1.1 to 5.8 when excluding distance to the ice edge but reach a maximum of 8.9 when including distance to the ice edge, thus distance to the ice edge was eliminated as it is highly correlated with latitude and SST and its GVIF value was close to the elimination threshold of 10 (Hair *et al.* 2009).

RF models are known to provide higher performance and have a number of advantages over standard regression methods like generalized additive models (Leathwick *et al.* 2006; Elith *et al.* 2008; James *et al.* 2013). RF uses a set of unpruned decision trees that are bootstrapped as they grow with trained sample data, and rely on randomly chosen subsets of the predictor variables as candidate splitting tree nodes (Hastie *et al.* 2009; James *et al.* 2013). RF does not discount some variables completely and candidate split-variable selection increases the probability of any solitary variable being included (Hastie *et al.* 2009; James *et al.* 2013). A generalised boosted regression trees model (GBM) was also used to model the occurrence and acoustic behaviour of blue whales but RF was found to be better at detecting signals and had a higher prediction accuracy than GBM.

RF model was used to determine which environmental parameters influenced the acoustic occurrence (presence/absence of calls) and acoustic behaviour (call rates) of the Antarctic blue whales during the Southern Ocean summer. The chl-a data were log-transformed before model fitting due to the skewness of their distribution. Pearson’s correlation coefficients (r) were calculated to measure the linear correlation (dependence) between the call rate of each call type.

The relative importance of predictor variables in the model was assessed by computing the influence of each of the variables on the prediction error of the model. The relative importance of each of the variables in the model can be computed by permuting the Out Of the Bag (OOB)/test data sample or by determining the decrease in node impurity, as measured by the mean sum of squares, resulting from splitting of the variable of interest and averaging over all trees. For each tree the prediction error is computed on the OOB data and the permuted data are calculated and averaged across all trees and normalized by the standard deviation of the difference. This normalized index is calculated for each of the variables and used as index of relative importance. RF model was fitted to determine the importance of the following predictors on blue whale occurrence: longitude, latitude, log-transformed chl-a, SST, SSH, water depth, distance from the shoreline, distance from the nearest SBACC, wind stress, wind speed, wind direction, station duration, day/night, and month. RF model for call rates determined the importance of the following predictors: longitude, latitude, log-transformed chl-a, SST, SSH, water depth, distance from the shoreline, distance from the nearest SBACC, wind stress, wind speed, wind direction, station type, whale numbers, day/night, month and whale groups.

The RF optimal parameter configurations for both call rate models were: the number of growing trees ntrees = 500 for Z-calls and 3,000 for D-calls; the splitting minimum size of terminal nodes of trees nodesize = 2 for Z-calls and 1 for D-calls; and the number of call rates randomly selected at tree node mtry = 3 for Z-calls and 2 for D-calls. The RF optimal parameter configurations for blue whale occurrence modelling: ntree = 500, nodesize = 1, and mtry = 6.

Since the detection ranges of sonobuoys were not estimated here, we ran the RF model with and without sighting data using the above optimal parameter configurations to evaluate effects of detection ranges on blue whale call rates. The model produced relatively similar sets of outputs in both cases. The modelling was performed with the R statistical software package using libraries randomForest (Breiman *et al.* 2014) and ranger (Wright and Ziegler 2016).

We used the 5-fold cross-validation (5-foldCV) and the Leave Group Out Cross Validation (LGOCV, also known as Monte-Carlo cross validation), to quantify the predictive accuracy of our classification model type between the predicted values and observed values of blue whale occurrence (Kuhn and Johnson, 2013). The area under the receiver operating characteristic curve (AUC) was used to measure the predictive accuracy of our classification model, i.e. how well the model correctly classified the classes included in the model (here the presence/absence of call whales). AUC normally takes values between 0.5 and 1, where values closer to 1 indicate better classification ability. The number of replicates (nrep) was set to 200 for the model performance assessment.

Using 70% of the data for training and the remaining for validation, the performance of RF for call rate modelling was assessed. Root mean square prediction error (RMSPE) was used to measure the difference between values predicted by the model and observed values. In addition, Spearman's rank correlation coefficient (rho) was applied as a qualitative measure of the performance of the model. A low RMSPE value indicates a better model whereas the opposite is true for rho.

The AUC values indicated better performance for RF than GBM (Table 4.1). The correlations between the predicted and observed values of both call rates were also highest for RF (Table 4.2). The 5-fold cross validation and LGOCV broadly produced remarkably similar results (Tables 4.1 and 4.2).

Table 4.1. RF model performance for blue whale occurrence based on AUC. TypePerf is the type of performance and SD is the standard deviation.

TypePerf	**Mean**	**SD**
5-foldCV	0.957	0.004
LGOCV	0.957	0.008

Table 4.2. RF model performance for blue whale call rates based on RMSPE and Spearmen's rho.

		rho		**RMSPE**	
Call type	**TypePerf**	**Mean**	**SD**	**Mean**	**SD**
D	5-foldCV	0.647	0.012	23.567	0.754
D	LGOCV	0.645	0.026	23.425	1.663
Z	5-foldCV	0.842	0.009	8.651	0.483
Z	LGOCV	0.841	0.018	8.722	0.872

4.3 Results

4.3.1 Southern Ocean environmental conditions

Southern Ocean environmental parameters varied across the 14 years of the IWC SOWER cruises (Figure 4.4), although it must be noted that different regions were normally visited in different years. The blended log-transformed chl-a concentrations for all surveyed years ranged between -2.5 and 1.7 mg m^{-3} (equivalent to 0.1 and 5.3 mg m^{-3} untransformed chl-a concentations; Figure 4.4a). The highest chl-a concentration was found at 62.78°S and 57.65°W for a station from February 2000 whilst the lowest was at 62.58°S and 119.28°E for a station from February 1999. Chl-a concentrations were generally higher for December and February between years (Figure 4.4a). The highest SST value of 20.6°C was derived in the Atlantic Ocean at 38.25°S and 18.29°E during the 2005/2006 cruise and the lowest recorded SST of -1.6 °C was off the ice edge at 63.55°S and 64.4°W during 1999/2000 cruise (Figure 4.4b).

Sea surface height was generally below -1 m with December and January having higher SSH values (Figure 4.4c). Wind speeds fluctuated across all years (Figure 4.4d). Wind direction medians ranged between 100° and 150° (Figure 4.4e). Wind stress medians for all the years were well below 0.4 N m^{-2} (Figure 4.4f). January 2006 had the highest value of 2.5 N m^{-2} wind stress observed at 62.75°S and 178.89°W that corresponds to wind speeds of 70 kts we observed during that IWC SOWER cruise. The year 2007/08 had environmental anomalies where SST, SSH, wind speed, wind direction and wind stress were higher than previous years (Figure 4.4). The distributions of the main six satellite-derived environmental variables across the data distribution in the Southern Ocean show both latitudinal and longitudinal trends over the study period (Figure 4.5).

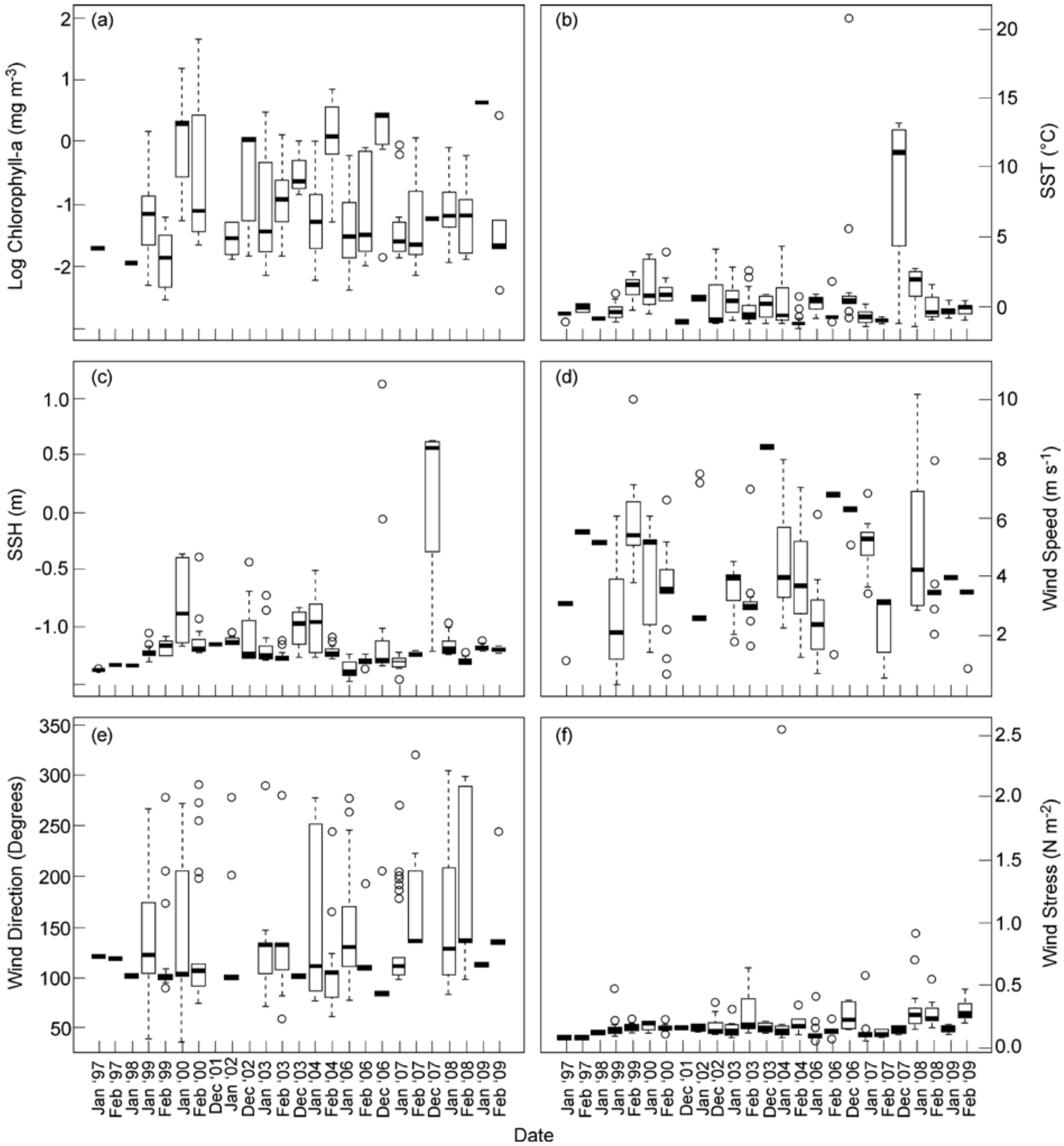


Figure 4.4. Monthly variations of the six satellite-derived environmental predictors used in models for the summer (December – February) of 1997 to 2009 in areas surveyed by the IWC SOWER cruises in the Southern Ocean (38- 78°S, -180-180°E). (a) Log transformed blended chl-a concentrations (mg m^{-3}), (b) Sea surface temperatures (°C), (c) Sea surface heights (m), (d) Wind speed (m s^{-1}), (e) Wind direction (degrees), and (f) Wind stress (N m^{-2}). Note that not all environmental variables were acquired for all months of our study period due to satellite data unavailability.

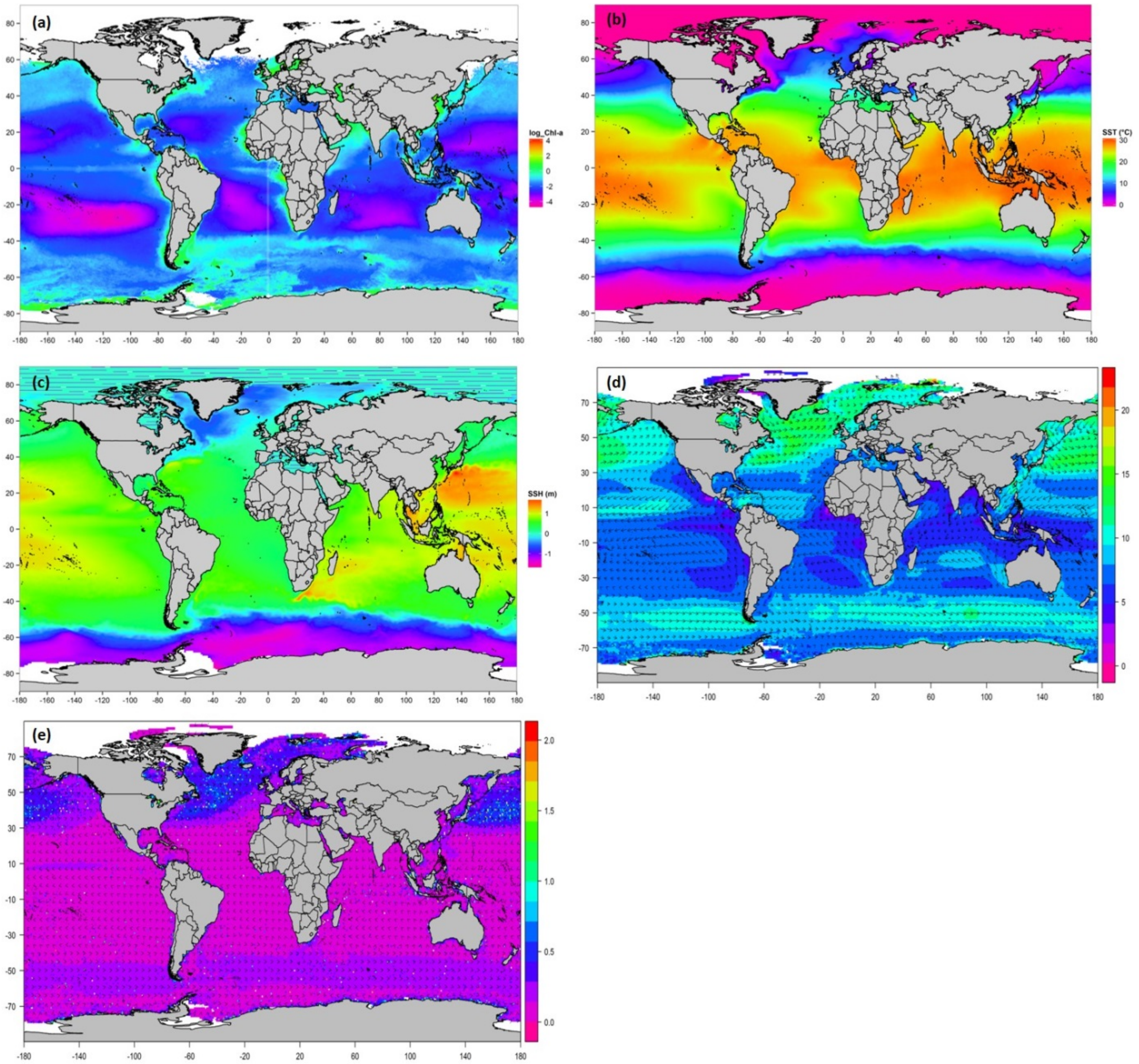


Figure 4.5. Global climatology of environmental variables observed during the austral summers (December- February) of 1997-2009. Horizontal distribution of the (a) log-transformed chl-a, (b) SST, (c) SSH, (d) sea surface wind speed (color) in m s^{-1} and vector (arrows), (e) sea surface wind stress (color) in N m^{-2} and vector (arrows). Only SeaWifs chl-a data were used for plotting the relative distribution of chl-a concentrations.

4.3.2 Blue whale call rates

Vocalisation or call rates are important for determining the approximate acoustic behaviour of whales at a given time and place (Matthews *et al.* 2001). Type 1 stations included 375 blue whales sighted in 173 groups associated with the call rates, and call occurrence, from 107 acoustic stations. Antarctic blue whale Z- and D-call rates generally increased between January and February of each year (Figure 4.6). Median D-call vocalisation rates for stations during most IWC SOWER years were well below 10 calls per hour (Figure 4.6). Blue whale call rates for both call types were generally low during December months for all the years. D-call rates for all the IWC SOWER cruises were observed to be highly correlated (r = 0.68) with the Z-call rates.

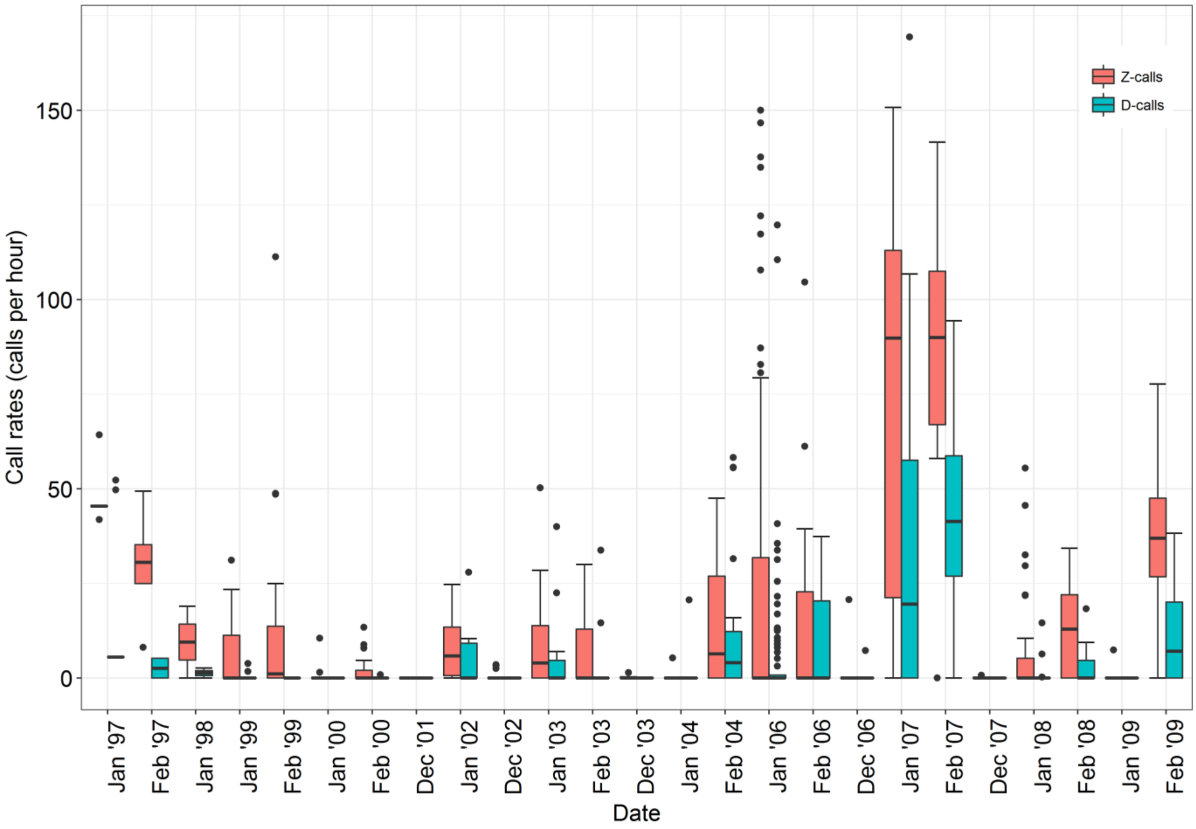


Figure 4.6. Box and whisker plots showing the Antarctic blue whales vocalization rate trends for the Z- and D- calls detected over the summer months during the IWC SOWER surveys. The box represent the first quartile to the third quartile (the interquartile range), and the segment inside the box is the median. The whisker delineates 1.5 times the interquartile width, and the closed circles are observations that are outside the range covered by the whisker.

4.3.3 Acoustically detected whale occurrence modelling outputs

Presence or absence of a species (Figure 4.1) can be used to determine preferred habitat, and the response curves of the effects of different environmental parameters on the occurrence of blue whales show such preferences. Blue whale call presence showed variation relative to different predictor parameters (Figure 4.7). The effects of each of the parameters on the occurrence of blue whale calls are shown on the response curves in Figure 4.8. Distance from nearest SBACC, latitude,distance from the nearest Antarctic shores and longitude, were the most important predictors of blue whale occurrence (Figure 4.9). SSH, SST, log chl-a, station duration, wind speed, wind direction, depth, and wind stress were moderately important predictors of occurrence, whereas month and day/night were the least important predictors of occurrence (Figure 4.9). Blue whales were only heard in water depths between 308 and 5,888 m.

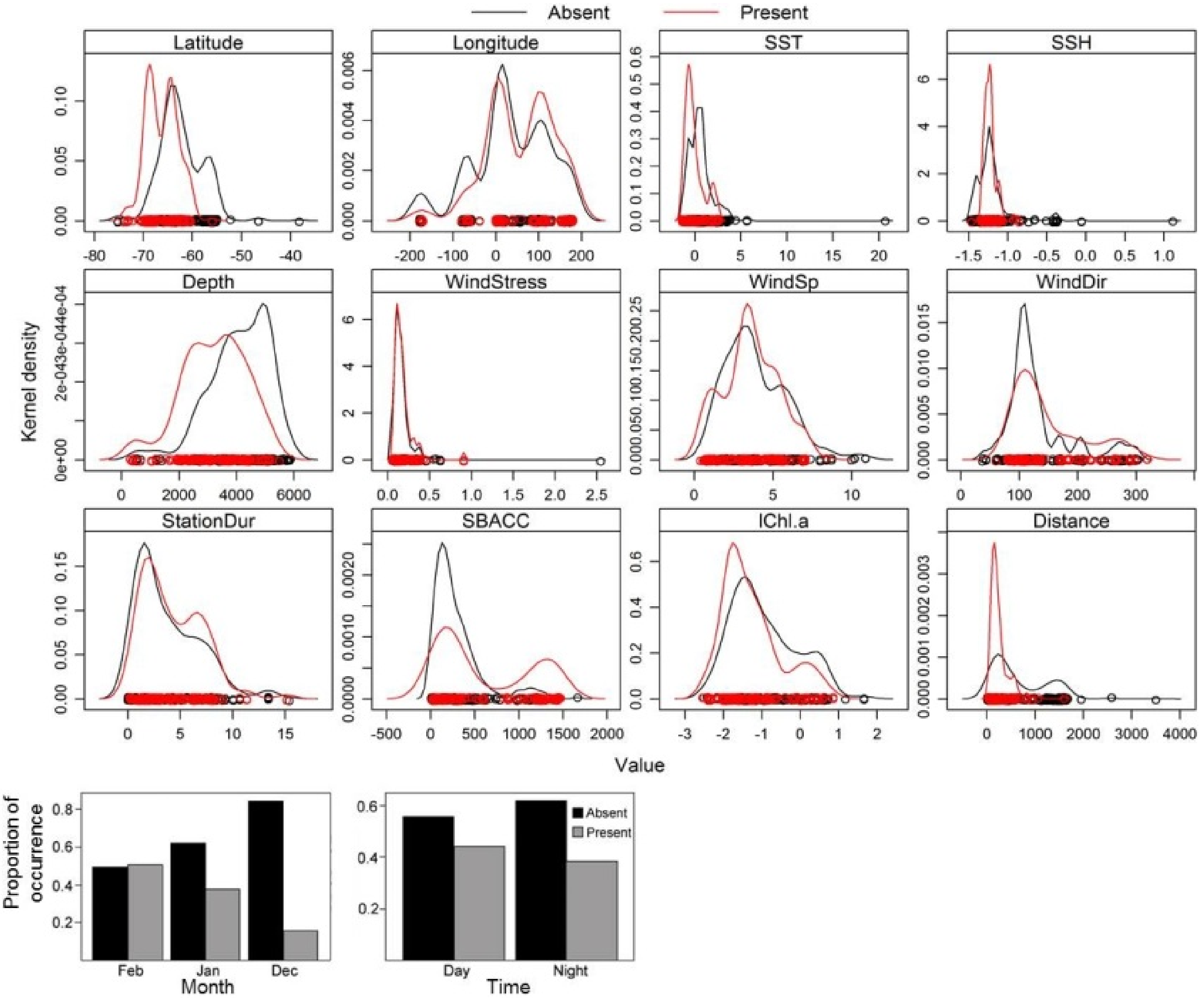


Figure 4.7. Kernel density distribution of each of the variables used in this study to define the occurrence of both blue whale calls in the Southern Ocean. Open circles represent each presence and absence of blue whales while barplots are for factor variables. SBACC is the distance of acoustic station from the nearest southern boundary of ACC (km), StationDur is station duration (hrs), lChl.a is log chlorophyll-a (mg m^{-3}), Distance is the distance from the nearest Antarctic shore (km), WindSp is wind speed (m s^{-1}), and WindDir is wind direction (º).

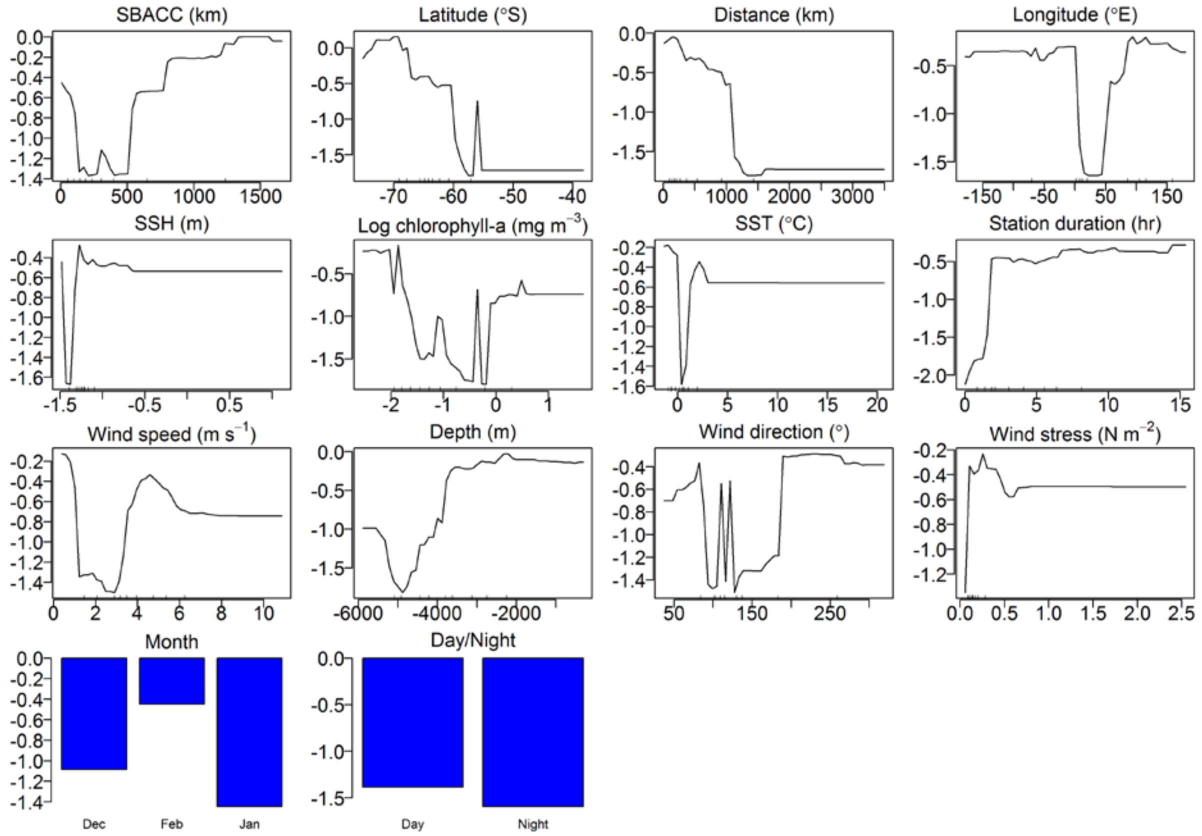


Figure 4.8. RF model plots of partial effects of the different predictors on the occurrence of blue whale D- and Z-calls. Y-axis is the partial effect of each predictor on occurrence (in logit-scale).

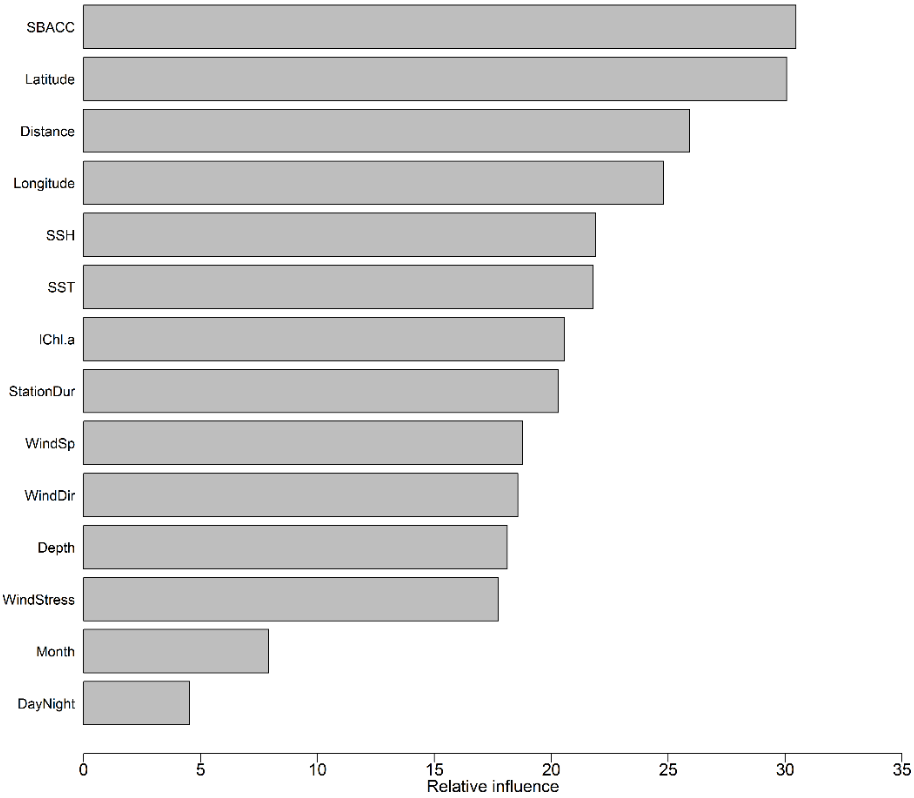


Figure 4.9. Relative importance of the different predictors influencing the occurrence of blue whales based on RF. Relative variable importance is measured by residual sum of squares and expressed relative to the maximum.

4.3.4 Acoustic behaviour modelling outputs

Model response curves of the effects of 15 different summer environmental parameters on the call rates of the two blue whale call types based on the 14 years acoustic time series are shown in Figures. 4.10-4.11. The RF model found that the distance from the SBACC, latitude and number of whales at a station were the most important predictors of D-call vocalisation rates (Figure 4.12). Longitude followed by whale groups (number of group sizes of 1, 2 and 4 were mostly influential), depth, wind stress, wind speed, SST, the distance from the Antarctic shore, wind direction, and SSH were moderately important predictors of acoustic behaviour (Figure 4.12). Log chl-a, month and time of day were the least important predictors of D-call rates (Figure 4.12). Distance from the SBACC, latitude and longitude were the most important predictors of the blue whale Z-call vocalisation rate by the RF model (Figure 4.12). Whale groups (number of group sizes of 1, 2 and 4 were mostly influential) followed by SSH, the distance from the Antarctic shore, depth, number of whales, wind direction, log chl-a, wind stress, and SST were the moderately important predictors of behaviour (Figure 4.12). Wind speed, month and time of day were the least important predictors of Z-call rates.

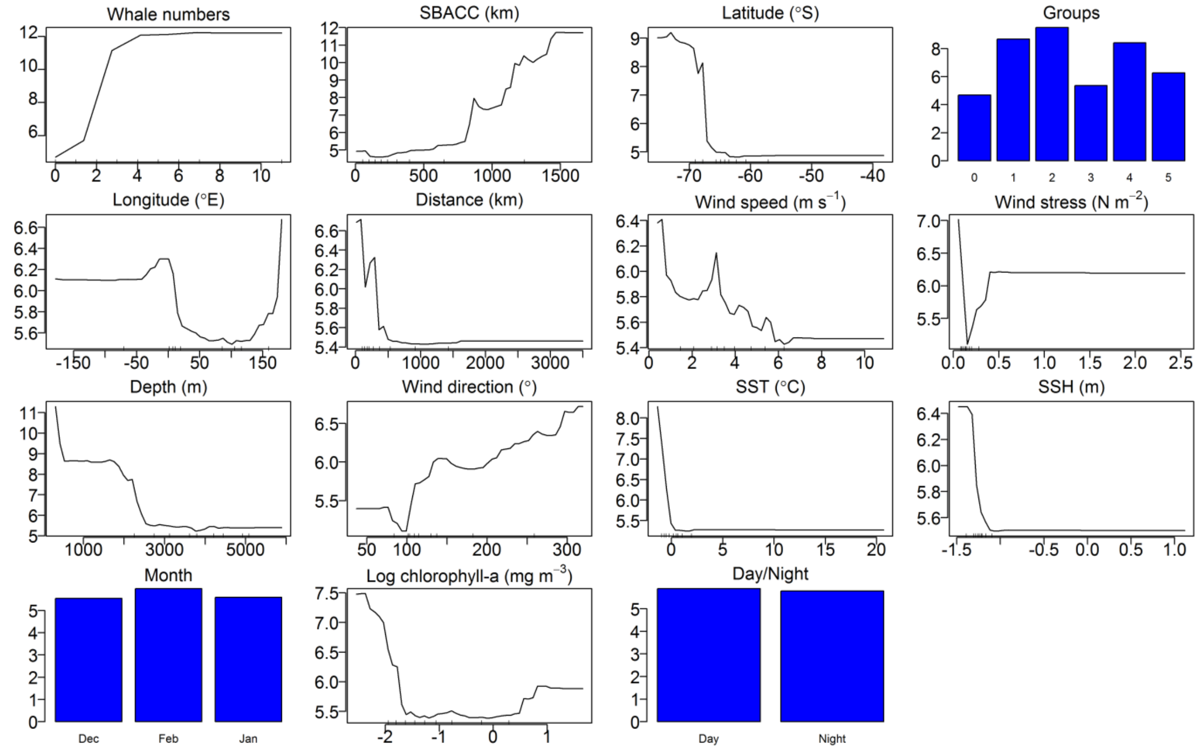


Figure 4.10. Partial effects of the different predictors on D-call rates of blue whales using the RF model. Plots indicate the marginal effect on blue whale call occurrence (y-axes) by each predictor variable (x-axis).

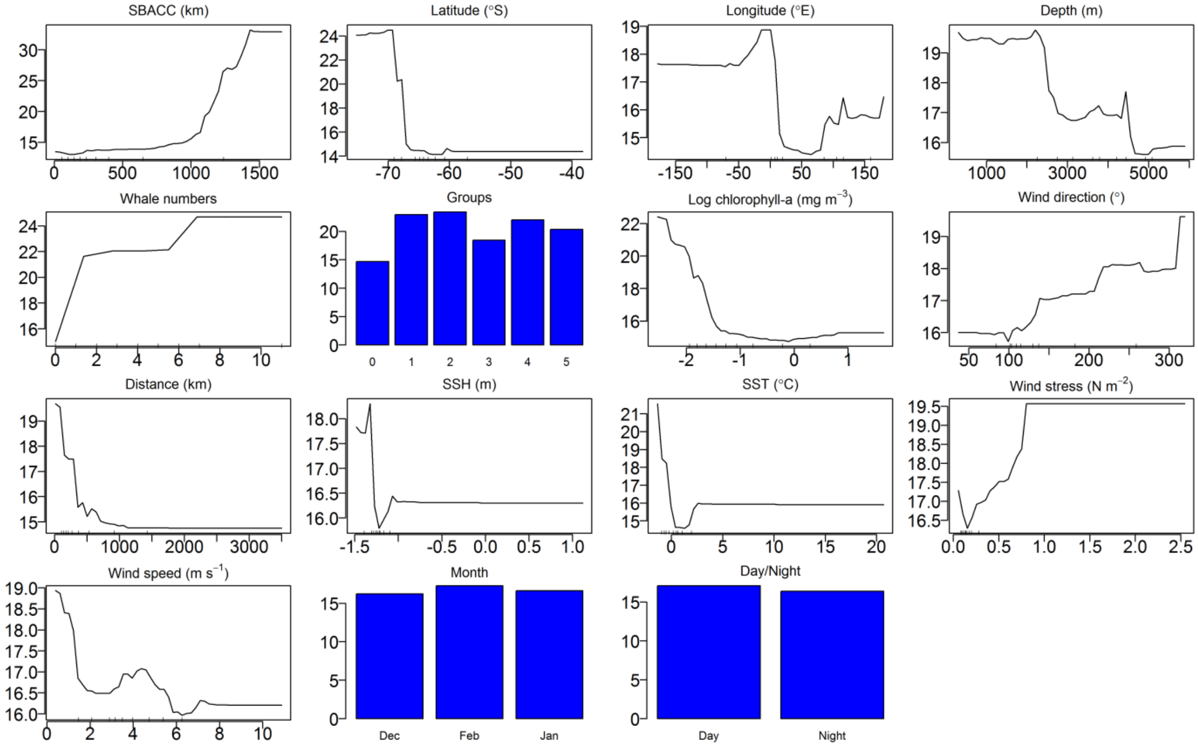


Figure 4.11. Partial effects of the different predictors on Z-call rates of blue whales using the RF model. Plots indicate the marginal effect on blue whale call occurrence (y-axes) by each predictor variable (x-axis). Contribution of each variable to the model given below the function. Y-axes are different across all plots. Scale of x-axes is different across each predictor variable.

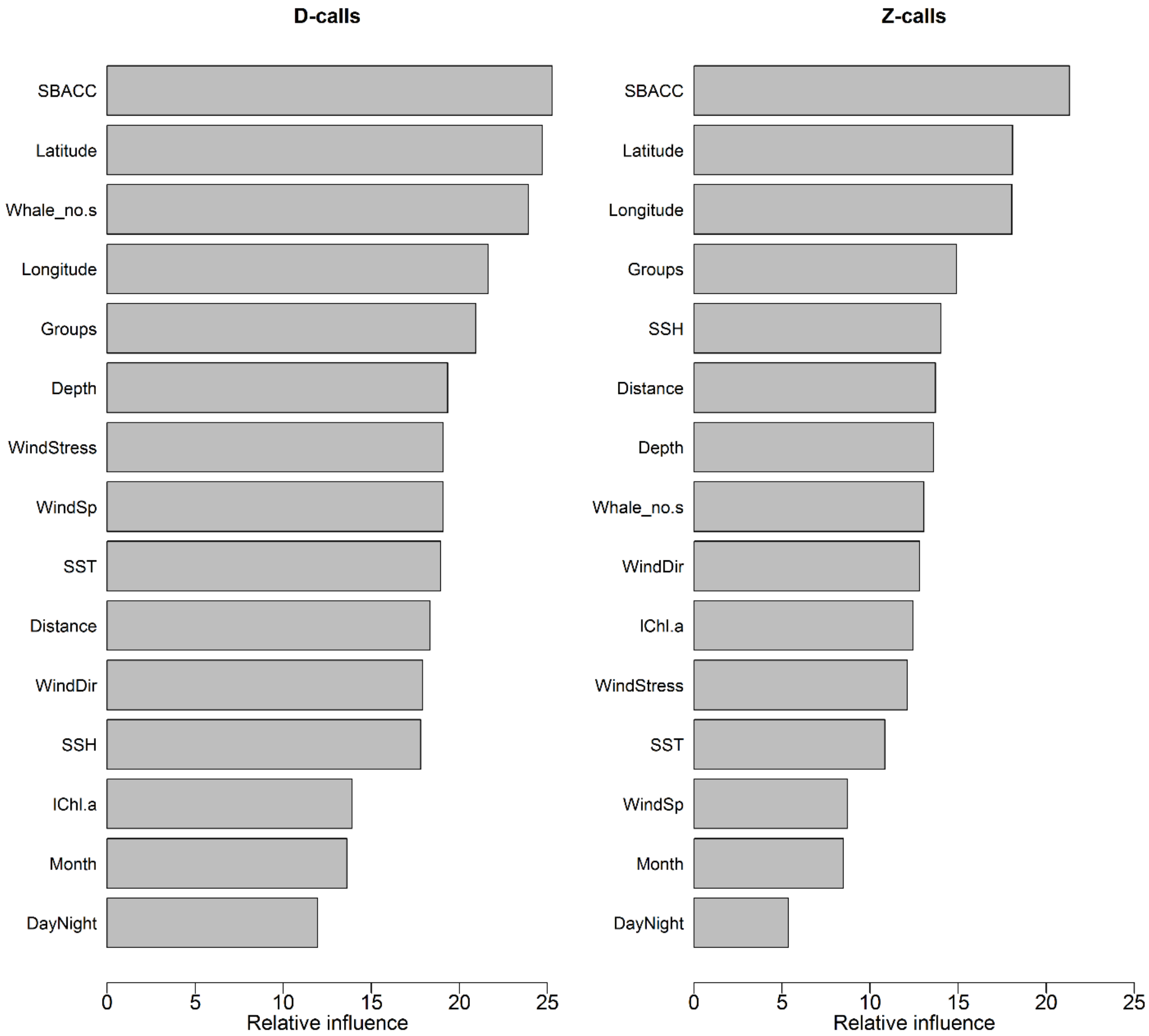


Figure 4.12. Relative importance of the different predictors in influencing the acoustic behaviour of blue whales based on RF model results. Relative variable importance is measured by residual sum of squares and expressed relative to the maximum.

4.4 Discussion

Environmental conditions were important in predicting the call occurrence and acoustic behaviour of blue whales in the Southern Ocean. Call rates increased in January and February of each year, likely due to the increasing numbers of blue whales arriving in the Southern Ocean from their overwintering grounds relative to December where more extensive sea ice extent could potentially have affected the distribution of vocal Antarctic blue whales (Mackintosh and Wheeler, 1929; Širović *et al.* 2004; Miller *et al.* 2014). However, month of survey was the least important predictor of both call occurrence and vocalisation rates in our modelling outputs. We suspect that this is because the survey months of all IWC SOWER cruises fall within the same season, hence their overall results are comparable although there might be some inter-month differences.

Not surprisingly, the type 1 (presence of whale group ≥1) station had a higher effect on call rates than type 2 (no whale groups present) station (Figures 4.10 and 4.11), confirming that deploying an acoustic instrument in the visual presence of whales increased the probabilities of recording their sounds, and that there might be other unobserved vocally active whales in the area interacting with the sighted whales. Acoustic stations where blue whales were not detected might indicate that whales were absent from the area or silent. Call rates increased with number of whales and groups in an area, a behaviour also noted in North Atlantic right whales *Eubalaena glacialis* (Matthews *et al.* 2001). The recording duration of stations was found to be a moderately important predictor of the call occurrence of blue whales by the RF model, reflecting that the length of the acoustic recording affects the probability of detecting blue whales within an area (Rankin *et al.* 2005). Although higher call rates were recorded during the day than at night, time of the day was the least important predictor because acoustic occurrence and vocalisations occurred independently of time of the day.

In this study, Antarctic blue whales were commonly found in waters with SSTs between -1.4°C and 3.5°C, which suggests that this species has a broad temperature tolerance in the Southern Ocean. This could also explain the latitudinal dependence of blue whales, as the colder waters are generally found further south near the ice edge. D-call rates increased when SSTs were below 0.3°C illustrating a preference for temperatures associated with high zooplankton productivity of the ACC thermal fronts. Inter-annual variability in SST and mesoscale ocean circulation affect the inherent Antarctic ice cover that is critical to the distribution of blue whale prey species *Euphausia superba* (White and Peterson, 1996; Behrenfeld *et al.* 2006). SST values between 0-3.5°C were demonstrated by the RF model as most preferred range for the Z-call rates.

The area between the ice edge and 800 km from the nearest Antarctic shore was determined by the model to be important for call occurrence and call rates of Antarctic blue whales in summer. This indicates that not all blue whales transit to the ice edge to feed, but that some animals remain well north of the ice edge. The SBACC is associated with high primary production, krill and whales, suggesting that it provides predictably productive foraging for many species; it is of critical importance to the function of the Southern Ocean ecosystem (Tynan, 1998; Matsuoka *et al.* 2003b). However, our results showed that regions further away from the SBACC but closer to the ice edge, were the most preferred by blue whales. This result shows that blue whales in the Southern Ocean prefer productive areas closer to the Antarctic shores.

Water depths between 380 and 5,900 m at the ice edge and open sea, respectively, were of importance for both the occurrence and acoustic behaviour of whales reflecting a wide bathymetric preference by the species. It is important to note that the location of the ice edge in summer generally approximates the continental slope front (i.e. the shallower isobaths in this study) and is normally a region of high chl-a (Figure 4.7a) and prey availability. Kasamatsu *et al.* (2000) also found that blue whales preferred the ice edge regions. Latitudes between 60°S and 75°S were important for the occurrence and vocalisation rates of blue whales. Longitudes between 50°W and 30°E, and 90°E and 180°E were important longitudinal bands for the blue whale occurrence and vocalisation rates reflecting that these areas are associated with bathymetric features that are important for phytoplankton blooms in the Southern Ocean (Rintoul, 2011). Not surprisingly, more devoted survey effort in these longitudinal bands resulted in higher probability of encountering blue whales (Rankin *et al.* 2005). High historical blue whale catches recorded in these longitudinal bands confirm these areas as preferred habitats for blue whales in the Southern Ocean (Branch *et al.* 2007).

SSH values of less than -1 m were important to blue whale occurrence and call rates, indicating that blue whales occurred closer to the Antarctic Peninsula as SSH decreased closer to the Antarctic Peninsula (Sokolov and Rintoul, 2009). Specific values of SSH are known to define fronts and eddies in the Southern Ocean which in turn increase prey abundance or availability by enhancing primary production (Langlais *et al.* 2010; Nowlin and Klinck, 1986). Sea surface wind stress is considered important in the Ekman's transport of the wind-driven currents such as the ACC by leading to upwelling and downwelling in different areas of the ocean (Nowlin and Klinck, 1986; Chereskin and Price, 2011; Rintoul, 2011). The satellite-derived wind stress values of this study were within the 0.5-1.0 N m^{-2} range observed by Nowlin and Klinck (1986) and Thomalla *et al.* (2015) for the Southern Ocean, although Nowlin and Klinck (1986) observed wind stress values around 2.5 N m^{-2} between 20°W and 110°E. Wind direction controls the supply of nutrient carrying sediments to the continental margin, thus is an important sign of ocean productivity which is closely coupled to climate variability (Behrenfeld *et al.* 2006). The occurrence and vocalisation rates of blue whales showed strong preferences for south-easterly to north-westerly winds that are consistent with winds away from, and returning to, the Antarctic continent suggesting evidence of high productivity associated with those wind directions.

Satellite derived sea surface wind speeds of less than 10 m s^{-1} were experienced across the survey regions, and these wind speeds were typical for the Southern Ocean (Yuan, 2004; Zhang *et al.* 2006). These wind speeds coincide with the good to moderately good weather conditions required to conduct line transect visual surveys and sonobuoy deployments. Furthermore, such wind speeds are important for ocean circulation, air-sea gas and chemical exchanges and nutrient transport (e.g., Nowlin and Klinck, 1986; Rintoul, 2011) and are generally indicative of phytoplankton productive areas associated with fronts and eddies. Wind speed is also important acoustically in the generation of oceanic underwater noise (Urick, 1983), and may influence the acoustic behaviour of marine mammals (Au and Hastings, 2008). Our RF results showed that detections of vocalisation by blue whales were higher at wind speeds below 6 m s^{-1} (Figures 4.10- 4.11).

Deployments of acoustic instruments in poor weather conditions (at wind speeds above 10 m s^{-1}) are needed to further predict the temporal and spatial effects of wind-induced noise on the acoustic behaviour of blue whales (although wind noise might impact the detection of calls). High wind speeds are also known to introduce air bubbles in the upper water column that absorb and refract sound (Shabangu *et al.* 2014). The uses of stationary or moored hydrophone such as autonomous acoustic recorders or mobile ocean gliders to record animal sounds have the potential to reveal the possible effects of wind on the acoustic behaviour of blue whales at a high spatial and temporal resolution. This can also provide some information on whether eddies are able to induce high chl-a that attract blue whales. As these dynamic instruments (i.e. gliders) are capable of being controlled remotely, they have the potential to follow a particular feature of interest such as a meandering front or eddy.

Available evidence demonstrate that krill are most abundant in areas with the highest-productivity within their habitats (e.g., Atkinson *et al.* 2004), yet simplistic correlations have not been found between productivity in the Southern Ocean and krill abundance (Weber and El-Sayed, 1984; Constable *et al.* 2003). Negative krill-phytoplankton relationships found in the Southern Ocean may reflect locally high krill densities that drive down the phytoplankton biomass (Weber and El-Sayed, 1984; Whitehouse *et al.* 2009), thus high krill densities (the major phytoplankton consumer in the Southern Ocean) can be associated with locally low chl-a concentrations. Considerable variation in chl-a concentration was observed among different years and locations across the survey area, and there was a negative relationship between the acoustic occurrence of blue whales and chl-a concentrations. Branch *et al.* (2007) and Širović and Hildebrand (2011) also observed a negative relationship between blue whales and chl-a concentrations derived from SeaWIFS and *in situ* water sampling, respectively. This may reflect that blue whales aggregate and vocalize in areas with high zooplankton biomass. Similarly, RF indicated that low chl-a is highly important for the production of Z-calls (i.e. the non-feeding call), which could indicate that Antarctic blue whales may be acoustically more active when not feeding.

The results of the RF model provide evidence that blue whale occurrence and acoustic behaviour are sensitive to annual variabilities of major environmental parameters such as chl-a, wind speed, wind direction and stress, SSH and SST. Consequently, blue whales might be vulnerable to either gradual long-term changes or abrupt and persistent short-term changes or variability (i.e. climate change) of those key environmental factors. This might hamper the recovery of this species and lead to habitat loss and local distributional shifts (Elliot and Simmonds, 2007; Attard *et al.* 2012) as climate variability/change effects may influence the availability and distribution of prey (i.e. Antarctic krill). The Northern Hemisphere blue whale *Balaenoptera musculus* population is considered highly vulnerable to climate change (Babij *et al.* 2013); the vulnerability of Antarctic blue whales to climate change seems to be just as high.

4.5 Conclusions

The RF modelling enabled the explicit interpretation of the complex relationships between blue whales and their environment from our long term acoustic data set. RF performed well for call rates and occurrence modelling, it holds perhaps the greatest promise for acoustic behaviour and occurrence modelling because of its wide versatility that allows it to assume simpler, faster and more interpretable forms with incorporable automatic predictor selection.

Antarctic blue whales showed both latitudinal and longitudinal preferences in the Southern Ocean. Passive acoustic techniques provided useful information on blue whale occurrence and behaviour, however, more direct and continuous acoustic recording of blue whales are needed. Whales preferred relatively colder waters closer to the ice edge with potentially high krill abundances and occurred closer to the ice edge. The year 2007/08 was an environmental anomaly and blue whale call rates responded to the change, suggesting that future changes in environmental conditions have the potential to affect blue whale behaviour and occurrence. The link between environmental conditions and blue whale occurrence and behaviour revealed important biological information essential for improving the management and conservation of this depleted whale species. This study shows the potential influence of long-term systematic environmental change on Antarctic blue whales.

4.6 Acknowledgements

We are greatly indebted to the International Whaling Commission for granting permission to use the IWC SOWER passive acoustic data together with the cruise reports, acoustic data records and visual survey data. We thank the captains, crew and researchers aboard the IWC SOWER survey vessels, the *Shonan Maru* and the *Shonan Maru No 2* for the collection of these data. South African National Antarctic Programme and National Research Foundation funded the South African Blue Whale Project. Marcel du Plessis and Hazel Little of the Department of Oceanography, University of Cape Town, are thanked for the fruitful discussions regarding the best satellite products to use to obtain chlorophyll-a data for the cloudy Southern Ocean. Cathy Boucher, Department of Agriculture, Fisheries and Forestry, is acknowledged for collating some of our figures. GlobColour data (http://globcolour.info) used in this study has been developed, validated, and distributed by ACRI-ST, France. We are grateful to two anonymous reviewers for their constructive comments that improved the structure of this paper.

4.7 References

Amante, C. and B.W. Eakins, 2009. ETOPO1 1 Arc-Minute Global Relief Model: Procedures, Data Sources and Analysis. NOAA Technical Memorandum NESDIS NGDC-24. National Geophysical Data Center, NOAA. doi:10.7289/V5C8276M.

Atkinson, A.A., Siegel, V., Pakhomov, E., and Rothery, P. 2004. Long-term decline in krill stock and increase in salps within the Southern Ocean. Nature 432: 100–103.

Attard, C.R., Beheregaray, L.B., Jenner, K.C.S., Gill, P.C., Jenner, M.N., Morrice, M.G., Robertson, K.M. and Möller, L.M. 2012. Hybridization of Southern Hemisphere blue whale subspecies and a sympatric area off Antarctica: impacts of whaling or climate change? Molecular ecology 21: 5715–5727.

Au, W.W.L., and Hastings, M.C. 2008. Principles of marine bioacoustics. New York: Springer. 679 p.

Babij, E., Hayum, B., Himes-Cornell, A., Hollowed, A., Little, P., Orbach, M. and Pidgeon, E. 2013. International implications of climate change. In: Griffis R, Horward J, editors. Oceans and Marine Resources in a Changing Climate: A Technical Input to the 2013 National Climate Assessment. Washington, DC: Island Press. pp. 119–139.

Balance, L.T. 2009. Cetacean Ecology. *In:* Perrin, W.F., Wursig, B., and Thewissen, J.G.M., editors. Encyclopedia of marine mammals. 2nd ed. California: Academic Press. pp. 196–201.

Bates, D., and Maechler, M. 2015. Matrix: Sparse and Dense Matrix Classes and Methods. R package version 1.2-2. Available: http://CRAN.R-project.org/package=Matrix.

Behrenfeld, M.J., O'malley, R.T., Siegel, D.A., Mcclain, C.R., Sarmiento, J.L., Feldman, G.C., Milligan, A.J., Falkowski, P., Letelier, R.M., and Boss, E.S. 2006. Climate-driven trends in contemporary ocean productivity. Nature 444: 752–755.

Best, P.B. 2007. Whales and dolphins of the Southern African subregion. Cape Town: Cambridge University Press. 338 p.

Bivand. R., Keitt, T., Rowlingson, B., Pebesma, E., Sumner, M., Hijmans, R., and Rouault, E. 2015. Package 'rgdal'. (Bindings for the Geospatial Data Abstraction Library.) https://cran.rproject.org/web/packages/rgdal/.

Branch, T.A., Stafford, K.M., Palacios, D.M., Allison, C., Bannister, J.L., Burton, C.L.K., Cabrera, E., Carlson, C.A., Vernazzani, B.G., Gill, P.C., Hucke-Gaete, R., Jenner, K.C.S., Jenner, M.N.M., Matsuoka, K., Mikhalev, Y.A., Miyashita, T., Morrice, M.G., Nishiwaki, S., Sturrock, V.J., Tormosov, D., Anderson, R.C., Baker, A.N., Best, P.B., Borsa, P., Brownell, R.L., Childerhouse, S., Findlay, K.P., Gerrodette, T., Ilangakoon, A.D., Joergensen, M., Kahn, B., Ljungblad, D.K., Maughan, B., McCauley, R.D., McKay, S., Norris, T.F., Whale, O., Rankin, S., Samaran, F., Thiele, D., Van Waerebeek, K., and Warneke, R.M. 2007. Past and present distribution, densities and movements of blue whales (*Balaenoptera musculus*) in the Southern Hemisphere and northern Indian Ocean. Mammal Review 37(2):116–175.

Branch, T.A., Matsuoka, K., and Miyashita, T. 2004. Evidence for increases in Antarctic blue whales based on Bayesian modelling. Marine Mammal Science 20: 726–754.

Breiman, L., Cutler, A., Liaw, A., and Wiener, M. 2014. RandomForest: Breiman and Cutler's Random Forests for Classification and Regression. Available: http://CRAN.R-project.org/package=randomForest.

Chamberlain, S. 2016. rerddap: General Purpose Client for 'ERDDAP' Servers. R package version 0.3.4. Available: https://CRAN.R-project.org/package=rerddap.

Chereskin, T.K., and Price, J.F. 2011. Ekman transport and pumping. *In:* Steele JH, Thorpe SA, Turekian KK, editors. Encyclopedia of ocean sciences. 2nd ed. 4 Vol. London: Academic Press. pp. 222–227.

Constable, A.J., Nicol, S., and Strutton, P.G. 2003. Southern Ocean productivity in relation to spatial and temporal variation in the physical environment. Journal of Geophysical Research 108(C4), 8079. doi:10.1029/2001JC001270.

Donlon, C., Robinson. I., Casey, K.S., Vazquez-Cuervo, J., Armstrong, E., Arino, O., Gentemann, C., May, D., Leborgne, P., Piollé, J., Barton, I., Beggs, H., Poulter, D.J.S., Merchant, C.J., Bingham, A., Heinz, S., Harris, A., Wick, G., Emery, B., Minnett, P., Evans, R., Llewellyn-Jones, D., Mutlow, C., Reynolds, R.W., Kawamura, H., and Rayner, N. 2007. The Global Ocean Data Assimilation Experiment High-resolution Sea Surface Temperature Pilot Project. Bulletin of the American Meteorological Society 88(8): 1197–1213.

Ducet, N., Le Traon, P.-Y., and Reverdin, G. 2000. Global high resolution mapping of ocean circulation from TOPEX/Poseidon and ERS-1 and -2. Journal of Geophysical Research 105: 19477–19498.

Elith, J., Leathwick, J.R., and Hastie, T. 2008. A working guide to boosted regression trees. Journal of Animal Ecology 77(4): 802–813.

Elliott, W., and Simmonds, M. 2007. Whales in hot water? The impact of a changing climate on whales, dolphins and porpoises: A call for action. Chippenham, UK: WWF-International, Gland Switzerland / WDCS. 14 p.

Etnoyer, P., Canny, D., Mate, B.R., Morgan, L.E., Ortega-Ortiz, J.G., and Nichols, W.J. 2006. Sea-surface temperature gradients across blue whale and sea turtle foraging trajectories off the Baja California Peninsula, Mexico. Deep-Sea Research II 53(3–4): 340–358.

Fetterer, F., Knowles, K., Meier, W., and Savoie, M. 2016.Sea Ice Index, Version 2. Boulder, Colorado USA. NSIDC: National Snow and Ice Data Center. doi: http://dx.doi.org/10.7265/N5736NV7.

Fox, J., and Monette, G. 1992. Generalized collinearity diagnostics. Journal of the American Statistical Association 87: 178–183.

Fox, J., and Weisberg, S. 2011. An R Companion to Applied Regression, Second Edition. Thousand Oaks, CA: SAGE Publications Inc. 472 p.

Figueroa, H.K. 2006. XBAT: Extensible BioAcoustic Tool. Available: http://xbat.org.

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

Hair Jr, J.F., Black, W.C., Babin, B.J., and Anderson, R.E. 2009. Multivariate data analysis, 7th Edition. Upper Saddle River, NJ: Pearson Education. 761 p.

Hastie, T.J., Tibshirani, R., and Friedman, J. 2009. The elements of statistical learning. New York: Springer. 739 p.

James, G., Witten, D., and Hastie, T. 2013. An introduction to statistical learning: with applications in R. New York: Taylor and Francis Group. 426 p.

Kahru, M., and Mitchell, B.G. 2010. Blending of ocean colour algorithms applied to the Southern Ocean. Remote Sensing Letters 1(2): 119–124.

Kasamatsu, F., Matsuoka, K., and Hakamada, T. 2000. Interspecific relationships in density among the whale community in the Antarctic. Polar Biology 23: 466–473.

Kuhn, M., and Johnson, K. 2013. Applied predictive modelling. New York: Springer. 600 p.

Langlais, C., Schiller, A., and Oke, P.R. 2010. Southern Ocean Fronts in the Bluelink Reanalysis. Mercator Ocean Quarterly Newsletter 36: 50–57.

Leathwick, J.R., Elith, J., Francis, M.P., Hastie, T., and Taylor, P. 2006. Variation in demersal fish species richness in the oceans surrounding New Zealand: an analysis using boosted regression trees. Marine Ecology Progress Series 321: 267–281.

Mackintosh, N.A., and Wheeler, J.F.G. 1929. Southern blue and fin whales. Discovery Reports I: 259–540.

Maritorena, S., Fanton d’Andon, O.H., Mangin, A., and Siegel, D.A. 2010. Merged satellite ocean color data products using a bio-optical model: Characteristics, benefits and issues. Remote Sensing of Environment 114: 1791–1804.

Matsuoka, K., Ensor, P., Hakamada, T., Shimada, H., Nishiwaki, S., Kasamatsu, F., Kato, H. 2003. Overview of minke whale sightings surveys conducted on IWC/IDCR and SOWER Antarctic cruise from 1989/79 to 2000/01. Journal of Cetacean Research and Management 5(2): 173–201.

Matsuoka, K., Watanabe, T., Ichi, T., Shimada, H., and Nishiwaki, S. 2003. Large whale distributions (south of 60°S, 35°E-130°E) in relation to the southern boundary of the ACC. *In:* Huiske, A.H.L., Gieskes, W.W.C., Rozema, J., Schrno, R.M.L., van der Vies, S.M., Wolff, W.J., editors. Antarctic Biology in a Global Context. Leiden, The Netherlands: Backhuys Publishers. pp. 26–30.

Matthews, J.N., Brown, S., Gillespie, D., Johnson, M., McLanaghan, R., Moscrop, A. and Nowacek, D., Leaper, R., Lewis, T., and Tyack, P. 2001. Vocalisation rates of the North

Atlantic right whale (*Eubalaena glacialis*). Journal of Cetacean Research and Management 3(3): 271–282.

Matworks Inc, 2014. MATLAB R2014a version 8.3.0.532. The MathWorks, Inc., Natick, Massachusetts, United States.

Mellinger, D.K., and Clark, C.W. 2000. Recognizing transient low-frequency whale sounds byspectrogram correlation. Journal of the Acoustical Society of America 107: 3518–3529.

Mendelssohn, R. 2015. xtractomatic: Extracts Environmental Data from ERD's ERDDAP Web Service. R package version 3.0.0. Available: https://github.com/rmendels/xtractomatic.

Miller, B.S., Barlow, J., Calderan, S., Collins, K., Leaper, R., Kelly, N., Peel, D., Olson, P., Ensor, P. and Double, M.C. 2013. Long-range acoustic tracking of Antarctic blue whales. Paper submitted for consideration by the IWC Scientific Committee SC/65/SH18.

Miller, B.S., Leaper, R., Calderan, S., and Gedamke, J. 2014. Red Shift, Blue Shift: Investigating Doppler Shifts, Blubber Thickness, and Migration as Explanations of Seasonal Variation in the Tonality of Antarctic Blue Whale Song. PLoS ONE 9(9): e107740. doi:10.1371/journal.pone.0107740

Moore, S.E. 2009. Climate Change. In: Perrin WF, Wursig B, Thewissen JGM, editors. Encyclopedia of marine mammals. 2nd ed. Academic Press, California. pp. 238–241.

National Climatic Data Center. 2007. GHRSST Level 4 AVHRR_OI Global Blended Sea Surface Temperature Analysis. Ver. 1.0. PO.DAAC, CA, USA. Dataset accessed [2015-04-12] at http://dx.doi.org/10.5067/GHAAO-4BC01

Nicol, S., Worby, A., Leaper, R. 2008. Changes in the Antarctic sea ice ecosystem: potential effects on krill and baleen whales. Marine and Freshwater Research 59: 361–382. doi:10.1071/MF07161

Nowlin, W., and Klinck, J. 1986. The physics of the Antarctic Circumpolar Current. Reviews of Geophysics 24(3): 469–491.

O'Brien, R.M. 2007. A caution regarding rules of thumb for variance inflation factors. Quality and quantity 41: 673–690.

Oleson, E.M., Calambokidis, J., Burgess, W.C., McDonald, M.A., LeDuc, C.A., and Hildebrand, J.A. 2007. Behavioral context of call production by eastern North Pacific blue whales. Marine Ecology Progress Series 330: 269–284.

Orsi, A.H., Whitworth III, T., and Nowlin Jr, W.D. 1995. On the meridional extent and fronts of the Antarctic Circumpolar Current. Deep-Sea Research 42(5): 641–673.

Pierce, D. 2014. ncdf4: Interface to Unidata netCDF (version 4 or earlier) format data files. R package version 1.12. Available: http://dwpierce.com/software

R Core Team, 2015. R: A Language and Environment for Statistical Computing. 3.1.1 version. Vienna, Austria: R Foundation for Statistical Computing. Available: https://www.R-project.org/.

Rahmstorf, S. 2009. Abrupt climate change. *In:* Steele JH, Thorpe SA, Turekian KK, editors. Encyclopedia of ocean sciences. 2nd ed. 4 vol. London: Academic Press. pp. 1–6.

Rankin, S., Ljungblad, D., Clark, C., and 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, Antarctica. Journal of Cetacean Research and Management 7: 13–20.

Rice, D.W. 1998. Marine mammals of the world: systematics and distribution. Society for Marine Mammalogy Special Publication No. 4. Lawrence, KS: Allen Press. 231 p.

Riffenburgh, B. 2007. Encyclopedia of the Antarctic. New York: Routledge. 1145 p.

Rintoul, S.R. 2011. Antarctic Circumpolar Current. *In:* Steele JH, Thorpe SA, Turekian KK, editors. Encyclopedia of ocean sciences. 2nd ed. 4 vol. London: Academic Press. pp. 178–190.

Samaran, F., Adam, O., and Guinet, C. 2010. Detection range modeling of blue whale calls in Southwestern Indian Ocean. Applied Acoustics 71: 1099–1106.

Samaran, F., Stafford, K.M., Branch, T.A., Gedamke, J., Royer, J-Y., Dziak, R.P., and Guinet, C. 2013. Seasonal and geographic variation of southern blue whale subspecies in the Indian Ocean. PLoS ONE, 8(8):e71561.

Shabangu, F.W., Ona, E., and Yemane, D. 2014. Measurements of acoustic attenuation at 38 kHz by wind-induced air bubbles with suggested correction factors for hull-mounted transducers. Fisheries Research 151: 47–56.

Širović, A.S., Hildebrand, J.A., Wiggins, S.M., McDonald, M.A., Moore, S.E., and Thiele. D. 2004. Seasonality of blue and fin whale calls and the influence of sea ice in the Western Antarctic Peninsula. Deep-Sea Research II 51: 2327–2344.

Širović, A. 2016. Variability in the performance of the spectrogram correlation detector for North-east Pacific blue whale calls. Bioacoustics 25(2): 145–160.

Širović, A., Hildebrand, J.A., and Wiggins, S.M. 2007. Blue and fin whale call source levels and propagation range in the Southern Ocean. Journal of Acoustical Society of America 122: 1208–15.

Širović, A., and Hildebrand, J.A. 2011. Using passive acoustics to model blue whale habitat off the Western Antarctic Peninsula. Deep-Sea Research II 58: 1719–1728.

Sokolov, S., and Rintoul, S.R. 2009. Circumpolar structure and distribution of the Antarctic Circumpolar Current fronts: 2. Variability and relationship to sea surface height. Journal of Geophysical Research 114: C11019. doi:10.1029/2008JC005248

Stafford, K.M., Bohnenstiehl, D.W.R., Tolstoy, M., Chapp, E., Mellinger, D.K., and Moore, S.E. 2004. Antarctic-type blue whale calls recorded at low latitudes in the Indian and eastern Pacific Oceans. Deep-Sea Research I 51: 1337–1346.

Swart, S., Thomalla, S.J., and Monteiro, P.M.S. 2014. The seasonal cycle of mixed layer dynamics and phytoplankton biomass in the Sub-Antarctic Zone: a high-resolution glider experiment. Journal of Marine Systems. doi:10.1016/j.jmarsys.2014.06.002.

Thomalla, S.J., Racault, M.-F., Swart, S., and Monteiro, P.M.S. 2015. High-resolution view of the spring bloom initiation and net community production in the Subantarctic Southern Ocean using glider data. ICES Journal of Marine Science. doi: 10.1093/icesjms/fsv105.

Thomas, P.O., Reeves, R.R., and Brownell Jr, R.L. 2016. Status of the world's baleen whales. Marine Mammal Science 32(2): 682–734.

Thompson, P.O., Findley, L.T., and Vidal, O., and Cummings, W.C. 1996. Underwater sounds of blue whales, *Balaenoptera musculus*, in the Gulf of California, Mexico. Marine Mammal Science 12 (2): 288–292.

Tynan, C. 1998. Ecological importance of the Southern Boundary of the Antarctic Circumpolar Current. Nature 392: 708–710.

Urick, R.J. 1983. Principles of underwater sound. 3rd ed. New York: McGraw Hill. 423 pp.

Weber, L.H., and El-Sayed, S.Z. 1985. Spatial variability of phytoplankton and the distribution and abundance of krill in the Indian Sector of the Southern Ocean. In: Siegfried WR, Condy PR, Laws RM, editors. Antarctic nutrient cycles and food webs. Berlin: Springer. pp. 284–293.

White, W.B. and Peterson, R.G. 1996. An Antarctic circumpolar wave in surface pressure, wind, temperature and sea-ice extent. Nature 380: 699–702.

Whitehouse, M.J., Atkinson, A., Ward, P., Korb, R.E., and Rothery, P., Fielding S. 2009. Role of krill versus bottom-up factors in controlling phytoplankton biomass in the northern Antarctic waters of South Georgia. Marine Ecology Progress Series 393: 69–82.

Wickham, H. 2015.Stringr: Simple, consistent wrappers for common string operations. Available: http://CRAN.Rproject.org/package=stringr.

Wright, M.N., and Ziegler, A. 2016. ranger: A Fast Implementation of Random Forests for High Dimensional Data in C++ and R. Journal of Statistical Software, in press. http://arxiv.org/abs/1508.04409.

Yuan, X. 2004. High-wind-speed evaluation in the Southern Ocean. Journal of Geophysical Research 109: D13101. doi:10.1029/2003JD004179.

Zhang, H.-M., Reynolds, R.W., and Bates, J.J. 2006. Blended and gridded high resolution global sea surface wind speed and climatology from multiple satellites: 1987–present. In: Proceedings of the American Meteorological Society 2006 Annual Meeting, Atlanta, GA, January 29- February; P2.23.

Chapter 5: Seasonal occurrence and diel calling behaviour of Antarctic blue whales and fin whales in relation to environmental conditions off the west coast of South Africa

Shabangu et al. Under review in Journal of Marine Systems

Abstract

Passive acoustic monitoring was used to detect the sounds of rarely sighted Antarctic blue and fin whales to investigate their seasonal occurrence (as presence or absence of whale calls) and behaviour (as determined from call rates) in the Benguela ecosystem. Data were collected using autonomous acoustic recorders deployed on oceanographic moorings for 16.26 months off the west coast of South Africa in 2014 and 2015. Our results show that migratory Antarctic blue and fin whales were present in South African waters between May and August with some fin whales extending their presence to November. Antarctic blue whales produced both their characteristic Z-call and their feeding associated D-call. Fin whales produced calls characteristic of animals from the eastern Antarctic fin whale acoustic population. Patterns of diel call rate of both whale species varied between seasons. A random forest model identified environmental parameters such as sea surface temperature, sea surface height, and log-transformed chlorophyll-a as the most important predictors of call occurrence and call rates of blue and fin whales. Here we present the first acoustic recordings of Antarctic blue and fin whales in the southeast Atlantic Ocean, and provide preliminary information to investigate seasonal abundance and distribution of these large baleen whale populations in the Benguela ecosystem. This work demonstrates the feasibility of cost-effectively monitoring Antarctic top-consumer baleen whales off the west coast of South Africa.

5.1 Introduction

Antarctic blue whales *Balaenoptera musculus intermedia* and fin whales *B. physalus* are rarely sighted off the coasts of South Africa (with fewer than 10 confirmed Antarctic blue whale sightings since 1975) due to their low abundance, inconspicuousness and the lack of search effort and monitoring in the offshore environment. As a result of their large size, they yielded more oil than any other whale species, and were therefore harvested to near-extinction in the Southern Hemisphere before modern whaling ceased in the 1960s (Hilborn *et al.* 2003; Branch *et al.* 2004, 2007; Best, 2007). Operating from 1909 onwards, the modern whaling stations at Saldanha Bay and Cape Hangklip (South Africa), as well as stations at Lüderitz and Walvis Bay (Namibia), were the main whaling stations to target blue and fin whales in the southern African west coast region (Best, 1994, 1998, 2007), although catches were also made from Angolan land stations.

By the time whaling ceased in the mid-1970s, only 0.7% (0.3%–1.3%) of the original blue whale population remained (Branch *et al.* 2004). At present, the Antarctic blue whale population remains low; the 1996 Southern Hemisphere estimate was 1,700 individuals (95% confidence interval: 860-2,900) and the population was estimated to be increasing at 8.2% (1.7-15.3%) per annum (Branch *et al.* 2004). There are fewer data available for fin whales but some evidence suggests that they, too, may be recovering although the current rate of increase is unknown (Branch and Butterworth, 2006). The International Union for the Conservation of Nature (IUCN) currently classifies Antarctic blue and fin whales as Critically Endangered and Endangered respectively (Reilly *et al.* 2013).

Both blue and fin whales produce low-frequency calls (< 120 Hz) with high intensities (~189±4 dB re: 1 µPa at 1 m) that can travel great distances underwater (Širović *et al.* 2007); such calls are believed to be whale population specific (McDonald *et al.* 2006; Širović *et al.* 2009). Antarctic blue whales produce two kinds of calls, D-call (McDonald *et al.* 2001; Oleson *et al.* 2007a,b) and Z-call (Ljungblad *et al.* 1998). The D-call is frequency modulated (FM) and downsweeps from about 106 to 22 Hz (Rankin *et al.* 2005). Males and females presumably produce D-calls during feeding and also use this call for group communication (McDonald *et al.* 2001; Oleson *et al.* 2007a,b). The characteristic Z-call (termed so due to its Z-shaped spectrogram signature) is a low frequency, stereotyped three-unit sequence of tonal sounds that lasts from 18 s to ~26 s (Ljungblad *et al.* 1998; Rankin *et al.* 2005). The first unit of the Z-call is a tone at ~27 Hz followed by a second unit that frequency modulates and downsweeps from ~27 to 20 Hz and third unit slightly frequency modulates from 20 to ~18 Hz. The Z-call is believed to be produced by Antarctic blue whale males only, as a long-distance contact call for sexual advertisement and likely other communication purposes, similar to other blue whale subspecies (McDonald *et al.* 2001; Oleson *et al.* 2007a,b).

Antarctic fin whales produce short (1 s) FM downsweeping from ~28 Hz to 15 Hz (also known as the 20 Hz pulse), and a second, simultaneously produced higher frequency pulse. These signals are repeated at 13 s intercall intervals (Širović *et al.* 2004). The higher frequency pulse has been used to delineate between two acoustic populations of fin whales in the Antarctic: the eastern Antarctic acoustic population with a secondary frequency peak at 99 Hz and the western Antarctic acoustic population with a peak at 89 Hz (Širović *et al.* 2009). Fin whales also make irregular and short (usually under 1 s) pulses that tend to downsweep from 70 to 40 Hz, termed hereafter the 40 Hz pulses. Unlike the 20 Hz pulses, the fin whale 40 Hz pulses are not repeated regularly and are sometimes confused with blue whale D-calls as they both cover a similar frequency band. However, the D-call is slightly slanted to the right as it downsweeps whereas the 40 Hz pulse downsweeps vertically without slanting.

Both male blue and fin whales produce calls in repeated sequences at regular intervals, these repeated stereotyped sequences of calls are considered songs (McDonald *et al.* 2001, 2006; Croll *et al.* 2002; Oleson *et al.* 2007c, 2014; Širović *et al.* 2017). Songs can last from minutes to hours, days or even weeks with only slight breaks, which have been attributed to a whale surfacing to breathe (Cummings and Thompson 1971; McDonald *et al.* 2001, 2006). A decrease has been observed in the vocalization frequency of the Z-call song from ~28 to ~26 Hz over the past 15 years and a wide variety of reasons have been suggested for this including cultural conformity, sex, body size, climate change and many others (McDonald *et al.* 2009; Gavrillov *et al.* 2012; Ward *et al.* 2017).

The Benguela Current Large Marine Ecosystem, hereafter the Benguela ecosystem, extends from east of the Cape of Good Hope (South Africa) equatorwards to near the southern border of Angola (Figure 1) and is generally characterized by its nutrient-rich upwelling regime (Shannon, 2006). Northwestward winds in the Benguela ecosystem induce the movement of cold nutrient-rich bottom waters to the sea surface which results in upwelling (Andrews and Hutchings, 1980; Lutjeharms and Meeuwis 1987; Jury and Bundrit, 1992; Grodsky *et al.* 2008; Goubanova *et al.* 2013). Such nutrient-rich water movement into the photic zone drives phytoplankton blooms and the productive food webs within the Benguela. This productivity drives the zooplankton biomass, which are prey for some economically important South African pelagic fisheries species including anchovy *Engraulis encrasicolus*, sardine *Sardinops sagax* and round herring *Etrumeus whiteheadi*. These are consumed by marine mammals, piscivorous fish and seabirds. Faecal matter from feeding whales and other top predators fertilises the Benguela ecosystem and presumably enhances the growth of phytoplankton as identified elsewhere in the world's oceans (Lavery *et al.* 2010; Roman *et al.* 2014; Doughty *et al.* 2016). Hence, large baleen whales potentially play an important role in the Benguela ecosystem functioning.

The aim of our study was to determine the seasonal occurrence and diel calling behaviour of blue and fin whales in relation to environmental conditions in the Benguela ecosystem using passive acoustic monitoring. Such acoustic monitoring in the low latitudes of large baleen whales from the Antarctic is potentially the most economical and reliable method of monitoring and tracking these whales. This study establishes the acoustic seasonal occurrence and behaviour of Antarctic blue and fin whales in the southeast Atlantic Ocean, which is important for the conservation and management strategies of these species.

5.2 Materials and Methods

5.2.1 Acoustic data collection

Acoustic data were collected off the west coast of South Africa in the southern Benguela ecosystem located in the southeast Atlantic Ocean (Figure 5.1). We used two passive acoustic monitoring stations each equipped with an Autonomous Acoustic Recorder (AAR) (Autonomous Underwater Recorder for Acoustic Listening-Model 2 version 04.1.3 manufactured by Multi-Electronique Inc., Canada) to record the acoustic data (Supplementary Figure S5.1). The first AAR (hereafter AAR1) was deployed at 34° 22.21’S, 17° 37.69’E from 24 July 2014 to 1 December 2014 in water depth of 855 m (Figure 5.1). The second AAR (hereafter AAR2) was deployed at 34° 23.64'S, 17° 35.66'E from 16 September 2014 to 1 December 2015 in water depth of 1,118 m (Figure 1). Both AARs (Supplementary Figure S5.1) were attached to the South Atlantic Meridional Overturning Circulation Basin-wide Array (SAMBA) of oceanographic moorings (Ansorge *et al.* 2014) and situated approximately 70 km from the coast (Figure 5.1). The SAMBA transect is a hydrographic transect that falls under the South Atlantic Meridional Overturning Circulation (SAMOC) global project. AAR1 recorded the first 30 minutes of every hour of each day, whereas AAR2 only recorded the first 20 minutes of every hour of each day to maximize battery lifespan. AAR1 was positioned at 200 m below the sea surface whereas AAR2 was slightly deeper at 300 m below the sea surface. Both AARs sampled at 4,096 Hz for an effective monitored bandwidth range of 10 Hz to 2,048 Hz and had receiving sensitivities of -169 dB re 1V/μPa when applying a AAR gain of 22 dB.

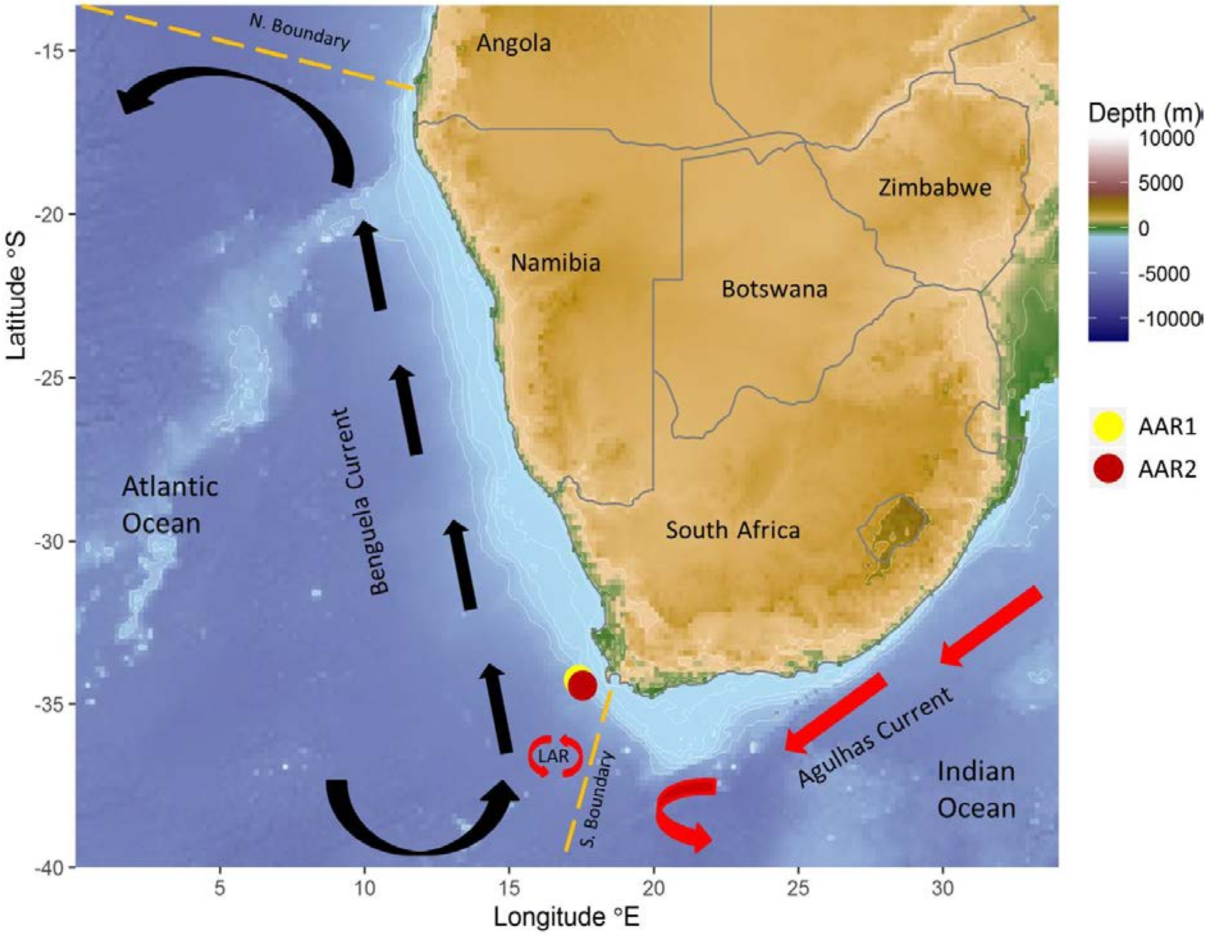


Figure 5.1. Location of AAR1 (🟡) and AAR2 (🔴) off the west coast of South Africa in the Benguela ecosystem, Atlantic Ocean. Moorings were located approximately 70 km from the nearest shoreline. The flow direction of the cold Benguela Current is shown by black arrows and the flow direction of the warm Agulhas Current is shown by red arrows. The dashed orange lines are the northern and southern boundaries of the Benguela Current respectively. LAR is the Agulhas Current leakage via Agulhas Rings introducing warm waters to the Bengulea ecosystem. Bathymetry data were obtained from the ETOPO1 dataset (Amante and Eakins, 2009).

A total of 5,057 hours were recorded from both listening stations: 1,567 hours from AAR1 and 3,489.75 hours from AAR2. Here we use Southern (austral) Hemisphere seasons of the year to parse our data into seasons: summer (December to February), autumn (March to May), winter (June to August), and spring (September to November). Different light regimes were classified over different seasons in accordance with the altitude of the sun (dawn (nautical twilight), daytime, dusk (nautical twilight) and nighttime) by averaging hourly sun altitudes over austral seasons. We used hourly sun altitudes for each day of the year from 34° 22”S, 17° 37”E for both AAR locations since there should be no difference in the light conditions between the two closely spaced locations. Sun altitudes were obtained from the

United States Naval Observatory Astronomical Applications Department (http://aa.usno.navy.mil). We defined the nautical dawn hours as periods when the centre of the sun was geometrically 12° below the horizon before sunrise. Daytime hours were between sunrise and sunset, and the nautical dusk hours were between sunset and the evening. Nighttime hours were instants when the geometric centre of the sun was 12° below the horizon in the evening, which is between dusk and dawn.

5.2.2 Whale call detections

Acoustic data were analysed using the eXtensible Bio-Acoustic Tool (XBAT) software (Figueroa, 2006) implemented as a MATLAB routine (MathWorks Inc, 2014) with automatic detection templates for fin whale calls, and Antarctic blue whale D- and Z-calls developed from the 2014-15 data and applied in XBAT. The D-call downsweeping from 70-30 Hz (Figure 5.2a) and a complete Z-call (Figure 5.2b) with all the three units were used as detection templates for Antarctic blue whales because they contained most of the energy of the calls. The 20 Hz pulse with a short downsweeping 28-15 Hz tone (Figure 5.2b) was used for automated detection of fin whale calls as it is the most abundant and reliable sound of fin whales. The 40 Hz pulse of fin whales was absent from our acoustic recordings. The template detector method operates on an acoustic time series of spectrograms by constructing a correlation kernel for the vocalization (Mellinger and Clark, 2000). Calls were recognized from spectrograms by cross-correlating with the template kernel based on a similarity level above a set threshold (i.e. the lowest detectable similarity percentage between a template and call). We used high signal-to-noise ratio calls to construct templates to automatically detect fin whale calls, D- and Z-calls. In order to estimate the number of false positive calls (detections that were not blue or fin whale calls) and false negative calls (missed blue or fin whale calls), the entire acoustic dataset was assessed visually. The visually identified false positive detections were manually excluded from further data analyses. Visually identified false negative detections were manually incorporated into the calculations of final total call number and rates but considered missed calls during the below detector accuracy test.

We tested seven different thresholds from 10% to 70% by increments of 10% to determine optimal thresholds for our analyses of Antarctic blue whale calls from AARs 1 and 2, and for fin whale calls from AAR1 (Figure 5.3). However, only six different thresholds from 20% to 70% by increments of 10% were tested for fin whale calls from AAR2 (Figure 3); the 10% threshold was not used because it produced many false positives. The 10% detection threshold was optimal for the detections of D- and Z-calls from both AARs and for the fin whale call detections from AAR1 as it produced the fewest missed calls. The 20% detection threshold was best suited for detecting fin whale calls from AAR2 (Figure 5.2). Detection templates for AAR1 produced false negative errors of 13% and 1% for the fin whale and Z-calls respectively; hence 87% and 99% accuracy rates for fin whale calls and Z-calls correspondingly (Figure 5.3). Detection templates from AAR2 produced false negative error rates of 13% and 11% for D- and Z-calls respectively; hence accuracy rates of 87% and 89% for D- and Z-calls respectively. The fin whale detection template from AAR2 produced 2% false negatives and a 98% accuracy rate (Figure 5.3).

The seasonal acoustic presence of blue and fin whales is defined herein as instances when calls of either whale species were detected within a sampling interval. The Z-call and 20 Hz pulse were used to determine acoustic occurrence of blue and fin whale respectively, since these were the most prevalent call types in our data. Acoustic absence refers to instances when neither blue nor fin whale calls were detected by AARs within a sampling interval.

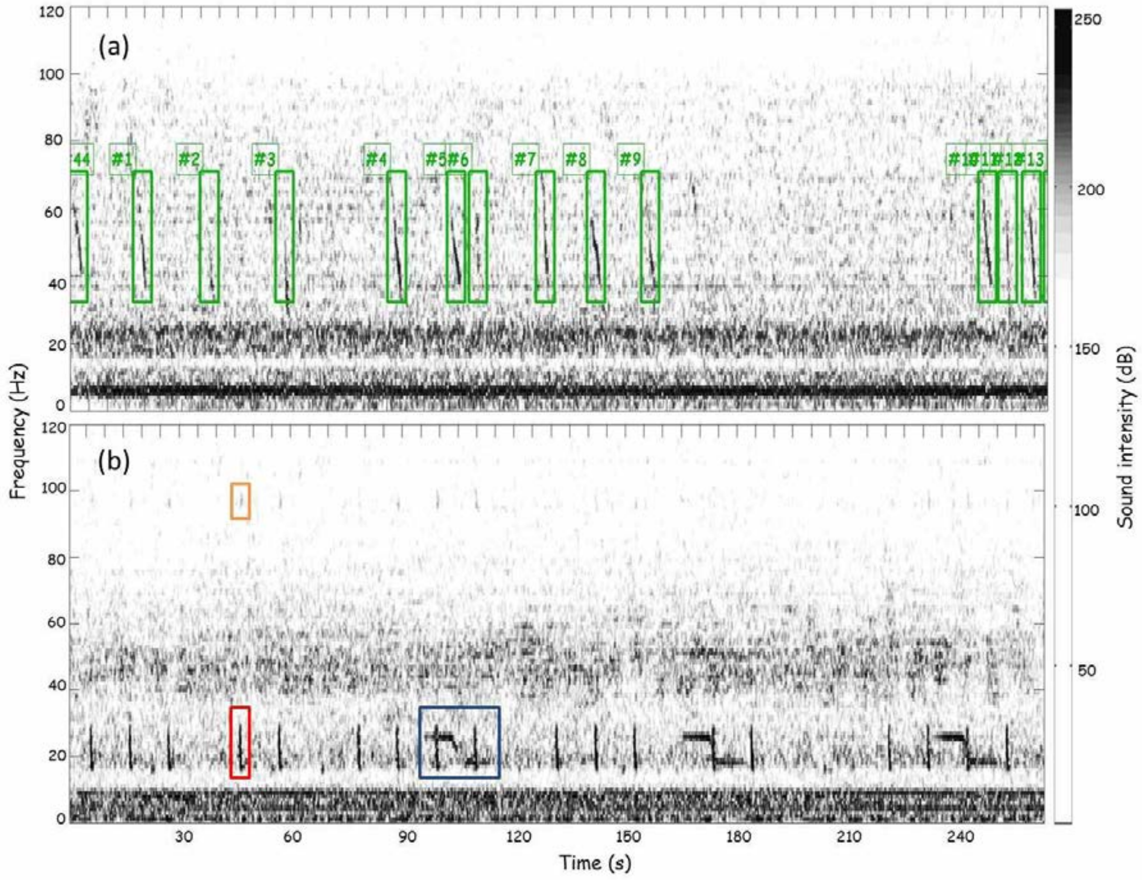


Figure 5.2. Spectrograms showing a) Antarctic blue whale D-calls (green boxes) and b) low frequency downsweeping ~28-15 Hz tone (red box) and high frequency 99 Hz tone (orange rectangle) of eastern Antarctic fin whale acoustic population and Z-calls (blue box) of Antarctic blue whales including co-occurring fin whale calls. Spectrogram parameters: frame size 1.28 s, 25% overlap, FFT size 4,096 points, Hanning window.

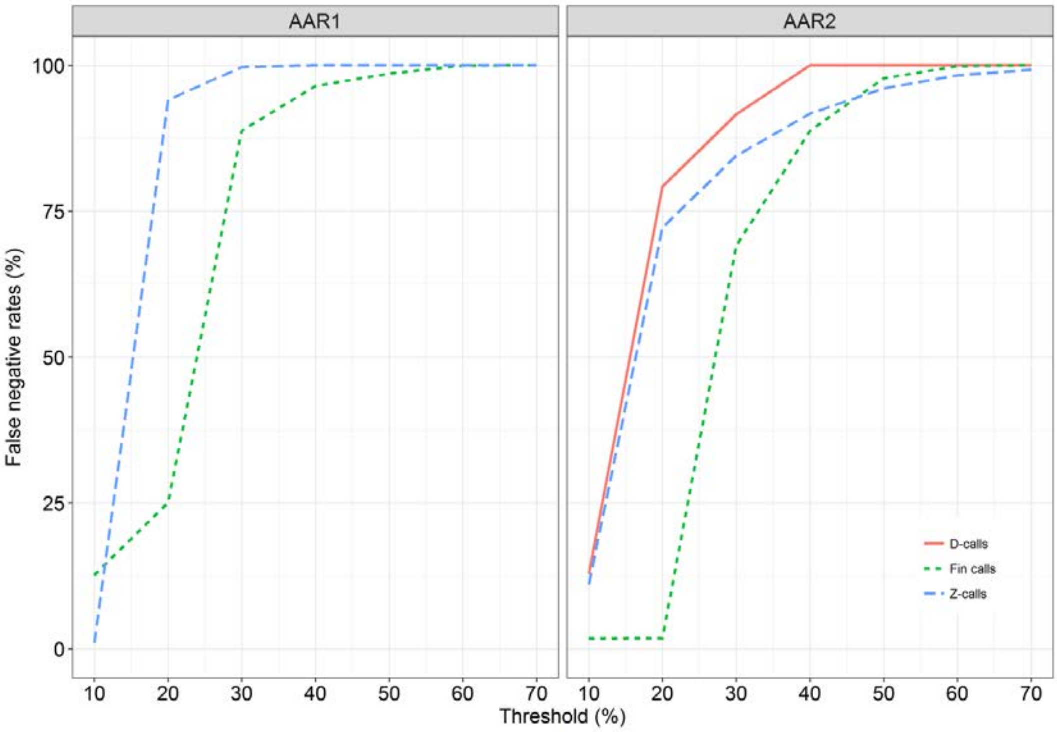


Figure 5.3. False negative rates at different thresholds for 28 Hz fin whale calls and Antarctic blue whale Z- and D-calls recorded from AAR1 (left) and AAR2 (right). No D-calls were recorded from AAR1.

5.2.3 Calculation of call rates

The actual recording time of sampling intervals (i.e. 30 minutes duty cycle for AAR1 and 20 minutes duty cycle for AAR2) were converted to full hour of the recording interval by dividing with 60 minutes of an hour. Call rates (expressed as calls detected per hour) of Antarctic blue and fin whales were calculated as the total number of calls recorded within a sampling interval divided by the duty cycle (0.50 h for AAR1 and 0.33 h for AAR2). The total hours with Z-, D-, and fin whales calls were calculated as the sum of the sampling periods with detections multiplied by the sampling intervals. The whale call rates refer to the overall call detection rate per unit time, not the number of calls per individual, which is unknown. Call rates reflected the acoustic behaviour of these whales in the Benguela ecosystem. The proportion of species call occurrence was calculated as the number of call presence of each species divided by the total number of samples recorded over time (month or season). We calculated the mean daily call rates as an average of call rates per day. Because the two listening stations were very close (4.8 km apart) and within the same regions from which the environmental data were extracted, we only used data from one of the instruments during the period of overlap (16 September to 1 December 2014). Smoothed means of the diel call rate patterns per season and environmental variables were calculated by the locally weighted polynomial regression using the function ‘loess’ (Cleveland *et al.* 1992) in R (R Core Team, 2016).

5.2.4 Environmental variables

Water temperature

We used daily sea surface temperature (SST) from the Operational Sea Surface Temperature and Sea Ice Analysis (OSTIA) data downloaded from the Copernicus Marine Environment Monitoring Service (ftp://cmems.isac.cnr.it/Core/SST_GLO_SST_L4_NRT_OBSERVATIONS

_010_001/METOFFICE-GLO-SST-L4-NRT-OBS-SST-V2/). OSTIA uses satellite data provided by the Group for High Resolution Sea Surface Temperature project (Donlon et al., 2012). The daily OSTIA SST data were first converted from Kelvin to degree Celsius (°C) by subtracting 273.15. SST was used to indicate changes in biological, physical, and chemical process that productivity and animal behaviour around the mooring.

Chlorophyll-a

Daily weighted average chlorophyll-a (chl-a) measurements of the GlobColour project (http://globcolour.info) were obtained from GlobColour developer, validator and distributor: ACRI-ST, France (ftp://ftp.hermes.acri.fr). The globally blended and binned high-resolution level-3 mapped grid, case-1 water GlobColour project merges the remotely sensed ocean colour measurements from two satellite data sources (Maritorena et al., 2010). About 90% of the records (dates) contained chl-a concentrations; for missing data, we used chl-a concentrations from the previous available record as there is a known spatial and temporal autocorrelation of daily chlorophyll-a within a time series (e.g., Mackas, 1984; Jutla et al., 2012). The replacement was done using the 'zoo' library (Zeileis and Grothendieck, 2005) in R. The chl-a concentration (i.e. phytoplankton pigment concentration) data were log-transformed for further analyses due to the skewness of their distribution.

Wind speed

Data on daily blended vector sea surface wind speed (at 10 m above sea level) were downloaded from the National Climatic Data Center (ftp://eclipse.ncdc.noaa.gov/pub/seawinds/SI/). These sea wind speeds were blended from multiple satellites on a global 0.25 degree spatial grid and a 6-hourly temporal resolution (see Zhang *et al.* 2006). Wind speed indicated oceanic circulation around our moorings and not used as proxy of ambient noise since previous studies found insignificant effect of wind-induced noise on sounds below 100 Hz (e.g., Wenz, 1962; Menze *et al.* 2017).

Sea surface height

Daily sea surface height (SSH) information to indicate sea state conditions around moorings were obtained from Archiving, Validation and Interpretation of Satellite Oceanographic (ftp.aviso.altimetry.fr) that uses the level 4 absolute dynamic topography.

Wind stress curl and Ekman upwelling index

Daily data on wind stress curl and Ekman upwelling index was measured by the meteorological operation’s advanced scatterometer that globally sampled at a 0.25 degree spatial grid (Bentamy and Croize-Fillon, 2012). Such data were obtained from Environmental Research Division's Data Access Program (http://coastwatch.pfeg.noaa.gov/erddap/griddap/erdQMstress1day.html) of the United States National Oceanic and Atmospheric Administration. Wind stress and Ekman upwelling index were used as indices of nutrient transport around the moorings.

All the above environmental data were processed and analysed using libraries of Pierce (2015) and Bivand *et al.* (2016) in R. To determine the oceanographic conditions around the AAR mooring, the above variables were averaged by 1° grid where the values of four 1° blocks adjacent to the AAR mooring were averaged. One degree of latitude and longitude closer to 40° south is approximately 111 km and 85 km respectively. The detection range for Antarctic blue whale calls in the Southern Ocean is estimated to be around 100 km (Thomisch *et al.* 2016), and 56 km for fin whale calls in the Southern Ocean (Širović *et al.* 2007). All whales from which calls were detected by the AARs would fall within the 111 km area making environmental variables directly comparable. The 111 km grid also falls within the large spatial scale (100-500 km) for foraging baleen whales (Torres, 2017).

5.2.5 Seasonal occurrence and behaviour modelling

We used random forest (RF) modelling (Ho, 1995; Breiman, 2001) to investigate the influence of different environmental variables (time of the day, SST, SSH, wind speed, Ekman upwelling index and log transformed chl-a) on the acoustic seasonal occurrence (i.e. presence and absence of species calls) and behaviour (i.e. species call rates) of Antarctic blue and fin whales. The RF model is an ensemble modelling approach for classification, regression and other functions with non-parametric inferential properties (Breiman, 2001; Hastie *et al.* 2009). As a machine learning method, RF modelling provides higher performance and has considerable benefits over standard regression methods such as generalized additive models (GAM; Guisan *et al.* 2002; Elith *et al.* 2008; James *et al.* 2013). RF modelling uses a set of unpruned decision trees in the forest that are bootstrapped as they grow with trained sample data, and rely on randomly chosen subsets of the predictor variables as candidate splitting tree nodes (Hastie *et al.* 2009; James *et al.* 2013).

Unlike generalised boosted regression trees model (GBM; Friedman *et al.* 2000), RF does not completely ignore some variables and its candidate split-variable selection increases the probability of any solitary variable being included (Hastie *et al.* 2009; James *et al.* 2013). Even though GBM and GAM are both regression methods, GBM is known as an iterative computer learning algorithm whereas GAM is a data driven model for dealing with very non-linear and non-monotonic relationships between predictor and response variable (Guisan *et al.* 2002; Friedman *et al.* 2000). The RF model is generally built to avoid overfitting of growing trees in the training data (e.g., Hastie *et al.* 2009). The RF model is furthermore known to be immune to autocorrelation. This RF model is also better at dealing with zero-inflated data from count data (Hastie *et al.* 2009; Mascaro *et al.* 2014).

The relative importance of predictor variables in the model was assessed by computing the influence of each of the variables on the prediction error of the model. The relative importance of each of the variables in the model was computed by permuting the out of the bag (OOB) data, as measured by the mean sum of squares, resulting from splitting of the variable of interest and averaging over all trees (Hastie *et al.* 2009). For each tree, the prediction error was computed on the OOB data and the permuted data were calculated and averaged across all trees. The average prediction error were then normalized by the standard deviation of the difference from the mean prediction error. This normalized index was calculated for each of the variables and used as an index of relative importance.

We investigated correlations between predictor variables (time of the day, months of the year, SST, SSH, wind speed, wind stress curl, Ekman upwelling and log transformed chl-a) prior to modelling to determine the effects of multi-collinearity using the generalised variance inflation factors (GVIF; Fox and Monette, 1992). We implemented GVIF through the 'car' library (Fox and Weisberg, 2011) in R. GVIF quantified how much variance of the estimated regression coefficients was amplified because of collinearity. Low GVIF values (around one) indicate weak or no correlations, GVIF values around five indicate moderate correlations, and high GVIF values around 10 or more indicate strong correlations (Fox and Monette, 1992; O'Brien, 2007; Hair *et al.* 2009). Months of the year and wind stress curl were eliminated from further analysis due to strong collinearity with the log transformed chl-a, Ekman upwelling index, SSH and SST. Highest values of 5900.13 and 90.37 GVIFs were obtained when wind stress curl and months of the year were included in the GVIF model and GVIF dropped to 1.04 when those two parameters were excluded. To improve the performance prediction of the RF model, time of the day was removed from the model of blue and fin whale call occurrence because the index of relative importance was negative. Wind speed and time of the day were removed from the RF model of D-call and fin whale call rates respectively due to negative importance. Negative relative importance generally indicates that variables are not important at all (Perrier, 2015).

Following the multicollinearity test, the RF model was fitted using the optimal configuration values in Table 5.1. The RF modelling was performed in R using the 'randomForest' library

(Liaw and Wiener, 2002), whilst the optimal parameter configuration values were determined using the ‘ranger’ library as a computational-time-saving method for the implementation of the RF model (Wright and Ziegler, 2016).

Table 5.1. Optimal parameter configuration values used in the RF model to investigate seasonal call occurrences and call rates. Mtry is the number of variables randomly selected at each tree node; ntrees is the number of growing trees, nodesize is the splitting minimum size of terminal nodes of trees, Z is Z-call, D is D-calls, F is fin whale calls, BP is Antarctic blue whale presence, and FP is fin whale presence.

Mtry	Ntrees	Nodesize	Group
4	1500	2	Z
1	500	5	D
1	1500	1	F
4	500	1	BP
1	500	1	FP

Two different ways of assessing model performance were used for count (presence and absence) and continuous (call rates) data. The area under the receiver operating characteristic curve (AUC) was used to measure the predictive accuracy of our RF classification model compared to GAM and GBM, i.e. how well the model correctly classified the classes included in the model (here the presence and absence of whale calls). AUC normally takes values between 0.5 and 1, where values closer to 1 indicate better classification ability (DeLong *et al.* 1988). The number of replicates was set to 200 for the model performance assessment. Using 80% of the data for training and the remaining for validation, the performances of GAM, GBM and RF models for blue and fin whale call rates modelling were assessed. Root mean square prediction error (RMSPE) was used to measure the difference between values predicted by the model and observed values (e.g., Chai and Draxler, 2014). In addition, Spearman's rank correlation coefficient (rho) was applied as a qualitative measure of the performance of models. A low RMSPE value indicates a better model and the opposite is true for rho.

Only the RF model was better at detecting signals and had higher prediction accuracy than GBM and GAM as it had higher AUC values (Table 5.2). The correlations between the predicted and observed values of all three call rates were also highest for RF model (Table 5.3).

Table 5.2. Model performance for acoustic seasonal occurrences of blue and fin whales according to AUC. SD is the standard deviation. Boldface indicates values of a model with better performance.

	GAM		GBM		**RF**	
Species type	Mean	SD	Mean	SD	Mean	SD
Blue whale	0.918	0.004	0.848	0.025	**0.969**	**0.008**
Fin whale	0.849	0.033	0.849	0.033	**0.981**	**0.007**

Table 5.3. Model performance for blue and fin whale call rates based on root mean square prediction error (RMSPE) and Spearman's rank correlation coefficient (rho). Boldface indicates values of a model with better performance.

	rho		RMSPE	
Call-model types	Mean	SD	Mean	SD
D-GAM	0.028	0.007	0.090	0.016
D-GBM	0.022	0.020	0.096	0.019
D-RF	**0.029**	**0.008**	**0.088**	**0.013**
F-GAM	0.305	0.007	1.008	0.012
F-GBM	0.307	0.009	1.129	0.020
F-RF	**0.368**	**0.007**	**0.568**	**0.021**
Z-GAM	0.286	0.007	0.675	0.008
Z-GBM	0.275	0.012	0.725	0.012
Z-RF	**0.346**	**0.008**	**0.491**	**0.013**

5.3 Results

5.3.1 Call detections and the Benguela environment

Of the 1,567 total hours of acoustic data recorded by AAR1 from 30-minute sampling intervals, only 14 hours contained fin whale calls and 79.5 hours contained Antarctic blue whale calls. The total numbers of post-processed and operator verified calls for the two species from AAR1 were 2,539 fin whale 20 Hz pulse signals; 2,602 Antarctic blue whale Z-calls and no Antarctic blue whale D-calls. Out of the 3,489.75 total hours recorded by the AAR2 from 20-minute sampling intervals, 211.86 hours contained fin whale sounds while 156.09 hours contained Antarctic blue whale calls. The total numbers of post-processed and operator verified calls for the two species from AAR2 were 53,964 fin whale 20 Hz pulse signals; 6,114 Antarctic blue whale Z-calls and 176 Antarctic blue whale D-calls. All recorded fin whale sounds were those of the eastern Antarctic fin whale population (Figure

3b; Sirovic *et al.* 2009). Antarctic blue whales were detected within the hydrophone detection radius in 29 days for 2014 and 48 days for 2015, whereas fin whales were detected in 11 days for 2014 and 50 days for 2015. No calls of either species were recorded in summer and no choruses of either whale species were recorded throughout the deployment period of our AARs.

Both Antarctic blue and fin whale calls occurred between July and October in 2014 and May through November in 2015 (Figure 5.4). The peak monthly call occurrences of both species (32% of the time for Antarctic blue whale and 40% of the time for fin whale) were recorded in July (austral winter) (Figure 5.4). Mean daily call rates for fin whale calls and Antarctic blue whale D- and Z-calls followed the same trend as the monthly proportion of call occurrences with peaks in June and July (Figure 5.5). The highest mean daily call rate for D-call was 11 calls per hour per day detected in June, for Z-calls it was 61 calls per hour per day in July (Figure 5.5a); and the highest mean daily call rate for fin whale 20 Hz pulse was 396 calls per hour per day in July (Figure 5.5b).

The mean environmental conditions showed strong variation by season (Figure 5.6). Lower values for SST and log transformed chl-a were observed in winter while highest values of those parameters were observed in summer. Wind speed increased in winter through spring and SSH was high in winter but low in spring through summer (Figure 5.6). There was a general inverse relationship between SSH and wind speed, and there was lag in the decrease of log transformed chl-a after the decrease in Ekman upwelling index (Figure 5.6).

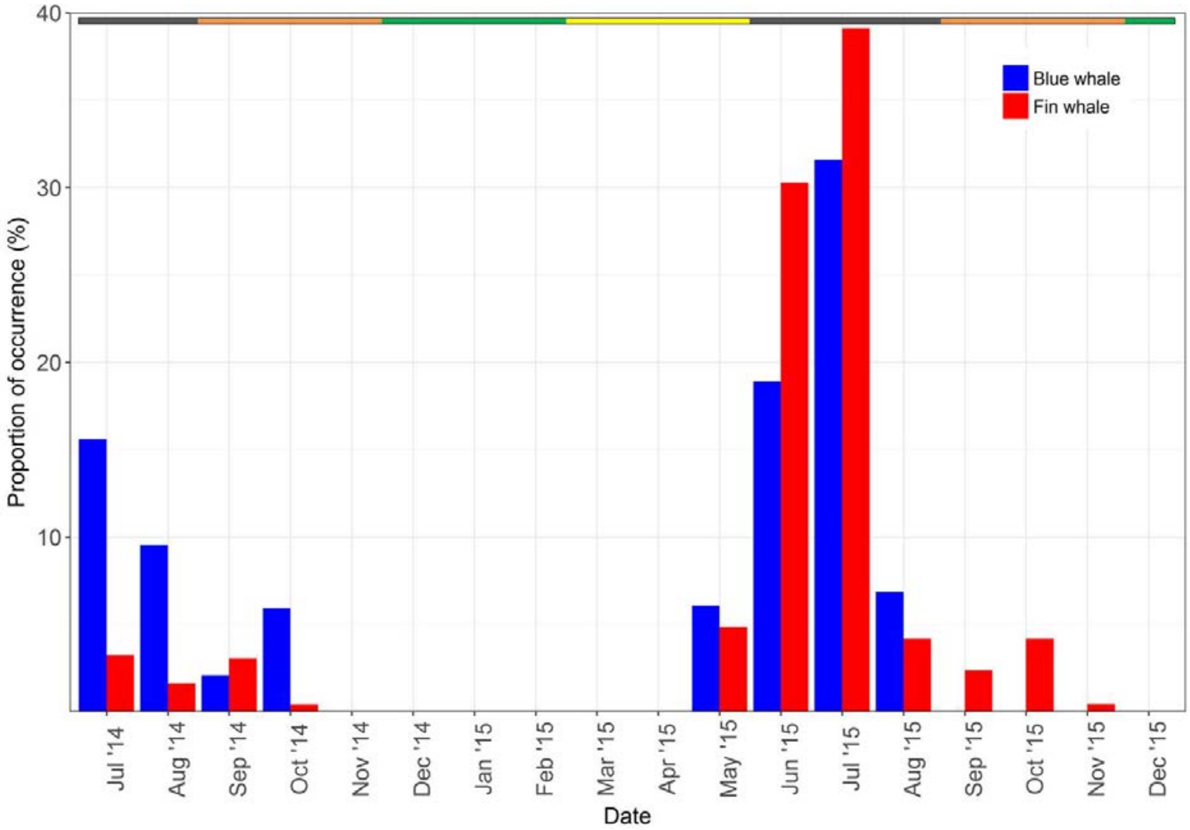


Figure 5.4. Monthly proportion of call occurrence of Antarctic blue and fin whales off the west coast of South Africa. Only seven days were sampled in July 2014 and one day was sampled in December 2015. Horizontal seasonal bar shading: green represents summer, yellow represents autumn, black represents winter, and orange represents spring.

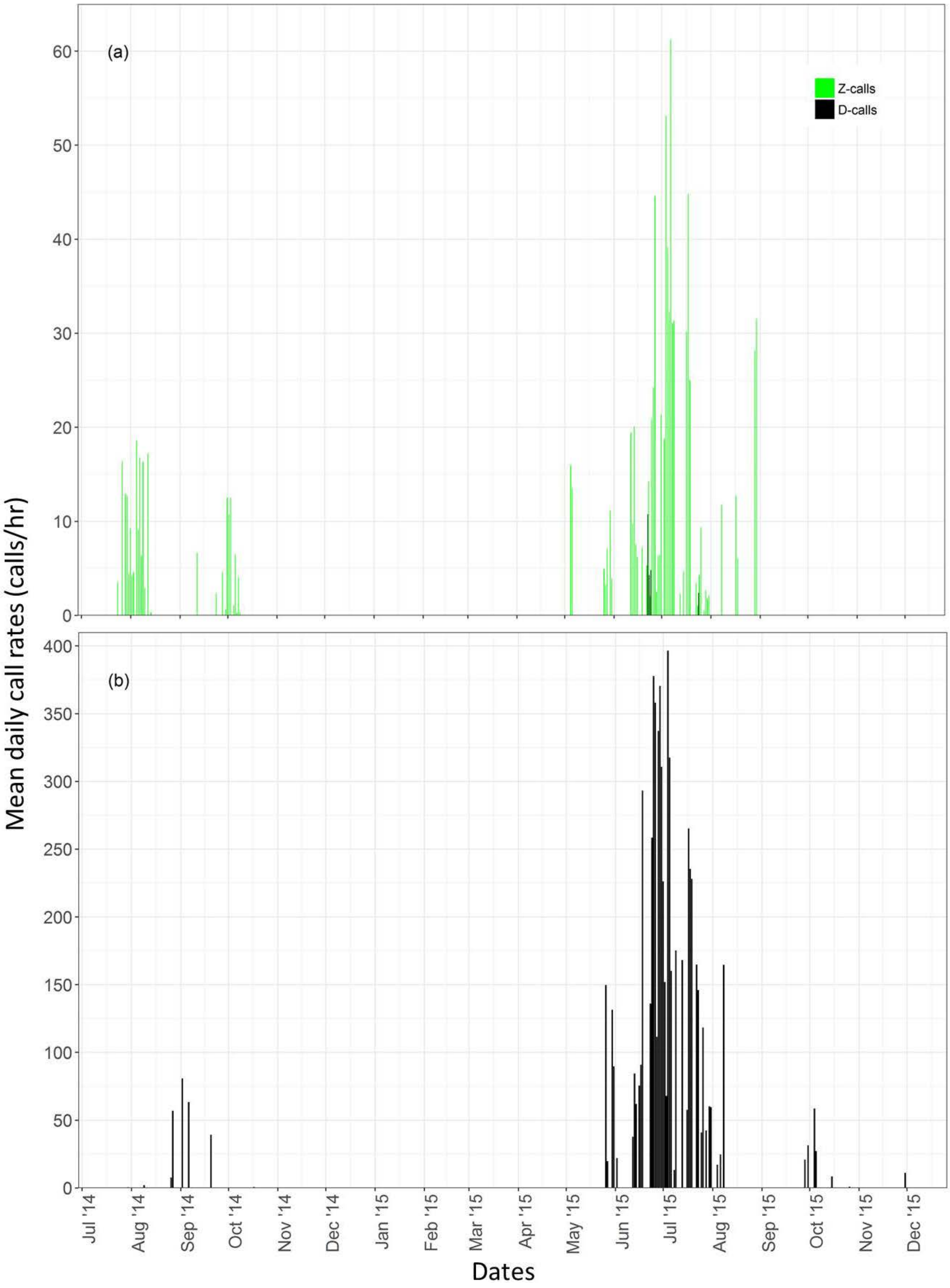


Figure 5.5. Mean daily call rates of Antarctic blue whales (a) and fin whale 20 Hz pulse (b) off the west coast of South Africa. Only seven days and one day were sampled in July 2014 and December 2015 respectively.

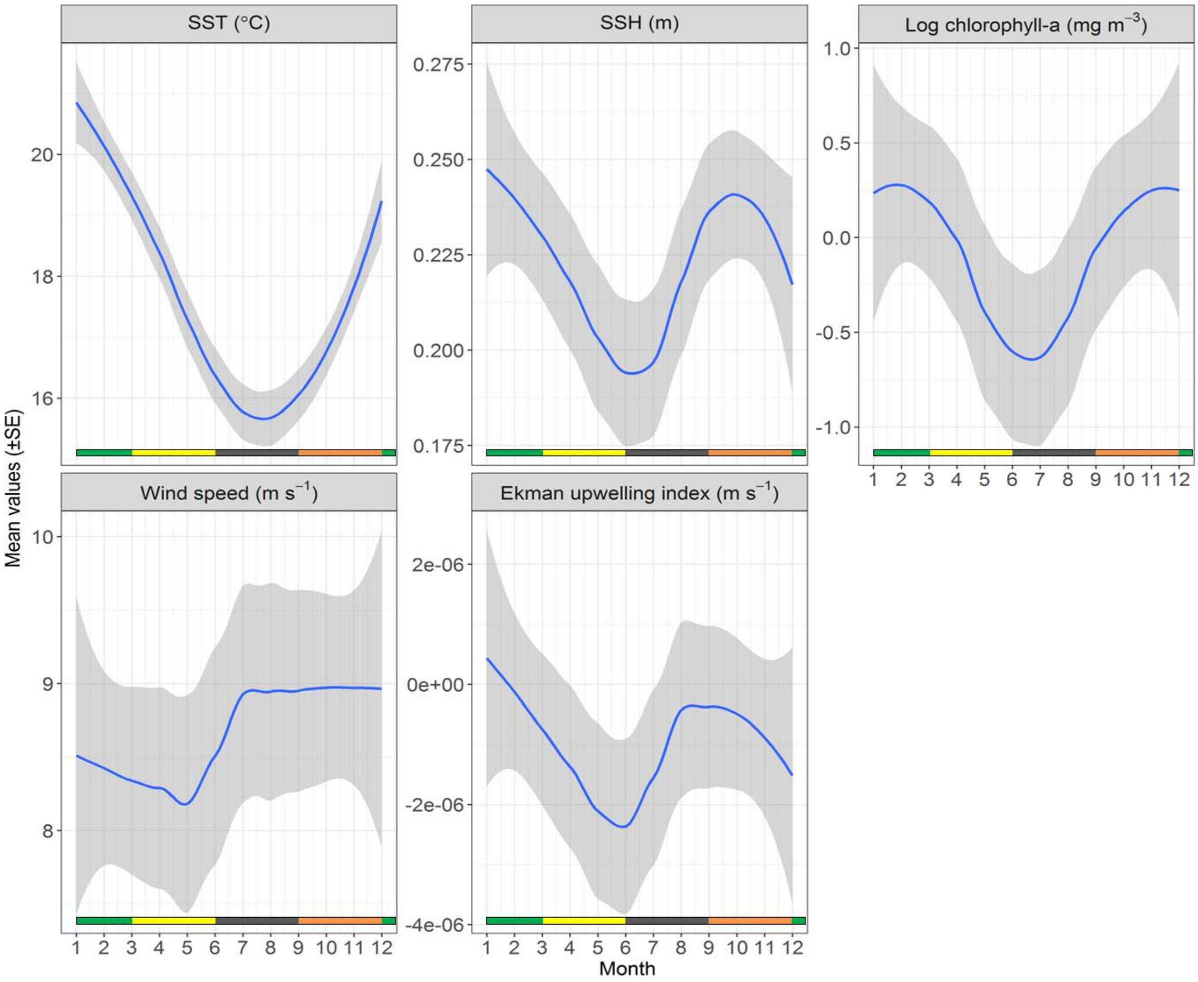


Figure 5.6. Smoothed monthly means of different environmental parameters off the west coast of South Africa. The grey shaded areas indicate the standard error (SE) of the smoothed mean (line). Horizontal seasonal bar shading: green represents summer, yellow represents autumn, black represents winter, and orange represents spring.

5.3.2 Seasonal call occurrences and rates

Both blue and fin whale call occurrence was greatest in winter (Figure 5.7). No whale calls were recorded in summer for either species. The proportion of call occurrence for Antarctic blue whales peaked during daytime in autumn, winter and spring (Figure 5.7); there were also some blue whale call occurrence peaks at night in spring. High Z-call rates of Antarctic blue whales were recorded during daytime in autumn and winter while fewer calls were recorded during daytime in spring (Figure 5.8a-c). D-call rates increased after midday to midnight in winter and no calls were recorded in other seasons (Figure 5.8d). In winter, the proportion of fin whale call occurrence peaked from midnight to dawn but decreased in the early morning; occurrence increased again from midday to dusk with a slight decrease after dusk and increased again towards night (Figure 5.7). In autumn and spring calls occurred more during dawn and daytime for fin whale (Figure 5.7). Fin whale call rates were high during daytime in autumn and spring but peaked after midnight and midday in winter (Figure 5.8e-g). There was no temporal segregation between the peaks of diel call rates of blue and fin whales in autumn and winter, however, spring had a strong temporal segregation of diel call rate peaks (Figure 5.8).

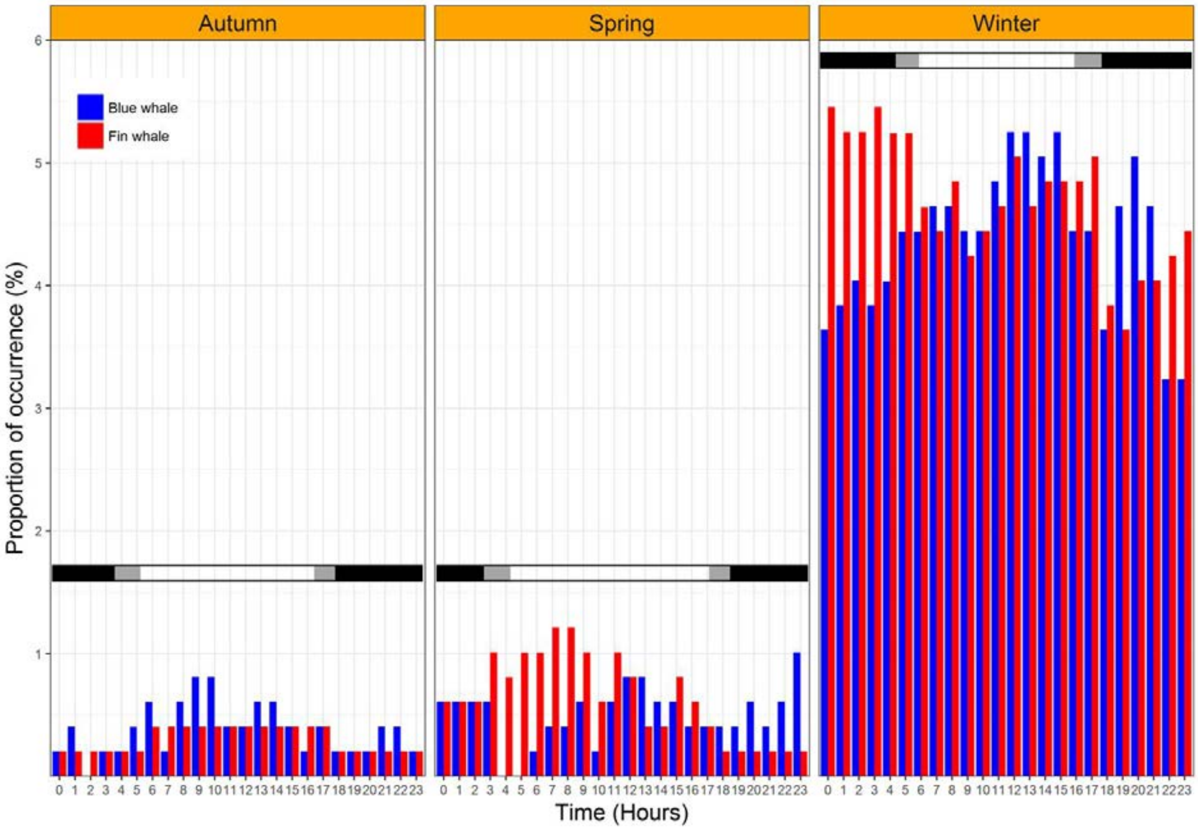


Figure 5.7. Diel proportion of call occurrence per season for blue and fin whales off the west coast of South Africa. Horizontal diel bar shading: black represents average nighttime hours, grey represents average twilight hours and white represents average daytime hours.

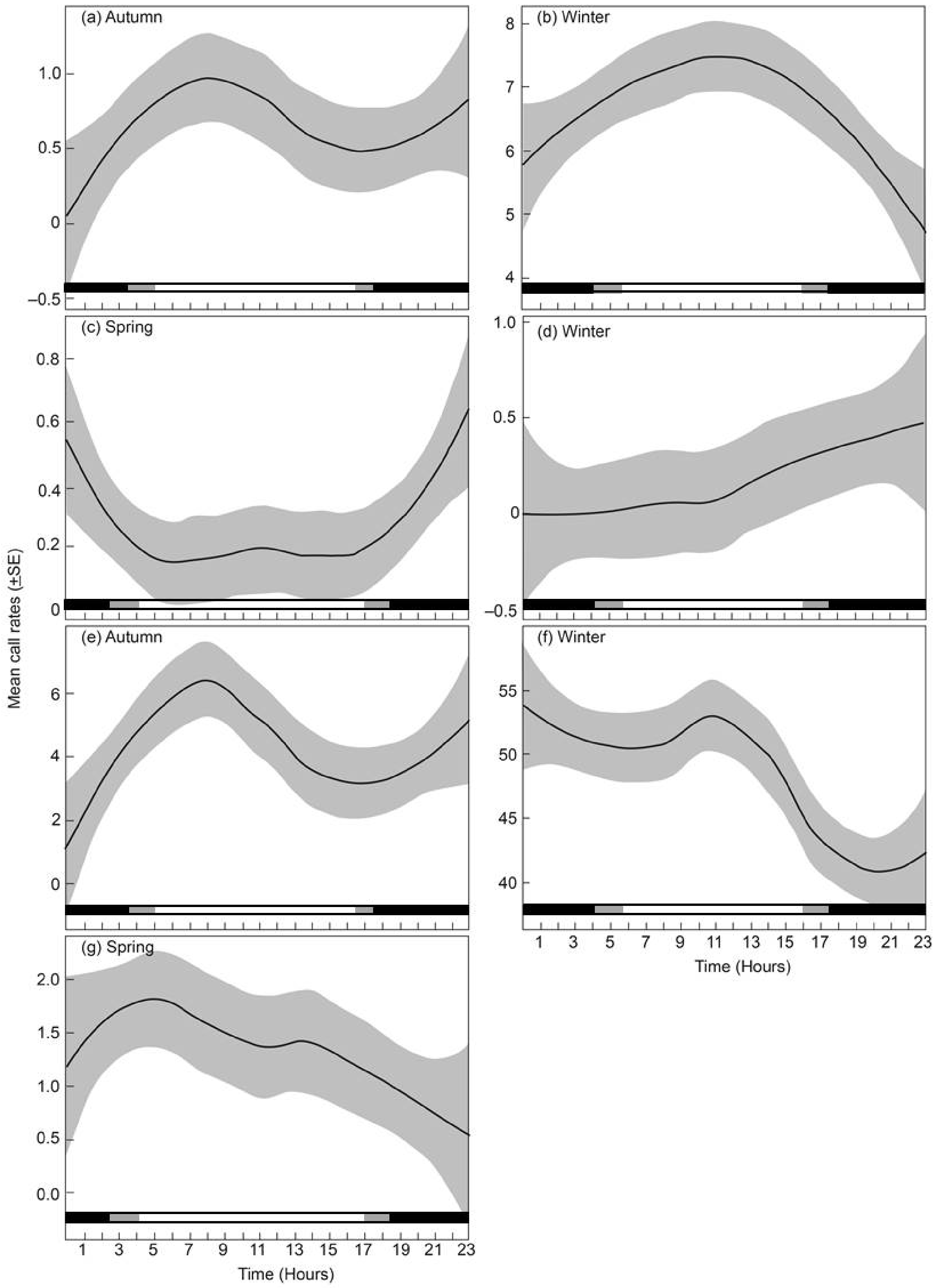


Figure 5.8. Smoothed mean diel call rate patterns per season of Antarctic blue and fin whale acoustic behaviour in the Benguela ecosystem. (a)-(c) Diel Z-call rates in autumn, winter and spring respectively; (d) diel D-call rate in winter; and (e)-(g) diel fin whale call rates in autumn, winter and spring respectively. The grey shaded areas of the line plot indicate the standard error (SE) of the smoothed mean (line). Horizontal diel bar shading: black represents average nighttime hours, grey represents average twilight hours and white represents average daytime hours. The above plots demonstrate the patterns of diel call rates over seasons and not a model predicted call rates.

Low log transformed chl-a (-2 to 1.5 mg m^{-3}), Ekman upwelling index (-3 to -0.5 x 10^{-5} m s^{-1}) and SST (14-17°C), but high SSH (0.17-0.21 m) had highest effect on the Antarctic blue whale call occurrence (Supplementary Figure S5.2). Effects of wind speed on Antarctic blue whale call occurrence was high at around 12 m s^{-1} (Supplementary Figure S5.2). The RF model identified SSH and SST as the most important predictors of Antarctic blue whale call occurrence (Figure 5.9). Wind speed and log transformed chl-a were moderately important predictors, while Ekman upwelling index was the least important predictor of overall Antarctic blue whale call occurrence (Figure 5.9). Low SST (14-16°C), Ekman upwelling index (-3 to -0.5 x 10^{-5} m s^{-1}) and wind speed (below 5 m s^{-1}), but high SSH (0.17-0.21 m) and log transformed chl-a (0.3-2.5 mg m^{-3}) were highly influential on Z-call rates (Supplementary Figure S5.3). Low SST (14-16°C) and Ekman upwelling index (-3 to -0.7 x 10^{-5} m s^{-1}), but high log transformed chl-a (0.5-2.5 mg m^{-3}) and SSH (>0.19 m) positively influenced D-call rates and there was an increase in call rates at night (Supplementary Figure S5.4). SST and log transformed chl-a were the most important predictors of D-call rates; SSH and SST were the most important predictor of Z-call rates (Figure 5.10). SSH and time of the day were moderately important predictors of the detection rate of D-calls with Ekman upwelling index being the least important predictor (Figure 5.10). Ekman upwelling index, log transformed chl-a and wind speed were moderately important predictors of Z-call rates, whereas time of the day was the least important predictor of Z-call rates (Figure 5.10).

Low SST (14-17.5°C) and Ekman upwelling index (-3 to -0.4 x 10^{-5} m s^{-1}) were highly influential on fin whale call occurrence (Supplementary Figure S5.5). Wind speed, SSH and log transformed chl-a had varying effects on fin whale call occurrence (Supplementary Figure S5.5). SST was the most important predictor of fin whale call occurrence (Figure 5.10). Low SST (14-16.1°C), Ekman upwelling index (-3 to -1 x 10^{-5} m s^{-1}) and log transformed chl-a (-2 to 0.5 mg m^{-3}) but high SSH (0.17-0.21 m) and varying wind speeds influenced fin whale call rates (Supplementary Figure S5.6). SSH, Ekman upwelling index and wind speed were moderately important predictors, and log transformed chl-a was the least important predictor of fin whale call occurrences (Figure 5.9). SST and SSH were the most important predictors of fin whale call rates; log transformed chl-a was moderately important predictor of fin whale call rates, whereas wind speed and Ekman upwelling index were the least important predictors (Figure 5.10).

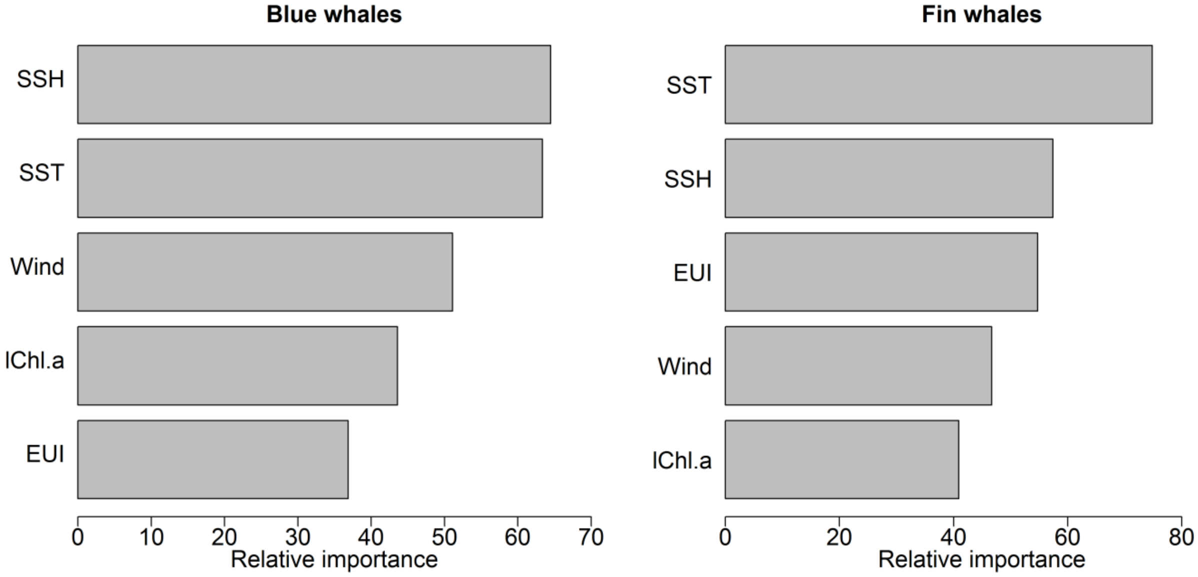


Figure 5.9. Ranked relative importance of different variables on call occurrences of blue (left) and fin (right) whales. lChl.a is log transformed chl-a, EUI is Ekman upwelling index and Wind is wind speed.

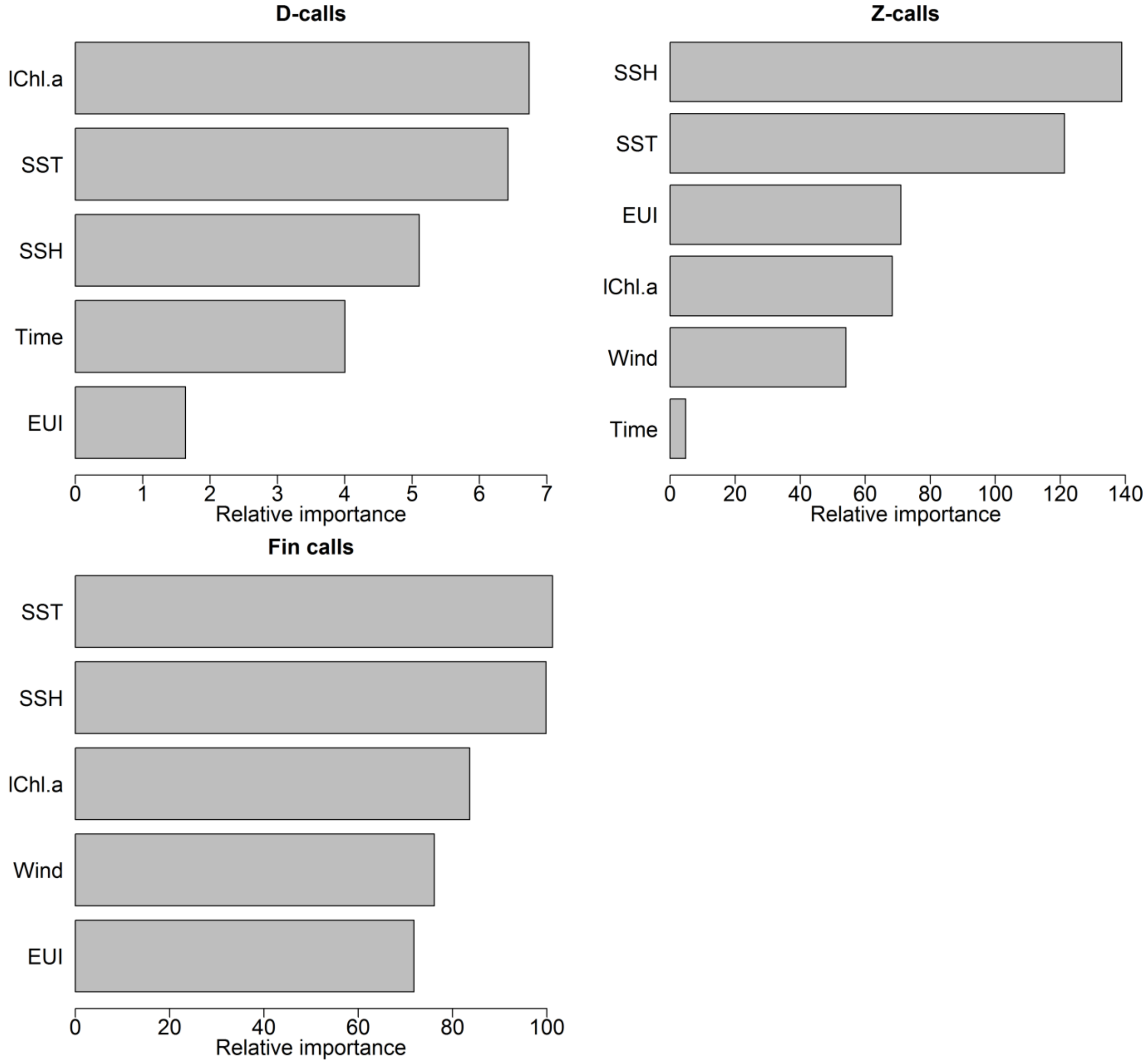


Figure 5.10. Ranked relative importance of different environmental conditions on call rates of Antarctic blue whale D- (top left) and Z-calls (top right); and fin whale (bottom left). lChl.a is the log transformed chl-a, EUI is Ekman upwelling index and WindSp is wind speed.

5.4 Discussion

Environmental and oceanographic conditions are excellent depicters of productivity and climate variability and/or change because they are influenced by changes in climate on both seasonal and inter-annual scales (Moore *et al.* 2008; Goubanova *et al.* 2013; Sydeman and Thompson, 2013). For example, the high wind speeds, SSH, log transformed chl-a, and Ekman upwelling index observed in summer in this study indicate the upwelling regime on the wide shelf in the southern Benguela (Jury and Bundrit, 1992; Veitch *et al.* 2010; Goubanova *et al.* 2013). Likewise, Brown (1992) noted high log transformed chl-a concentrations in summer and low concentrations of log transformed chl-a in winter in the southern Benguela ecosystem. Marine animals living in the Benguela ecosystem adapt to such environmental changes by varying their distribution and behaviour (Ekau *et al.* 2001). The remotely sensed environmental conditions (SST, SSH, wind speed, log transformed chl-a, and Ekman upwelling index) derived for our study showed seasonal trends that coincided with the seasonal acoustic occurrence of whales. For instance, winter had the lowest values of SST and log transformed chl-a but the highest occurrences of both whale species. A similar relationship was observed during summer in Antarctic between Antarctic blue whale acoustic occurrences and environmental conditions (Shabangu *et al.* 2017- Chapter 4).

The observed SST cooling from 21°C in summer to 15°C in winter could be due to weaker solar radiation (caused by cloud cover) and mean wind stress in winter (Goubanova *et al.* 2013) and the intrusions of cold sub-Antarctic surface waters (Lutjeharms and Meeuwis, 1987). SST and SSH were the most important predictor of fin whale acoustic occurrence and call rates (i.e., behaviour), suggesting environmental preference in this whale species, which might make it vulnerable to future environmental changes. Moreover, fin whale prey such as sardine and anchovy are known to prefer cold SST (17-20°C) in the Benguela ecosystem (Checkley *et al.* 2009; Mhlongo *et al.* 2015). North-directed winds along the southern Benguela coast reinforce the Ekman transport offshore and upwelling of nutrient-rich, cold water to the euphotic zones (Lutjeharms and Stockton, 1991; Jury and Bundrit, 1992). SSH and SST were the most important predictors of Antarctic blue whale call occurrence and Z-call rates because they describes upwelling events; it is well known that Antarctic blue whales are often reliant on upwelling regimes (Branch *et al.* 2007; Stafford *et al.* 2009; Shabangu *et al.* 2017- Chapter 4). Low wind speeds were important for Z-call rates suggesting that high wind speeds may have decreased acoustic detectability and possibly increased Benguela productivity. Ekman upwelling index was ranked by the RF model as a moderately or less important predictor of both whale call occurrence and call rates, likely indicating that nutrient recycling was well captured by variations in phytoplankton pigment concentration from the transformed chl-a measurements. The lack of temporal segregation between the peaks of diel call rates of blue and fin whales in autumn and winter is indicative that blue and fin whales are not only sympatrically but vocalise at similar times. The observed temporal segregation between peaks of diel call rates of blue and fin whales in spring could be due to few blue whales present in the Benguela ecosystem to yield comparable diel call rates to that of fin whales.

Blue and fin whales are thought to feed mainly in the Antarctic but to fast after migrating to lower latitudes to overwinter and mate (Mackintosh and Wheeler, 1929; Best, 2007). Our detections of Antarctic blue whale feeding associated D-call in the Benguela ecosystem might indicate that these animals could be foraging on their overwintering ground. While this has been hypothesized in the Indian Ocean (Samaran *et al.* 2013), to the best of our knowledge, this is the first indication that Antarctic blue whales might be feeding in the Benguela ecosystem. Log transformed chl-a and SST were the most important predictors of the Antarctic blue whale feeding associated D-call rates, indicating that productivity might have influenced whale feeding. As noted above, this is unsurprising given the documented association between Antarctic blue whales and regions of strong upwelling and high phytoplankton densities (Branch *et al.* 2007). Although the prey of Antarctic blue whales in the Benguela ecosystem is currently unidentified, we hypothesize that they might have been feeding on the local species of krill that form large enough swarms to be suitable prey. *Nematoscelis megalops* is the most abundant local krill species found in the outer-shelf waters of the Cape Peninsula while other krill species that also occur in the outer-shelf area do so in low numbers; these include *Euphausia recurva* and *Thysanoessa gregaria* (Pillar *et al.* 1992). Werner and Buchholz (2013) found low biomass but bigger sizes of *N. megalops* in winter on the Northern Benguela that corresponded well with changes in environmental conditions.

Barange *et al.* (1991) showed that *N. megalops* performs nocturnal vertical migrations from the deep sea to just below the thermocline positioned at around 20 to 40 m; this migration to near the surface corresponds well with the slight increase in the call rates of the Antarctic blue whale D-calls that we observed from dusk to midnight. The low numbers of D-calls (i.e. 176 calls) demonstrate that Antarctic blue whales rarely produce this call type as compared to Z-calls (with 6,114 calls detected). The socializing Z-call rates were higher during the day than at night in winter, which is similar acoustic behaviour to that observed in summer in the Southern Ocean (Shabangu *et al.* 2017- Chapter 4). This inverse relationship between calling and foraging-associated vocalizations in Antarctic blue whales might be an energy saving behaviour whereby animals socialize when their prey are at depth but forage when the prey are easily accessible close to the sea surface (Stafford *et al.* 2005). Similarly, Leroy *et al.* (2016) observed Antarctic blue whales in the Indian Ocean to be more vocally active during the day. Although there was a diurnal pattern in Antarctic blue and fin whale call rates, the RF model ranked the time of the day as moderately and least important predictor of D- and Z-call rates respectively. Such ranking indicates that time of the day cannot be reliably used to determine when whales will vocalise; this is further explained by the observed non-importance of time of the day on whale call occurrence.

In contrast to the Indian Ocean, where Antarctic blue whales were detected acoustically year-round (Samaran *et al.* 2010, 2013; Leroy *et al.* 2016), in the southeast Atlantic Ocean we detected Antarctic blue and fin whales only seasonally, most likely due to food limitations and the migratory behaviour of these species. Local krill species are not as abundant as *E. superba* is in the Antarctic and could not sustain a commercial fishery (Shabangu *et al.* 2016). Samaran *et al.* (2013) postulated that Antarctic blue whales could forage and move regionally and seasonally to utilize food resources available within the Indian Ocean. It is currently unknown whether fin whales were also feeding in the Benguela ecosystem as there has not been a feeding associated call yet documented for this species, but we suspect that they may have similar behaviour patterns to blue whales. SST was the strongest predictor of fin whale acoustic occurrence in the North Pacific (Stafford *et al.* 2009) and data from

Antarctic whaling grounds suggested that fin whales were most abundant in frontal zones with relatively colder water (Nasu, 1966).

Seasonal changes in the call occurrences of blue and fin whales might indicate a difference in the number of vocally active animals within recording radius of our AARs, an asynchronous whale migration, or they might be due to seasonal changes in call rates. Peaks observed in Antarctic blue whale call occurrences and rates by this study are the inverse of the seasonal peak observed by Širović *et al.* (2009) in the Southern Ocean. Širović *et al.* (2009) observed a peak in call numbers from late summer through autumn but low numbers in winter; then call numbers increasing again towards the end of spring. We observed an increase in Antarctic blue whale calls towards the end of autumn through winter and peaks in winter. Širović *et al.* (2009) also detected few fin whale calls by the late summer through autumn with the peak in autumn and no calls for the remainder of the year; however, we detected fin whale calls from late autumn until end of spring. Antarctic blue whale calls also peaked during the austral autumn and winter (May–September) in the Indian Ocean (Stafford *et al.* 2004; Samaran *et al.* 2010, 2013; Leroy *et al.* 2016).

These complementary patterns between high and low latitudes supports the idea that both species migrate between these regions annually and that the Benguela ecosystem forms an important overwintering, mating and calving ground for them (True, 1904; Best, 2007). The west coast of South Africa is most likely not used as a migration corridor to locations further north by either blue or fin whales because we did not record dual peaks in the acoustic presence of these species, where one peak might indicate a northward migration and a second peak might indicate a return southward migration to the Antarctica. Our results confirm the observation by Best (1998, 2007), based on whale catches in the northern and southern Benguela ecosystem, that Antarctic blue whales are most abundant between May and August and fin whales between May and November.

Antarctic blue whale calls detected here could be from any of the three recently genetically differentiated Antarctic blue whale populations that feed sympatrically in Antarctica but do not breed in the same Southern Hemisphere grounds (Attard *et al.* 2016). Acoustic presence of only eastern Antarctic fin whale acoustic population (Širović *et al.* 2009) in the southern Benguela ecosystem suggests that eastern and western Antarctic fin whales do not migrate sympatrically, and that western Antarctic fin whales do not use the Benguela ecosystem for overwintering, probably due to the long distance from their feeding grounds.

The passive acoustic data collection did not interfere with any oceanographic instruments on the moorings nor did such instruments interfere with the acoustic recordings, illustrating the value and efficacy of oceanographic moorings as acoustic platforms (Shabangu and Findlay, 2014- Chapter 2). Acoustic monitoring of these large Antarctic baleen whales off the west coast of South Africa can be considered the most economical and reliable method of monitoring and tracking the recovery of these marine mammals. We recommend continuous recording of acoustic data in an array series of moorings to track individual whales, estimate seasonal whale densities and identify whale migration corridors. Such recordings would also help to evaluate the effects of anthropogenic noise on the health of marine mammals in the Benguela ecosystem.

The results of this work have improved our understanding of the Benguela ecosystem by facilitating the incorporation of large baleen whales into the appropriate trophic level within the system. Blue and fin whales were believed to have largely been extirpated from the system due to whaling but may now be recovering. Sounds of humpback *Megaptera novaeangliae* and other whales were also observed from our acoustic recordings, expanding the efficacy of these systems for offshore large whale acoustic monitoring. Recent (i.e. July 2017) offshore sighting research efforts conducted along the SAMBA line during the SEAmester cruise, South Africa's Class Afloat programme (Ansorge *et al.* 2016), resulted in the sighting of fin, sperm *Physeter macrocephalus*, sei *B. borealis*, minke *B. bonaerensis*, and humpback whales but not Antarctic blue whales.

5.5 Conclusion

This study provides the first acoustic records of sympatric occurrence of Antarctic blue and fin whales off the west coast of South Africa and the first acoustic evidence of Antarctic blue whales possibly feeding in the Benguela ecosystem. The detection of the feeding associated D-calls of Antarctic blue whales might suggest that these whales do not necessarily fast while overwintering but feed opportunistically on available prey, contrary to earlier assumptions (e.g., Mackintosh and Wheeler, 1929). Our study confirms the west coast of South Africa as an overwintering and potentially mating/calving region of blue and fin whales. Both the call occurrences and diel acoustic behaviour of these whales in the southern Benguela ecosystem varied with season, and the peak in occurrence and call rates for both species was in July. This suggests a link with seasonal variation in environmental conditions. Using oceanographic moorings to collect passive acoustic data at the low latitude locations, a cost-effective method of monitoring whales was demonstrated. We recommend further research effort in the Benguela ecosystem to investigate abundance, and distribution of populations of these large Antarctic baleen whales over extended periods of time. The information produced here is vital for the management and conservation of these world’s largest animals through the identification of essential overwintering ground.

5.6 Acknowledgements

We acknowledge the National Research Foundation and the South African National Antarctic Programme for financial support of this South African Antarctic blue whale Project. The Department of Environmental Affairs is acknowledged for its kind assistance with the data collection. We thank Marcel du Plessis, Department of Oceanography, University of Cape Town, for his help with access to the AVISO SSH data. We are sincerely indebted to Prof

Isabelle Ansorge and other SAMOC oceanographers for permitting our AARs to “hitchhike” on their oceanographic moorings. We thank everyone who helped in the deployment and recovery of the AARs including captains and crew of RV *Algoa*. We are grateful to Dr Sheldon Dudley for his invaluable comments and suggestions on the earlier draft of this manuscript.

5.7 References

Amante, C. and Eakins, B.W. 2009. ETOPO1 1 Arc-Minute Global Relief Model: Procedures, Data Sources and Analysis. NOAA Technical Memorandum NESDIS NGDC-24. National Geophysical Data Center, NOAA. DOI:10.7289/V5C8276M.

Andrews, W.R.H. and Hutchings, L. 1980. Upwelling in the southern Benguela Current. Progress in Oceanography 9(1): 81.

Ansorge, I.J., Baringer, M.O., Campos, E.J.D., Dong, S., Fine, R.A., Garzoli, S.L., Goni, G., Meinen, C.S., Perez, R.C., Piola, A.R., Roberts, M.J., Speich, S., Sprintall, J., Terre, T., and van den Berg, M.A., 2014. Basin-wide oceanographic array bridges the South Atlantic. Eos 95(6): 53–54.

Ansorge, I.J., Brundrit, G., Brundrit, J., Dorrington, R., Fawcett, S., Gammon, D., Henry, T., Hermes, J., Hölscher, B., d’Hotman, J., Meiklejohn, I., Morris, T., Pinto, I., du Plessis, M., Roman, R., Saunders, C., Shabangu, F.W., de Vos, M., Walker, D.R., and Louw, G., 2016. SEAmester – South Africa’s first class afloat. South African Journal of Science 112(9/10): 1–4.

Attard, C.R.M., Beheregaray, L.B. and Möller, L.M. 2016. Towards population-level conservation in the critically endangered Antarctic blue whale: the number and distribution of their populations. Scientific Reports 6: 22291.

Barange, M., Gibbons, M.J., and Carola, M. 1991. Diet and feeding of *Euphausia hanseni* and *Nematoscelis megalops* (Euphausiacea) in the northern Benguela Current: ecological significance of vertical space partitioning. Marine Ecology Progress Series 73: 173–181.

Bentamy, A. and Croize-Fillon, D. 2012. Gridded surface wind fields from Metop/ASCAT measurements. International Journal of Remote Sensing 33(6): 1729–1754.

Best, P.B. 1994. A review of the catch statistics for modem whaling in southern Africa, 1908-1930. Report of the International Whaling Commission 44: 467–485.

Best, P.B. 1998. Blue whales off Namibia - a possible wintering ground for the Antarctic population. Paper SC/50/CAWS14 presented to the IWC Scientific Committee, April 1998, Muscat, Oman. 10 pp.

Best, P.B. 2007. Whales and dolphins of the Southern African subregion. Cambridge University Press, Cape Town.

Bivand, R., Keitt, T., and Rowlingson, B. 2016. rgdal: Bindings for the Geospatial Data Abstraction Library. R package version 1.1-10. https://CRAN.R-project.org/package=rgdal.

Branch, T.A., Matsuoka, K., and Miyashita, T. 2004. Evidence for increases in Antarctic blue whales based on Bayesian modelling. Marine Mammal Science 20(4): 726–754.

Branch, T.A. and Butterworth, D.S. 2006. Assessment of the East Greenland–Iceland fin whale population using a four-area model. Joint NAMMCO/IWC Scientific Workshop on the catch history, stock structure and abundance of North Atlantic fin whales, Reykjavik, Iceland, 23-26 March 2006. Document SC/14/FW/23 and SC/M06/FW23. 33 pp.

Branch, T.A., Stafford, K.M., Palacios, D.M., Allison, C., Bannister, J.L., Burton, C.L.K., Cabrera, E., Carlson, C.A., Vernazzani, B.G., Gill, P.C., Hucke-Gaete, R., Jenner, K.C.S., Jenner, M.N.M., Matsuoka, K., Mikhalev, Y.A., Miyashita, T., Morrice, M.G., Nishiwaki, S., Sturrock, V.J., Tormosov, D., Anderson, R.C., Baker, A.N., Best, P.B., Borsa, P., Brownell, R.L., Childerhouse, S., Findlay, K.P., Gerrodette, T., Ilangakoon, A.D., Joergensen, M., Kahn, B., Ljungblad, D.K., Maughan, B., McCauley, R.D., McKay, S., Norris, T.F., Whale, O., Rankin, S., Samaran, F., Thiele, D., Van Waerebeek, K., and Warneke, R.M. 2007. Past and present distribution, densities and movements of blue whales (*Balaenoptera musculus*) in the Southern Hemisphere and northern Indian Ocean. Mammal Review 37(2): 116–175.

Breiman, L. 2001. Random forests. Machine Learning 45: 5−32.

Brown, P.C. 1992. Spatial and seasonal variation in chlorophyll distribution in the upper 30 m of the photic zone in the Southern Benguela/Agulhas ecosystem. In: Payne, A.I.L., Brink, K.H., Mann, K.H., and Hilborn, R. (eds) Benguela trophic functioning. South African Journal of Marine Science l2: 515–525.

Chai, T., and Draxler, R.R. 2014. Root mean square error (RMSE) or mean absolute error (MAE)? – Arguments against avoiding RMSE in the literature. Geoscientific Model Development 7: 1247–1250.

Checkley Jr., D.M., Ayon, P., Baumgartner, T.R., Bernal, M., Coetzee, J.C., Emmett, R., Guevara, R., Hutchings, L., Ibaibariaga, L., Nakata, H., Oozeki, Y., Planque, B., Schweigert, J., Stratoudakis, Y., and van der Lingen, C.D. 2009. Habitats. In: Checkley Jr., D.M., Alheit, J., Oozeki, Y., and Roy, C. (eds.) Climate change and small pelagic fish. Cambridge University Press: New York. p. 12–44.

Cleveland, W.S., Grosse, E., and Shyu, W.M. 1992. Local regression models. In: Chambers, J.M., and Hastie, T.J. (eds) Statistical Models in S. Wadsworth and Brooks, Cole.

Croll, D.A., Clark, C.W., Acevedo, A., Tershy, B., Flores, S., Gedamke, J., and Urban, J. 2002. Only male fin whales sing loud songs. Nature 417: 809–811.

Cummings, W.C. and Thompson, P.O. 1971. Underwater sounds from the blue whale, *Balaenoptera musculus*. Journal of Acoustical Society of America 50(4): 1193–1198.

DeLong, E.R., Delong, D.M., and Clarke-Pearson, D.L. 1988. Comparing areas under two or more correlated Receiver Operating Characteristic curves: a nonparametric approach. Biometrics, 44(3): 837–845.

Donlon, C.J., Martin, M., Stark, J.D., Roberts-Jones, J., Fiedler, E., and Wimmer, W. 2012. The operational sea surface temperature and sea ice analysis (OSTIA) system. Remote Sensing of Environment 116: 140–158.

Doughty, C.E., Roman, J., Faurby, S., Wolf, A., Haque, A., Bakker, E.S., Malhi, Y., Dunning Jr, J.B., and Svenning, J.C. 2016. Global nutrient transport in a world of giants. PNAS 113(4): 868–873.

Ekau, W., Hendricks, A., Kadler, S., Koch, V., and Loick, N. 2001. Winter ichthyoplankton in the northern Benguela upwelling and Angola-Benguela Front regions. South African Journal of Science 97: 259–265.

Elith, J., Leathwick, J.R., and Hastie, T. 2008. A working guide to boosted regression trees. Journal of Animal Ecology 77(4): 802–813.

Figueroa, H.K. 2006. XBAT: Extensible BioAcoustic Tool. Available: http://xbat.org.

Fox, J., and Monette, G. 1992. Generalized collinearity diagnostics. Journal of the American Statistical Association 87: 178–183.

Fox, J., and Weisberg, S. 2011. An R companion to applied regression, second edition. SAGE Publications Inc, Thousand Oaks, CA.

Friedman, J.H., Hastie, T., and Tibshirani, R. 2000. Additive logistic regression: a statistical view of boosting. The Annals of Statistics 28: 337−407.

Gavrilov, A.N., McCauley, R.D., and Gedamke, J. 2012. Steady inter and intra-annual decrease in the vocalization frequency of Antarctic blue whales. Journal of the Acoustical Society of America 131: 4476–4480.

Goubanova, K., Illig, S., Machu, E., Garcon, V., and Dewitte, B. 2013. SST subseasonal variability in the central Benguela upwelling system as inferred from satellite observations (1999–2009). Journal of Geophysical Research: Oceans 118: 1–19.

Grodsky, S.A., Carton, J.A., and McClain, C.R. 2008. Variability of upwelling and chlorophyll in the equatorial Atlantic. Geophysical Research Letters 35:L03610. DOI: 10.1029/2007GL032466.

Guisan, A., Edwards, T.C., and Hastie, T. 2002. Generalized linear and generalized additive models in studies of species distributions: setting the scene. Ecological Modelling 157: 89−100.

Hair Jr, J.F., Black, W.C., Babin, B.J., and Anderson, R.E. 2009. Multivariate data analysis, 7th Edition. Pearson Education, Upper Saddle River, NJ.

Hastie, T.J., Tibshirani, R., and Friedman, J. 2009. The elements of statistical learning. New York: Springer.

Hilborn, R., Branch, T.A., Ernst, B., Magnusson, A., Minte-Vera, C.V., Scheuerell, M.D., and Valero, J.L. 2003. State of the world's fisheries. Annual Review of Environment and Resources 28: 359–399.

Ho, T.K. 1995. Random decision forests. Proceedings of the 3rd International Conference on Document Analysis and Recognition, Montreal, QC, 14–16 August 1995. p. 278–282.

James, G., Witten, D., and Hastie, T. 2013. An introduction to statistical learning: with applications in R. New York: Taylor and Francis Group.

Jury, M.R., and Brundrit, G.B. 1992. Temporal organization of upwelling in the southern Benguela ecosystem by resonant coastal trapped waves in the ocean and atmosphere. In: Payne, A.I.L., Brink, K.H., Mann, K.H., and Hilborn, R. (eds) Benguela Trophic Functioning. South African Journal of Marine Science 12: 219–224.

Jutla A.S., Akanda, A.S., and Islam, S. 2012. Satellite remote sensing of space–time plankton variability in the Bay of Bengal: Connections to cholera outbreaks. Remote Sensing of Environment 123: 196–206.

Lavery, T.J., Roudnew, B., Gill, P., Seymour, J., Seuront, L., Johnson, G., Mitchell, J.G., and Smetacek, V. 2010. Iron defecation by sperm whales stimulates carbon export in the Southern Ocean. Proceedings of the Royal Society B: Biological Sciences 277: 3527–3531.

Leroy, E.C., Samaran, F., Bonnel, J., and Royer, J.-Y. 2016. Seasonal and diel vocalization patterns of Antarctic blue whale (*Balaenoptera musculus intermedia*) in the Southern Indian Ocean: A multi-year and multi-site study. PLoS ONE 11(11): e0163587.

Liaw, A., and Wiener, M. 2002. Classification and Regression by randomForest. R News 2(3): 18–22.

Ljungblad, D.K., Clark, C.W., and Shimada, H. 1998. A comparison of sounds attributed to pygmy blue whales (*Balaenoptera musculus brevicauda*) recorded south of the Madagascar Plateau and those attributed to 'true' blue whales (*Balaenoptera musculus*) recorded of Antarctica. Report of International Whaling Commission 48: 439–442.

Lutjeharms, J.R.E., and Meeuwis, J.M. 1987. The extent and variability of South-East Atlantic upwelling. In: Payne, A.I.L., Brink, K.H., Mann, K.H, and Hilborn, R. (eds) Benguela Trophic Functioning. South African Journal of Marine Science 12: 51–62.

Lutjeharms, J.R.E., and Stockion, P.L. 1991. Aspects of the upwelling regime between Cape Point and Cape Agulhas, South Africa. South African Journal of Marine Science 10: 91–102.

Mackas, D.L. 1984. Spatial autocorrelation of plankton community composition in a continental shelf ecosystem. Limnology and Oceanography 29(3): 451-471.

Mackintosh, N.A., and Wheeler, J.F.G. 1929. Southern blue and fin whales. Discovery Reports I: 259–540.

Maritorena, S., Fanton d'Andon, O.H., Mangin, A., and Siegel, D.A. 2010. Merged satellite ocean color data products using a bio-optical model: Characteristics, benefits and issues. Remote Sensing of Environment 114: 1791–1804.

Mascaro, J., Asner, G.P., Knapp, D.E., Kennedy-Bowdoin, T., Martin, R.E., Anderson, C., Higgins, M., and Chadwick K.D. 2014. A tale of two ‘‘forests’’: Random forest machine learning aids tropical forest carbon mapping. PLoS ONE 9(1): e85993.

Matworks Inc, 2014. MATLAB R2014a version 8.3.0.532. The MathWorks, Inc., Natick, Massachusetts, United States.

McDonald, M.A., Calambokidis, J., Teranishi, A.M. and Hildebrand, J.A. 2001. The acoustic calls of blue whales off California with gender data. Journal of Acoustical Society of America 109(4): 1728–1735.

McDonald, M.A., Hildebrand, J.A., and Mesnick, S.L. 2006. Biogeographic characterization of blue whale song worldwide: using song to identify populations. Journal of Cetacean Research and Management 8: 55–65.

Mellinger, D.K., and Clark, C.W. 2000. Recognizing transient low-frequency whale sounds by spectrogram correlation. Journal of the Acoustical Society of America 107: 3518–3529.

Menze, S., Zitterbart, D.P., van Opzeeland, I., and Boebel, O. 2017. The influence of sea ice, wind speed and marine mammals on Southern Ocean ambient sound. Royal Society Open Science 4: 160370.

Mhlongo, N., Yemane, D., Hendricks, M., and van der Lingen, C.D. 2015. Have the spawning habitat preferences of anchovy (Engraulis encrasicolus) and sardine (Sardinops sagax) in the southern Benguela changed in recent years? Fisheries Oceanography 1(24): 1–14.

Moore, S.K., Trainer, V.L., Mantua, N.J., Parker, M.S., Laws, E.A., Backer, L.C., and Fleming, L.E. 2008. Impacts of climate variability and future climate change on harmful algal blooms and human health. Environmental Health 7(Suppl 2): S4. DOI: 10.1186/1476-069X-7-S2-S4.

Nasu, K. 1966. Fishery oceanographic study on the baleen whaling grounds. The Scientific Reports of the Whales Research Institute 20: 157–210.

O’Brien, R.M. 2007. A caution regarding rules of thumb for variance inflation factors. Quality and quantity 41: 673–690.

Oleson, E.M., Wiggins, S.M., and Hildebrand, J.A. 2007a. Temporal separation of blue whale call types on a southern California feeding ground. Animal Behaviour 74: 881–894.

Oleson, E.M., Calambokidis, J., Barlow, J., and Hildebrand, J.A. 2007b. Blue whales visual and acoustic encounter rates in the Southern California Bight. Marine Mammal Science 23(3): 574–597.

Oleson, E.M., Calambokidis, J., Burgess, W.C., McDonald, M.A., LeDuc, C.A., and Hildebrand, J.A. 2007c. Behavioral context of call production by eastern North Pacific blue whales. Marine Ecology Progress Series 330: 269–284.

Oleson, E.M., Širović, A., Bayless, A.R., and Hildebrand, J.A. 2014. Synchronous seasonal change in fin whale song in the North Pacific. PLoS ONE 9(12): e115678.

Perrier, A. 2015. Feature importance in random forests. http://alexperrier.github.io/jekyll/update/2015/08/27/feature-importance-random-forests-gini-accuracy.html

Pierce, D. 2015. ncdf4: Interface to Unidata netCDF (Version 4 or Earlier) Format Data Files. R package version 1.15. https://CRAN.R-project.org/package=ncdf4.

Pillar, S.C., Stuart, V., Barange, M., and Gibbons, M.J. 1992. Community structure and trophic ecology of euphausiids in the Benguela ecosystem. In: Payne, A.I.L., Brink, K.H., Mann, K.H., Hilborn, R. (eds) Benguela trophic functioning. South African Journal of Marine Science 12: 393–409.

R Core Team, 2016. R: A Language and Environment for Statistical Computing. 3.3.0 version. Vienna, Austria: R Foundation for Statistical Computing. Available: https://www.R-project.org/.

Rankin, S., Ljungblad, D., Clark, C.W., and 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, Antarctica. Journal of Cetacean Research and Management 7: 13–20.

Reilly, S.B., Bannister, J.L., Best, P.B., Brown, M., Brownell Jr, R.L., Butterworth, D.S., Clapham, P.J., Cooke, J., Donovan, G.P., Urbán, J., and Zerbini, A.N. 2013. *Balaenoptera physalus*. The IUCN Red List of Threatened Species 2013: e.T2478A44210520. http://dx.doi.org/10.2305/IUCN.UK.2013-1.RLTS.T2478A44210520.en.

Roman, J., Estes, J.A., Morissette, L., Smith, C., Costa, D., McCarthy, J., Nation, J.B., Nicol, S., Pershing. A., and Smetacek, V. 2014. Whales as marine ecosystem engineers. Frontiers in Ecology and the Environment 12: 377–385.

Samaran, F., Adam, O., and Guinet, C. 2010. Discovery of a mid-latitude sympatric area for two Southern Hemisphere blue whale subspecies. Endangered Species Research 12: 157–165.

Samaran, F., Stafford, K.M., Branch, T.A., Gedamke, J., Royer, J.-Y., Dziak, R.P., and Guinet, C. 2013. Seasonal and geographic variation of southern blue whale subspecies in the Indian Ocean. PLoS ONE 8(8): e71561.

Shabangu, F.W., and Findlay, K. 2014. Passive acoustic monitoring of marine mammals in South Africa, with special reference to Antarctic blue whales. In: Funke, N., Claassen, M., Meissner, R. and Nortje, K. (eds) Reflections on the state of research and development in the marine and maritime sectors in South Africa. Council for Scientific and Industrial Research, Pretoria. p. 153–173.

Shabangu, F.W., Somhlaba, S., and Leslie, R. 2016 Should South Africa harvest krill? Fishing Industry News Southern Africa 17(1): 18–20.

Shabangu, F.W., Yemane, D., Stafford, K.M., Ensor, P., and Findlay, K.P. 2017. Modelling the effects of environmental conditions on the acoustic occurrence and behaviour of Antarctic blue whales. PLoS ONE: e0172705.

Shannon, V. 2006. A plan comes together. In: Shannon, V., Hempel, G., Malanotte-Rizzoli, P., Moloney, C., and Woods, J. (eds) Benguela: Predicting a Large Marine Ecosystem. Large Marine Ecosystems 14, p. 3–10.

Širović, A., Hildebrand, J.A., Wiggins, S.M., McDonald, M.A., Moore, S.E., and Thiele, D. 2004. Seasonality of blue and fin whale calls and the influence of sea ice in the Western Antarctic Peninsula. Deep-Sea Research II 51: 2327–2344.

Širović, A., Hildebrand, J.A., and Wiggins, S.M. 2007. Blue and fin whale call source levels and propagation range in the Southern Ocean. Journal of Acoustical Society of America 122(2): 1208–1215.

Širović, A., Hildebrand, J.A., Wiggins, S.M., and Thiele, D. 2009. Blue and fin whale acoustic presence around Antarctica during 2003 and 2004. Marine Mammal Science 25(1): 125–136.

Širović, A., Oleson, E.M., Buccowich, J., Rice, A., and Bayless, A.R. 2017. Fin whale song variability in southern California and the Gulf of California. Scientific Reports 7: 10126.

Stafford, K.M., Bohnenstiehl, D.W.R., Tolstoy, M., Chapp, E., Mellinger, D.K., and Moore, S.E. 2004. Antarctic-type blue whale calls recorded at low latitudes in the Indian and eastern Pacific Oceans. Deep-Sea Research I 51: 1337–1346.

Stafford, K.M., Moore, S.E. and Fox, C.G. 2005. Diel variation in blue whale calls recorded in the eastern tropical Pacific. Animal Behaviour 69: 951–958.

Stafford, K.M., Citta, J.J., Moore, S.E., Daher, M.A., and George J.E. 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.

Sydeman, W., and Thompson, S.A. 2013. Potential impacts of climate change on California’s fish and fisheries. California Ocean Science Trust, Oakland, CA.

Thomisch, K., Boebel, O., Clark, C.W., Hagen, W., Spiesecke, S., Zitterbart, D.P., and Van Opzeeland, I. 2016. Spatio-temporal patterns in acoustic presence and distribution of Antarctic blue whales *Balaenoptera musculus intermedia* in the Weddell Sea. Endangered Species Research 30: 239–253.

Torres, L.G. 2017. A sense of scale: Foraging cetaceans' use of scale-dependent multimodal sensory systems. Marine Mammal Science 33(4): 1170–1193.

True, F.W. 1904. The whalebone whales of the western North Atlantic compared with those occurring in European waters with some observations on the species in the North Pacific. Smithsonian Contributions to Knowledge 33: 1–332.

Veitch, J., Penven, P., and Shillington, F. 2010. Modeling equilibrium dynamics of the Benguela Current system. Journal of Physical Oceanography 40: 1942–1964.

Ward, R., Gavrilov, A.N., and McCauley, R.D. 2017. “Spot” call: A common sound from an unidentified great whale in Australian temperate waters. Journal of the Acoustical Society of America 142(2): EL231–EL236.

Wenz, G. 1962. Acoustic ambient noise in the ocean: Spectra and sources. Journal of the Acoustical Society of America 34(12): 1936–1956.

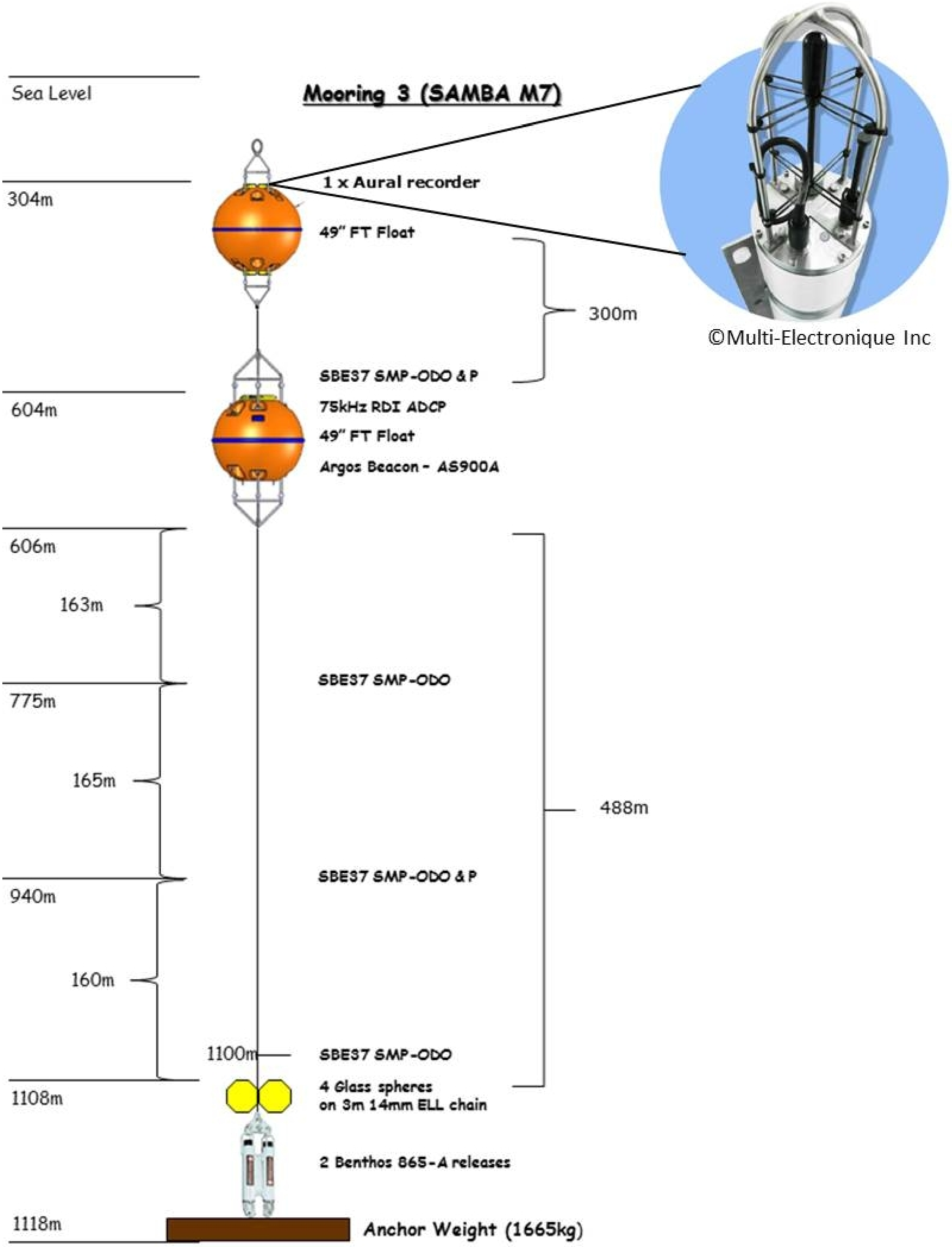
Werner, T. and Buchholz, F. 2013. Diel vertical migration behaviour in Euphausiids of the northern Benguela current: Seasonal adaptations to food availability and strong gradients of temperature and oxygen. Journal of Plankton Research 35(4): 792–812.

Wright, M.N. and Ziegler, A. 2016. ranger: A Fast Implementation of Random Forests for High Dimensional Data in C++ and R. ArXiv preprint. arXiv:1508.04409.

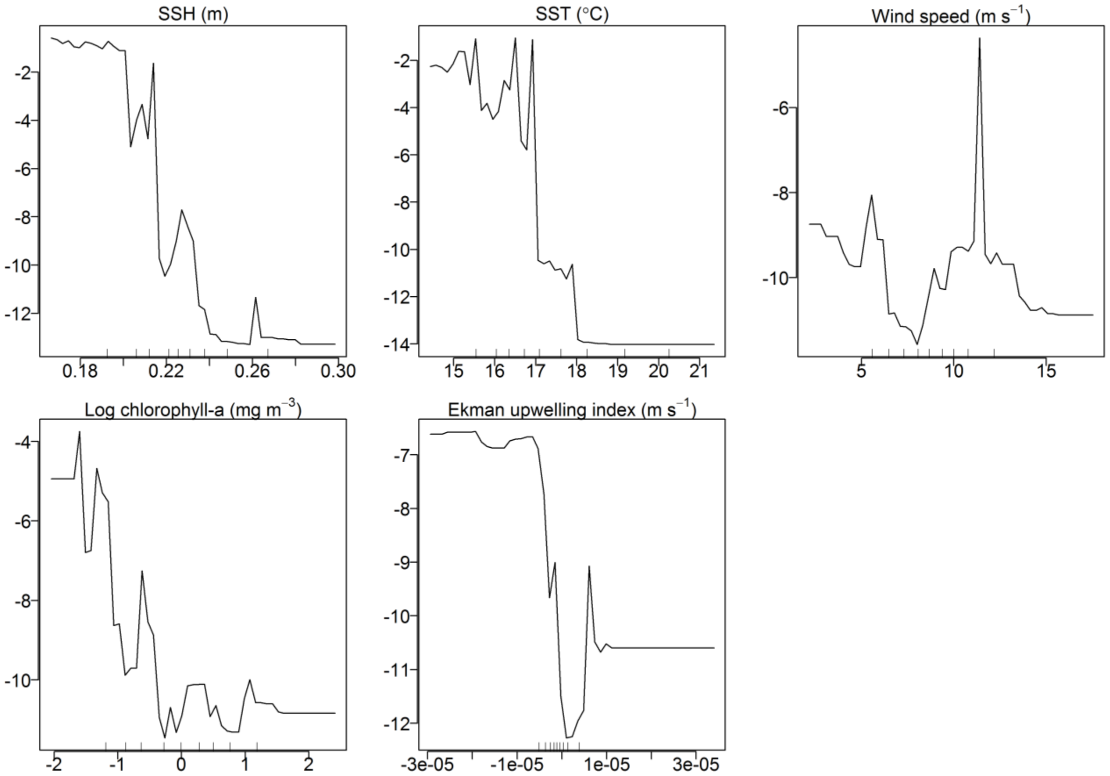
Zeileis, A., and Grothendieck, G. 2005. zoo: S3 Infrastructure for Regular and Irregular Time Series. Journal of Statistical Software 14(6): 1–27.

Zhang, H.-M., Reynolds, R.W., and Bates, J.J. 2006. Blended and gridded high resolution global sea surface wind speed and climatology from multiple satellites: 1987–present. In: Proceedings of the American Meteorological Society 2006 Annual Meeting, Atlanta, GA, January 29- February; P2.23.

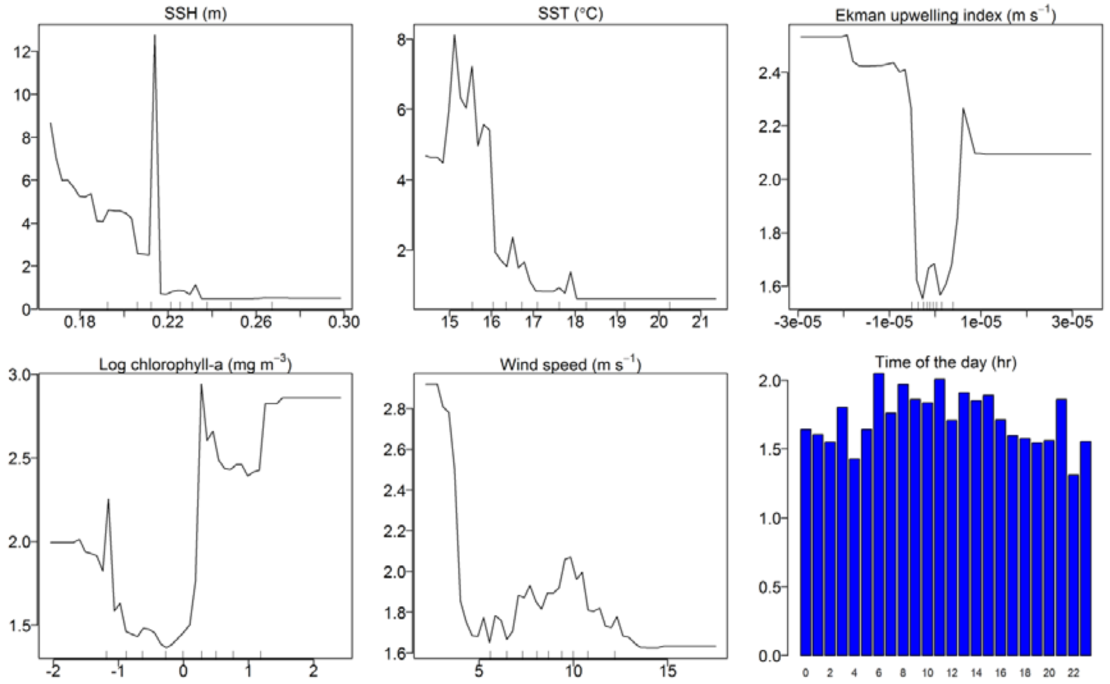
5.8. Supplementary material



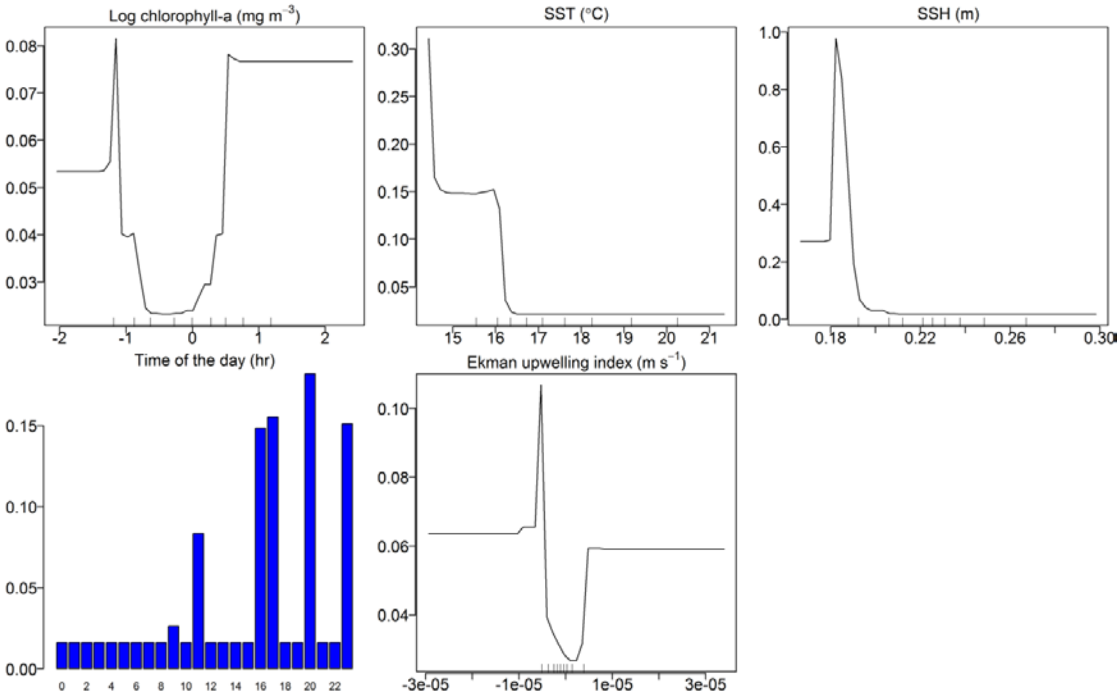
Supplementary Figure S5.1. Schematic representation of one of the SAMBA oceanographic moorings showing the position of AAR2 on the top buoy/float. The inset provides a magnified view of the hydrophone and protective bars on the AAR's head. Different oceanographic instruments are also seen attached at different depths of the mooring below the top buoy.



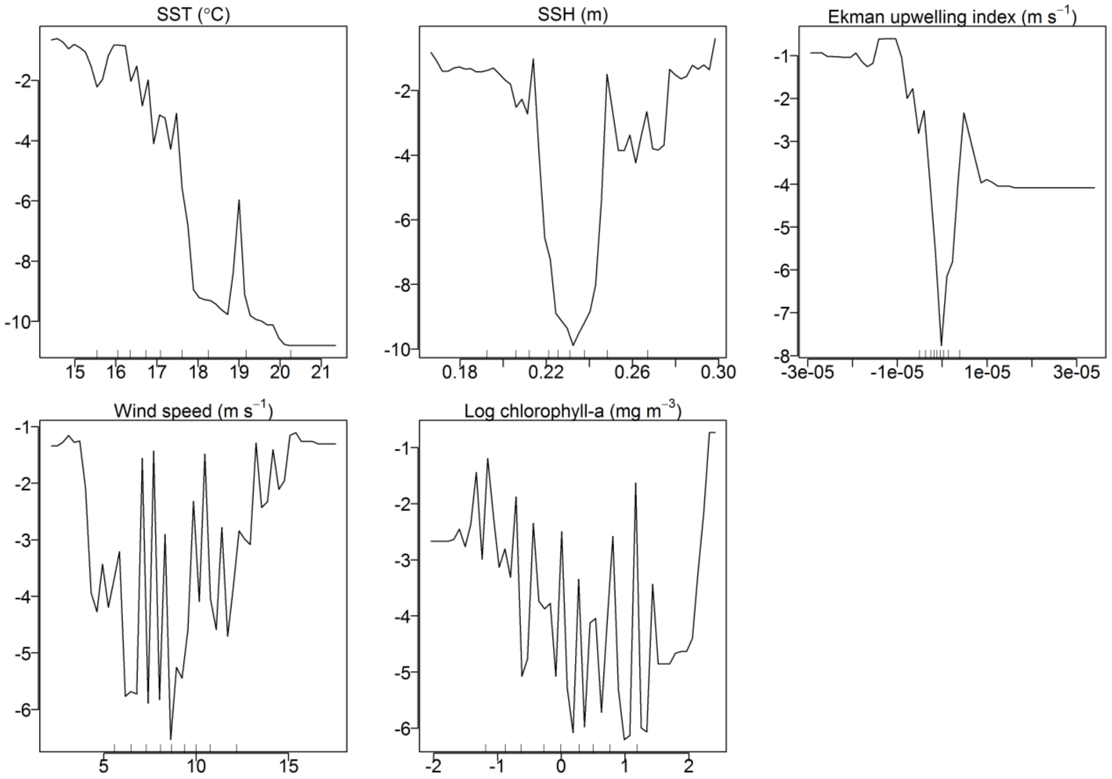
Supplementary Figure S5.2. Marginal effects of different variables on blue whale call occurrence. Y-axis is the partial effect of each predictor on occurrence (in logit-scale).



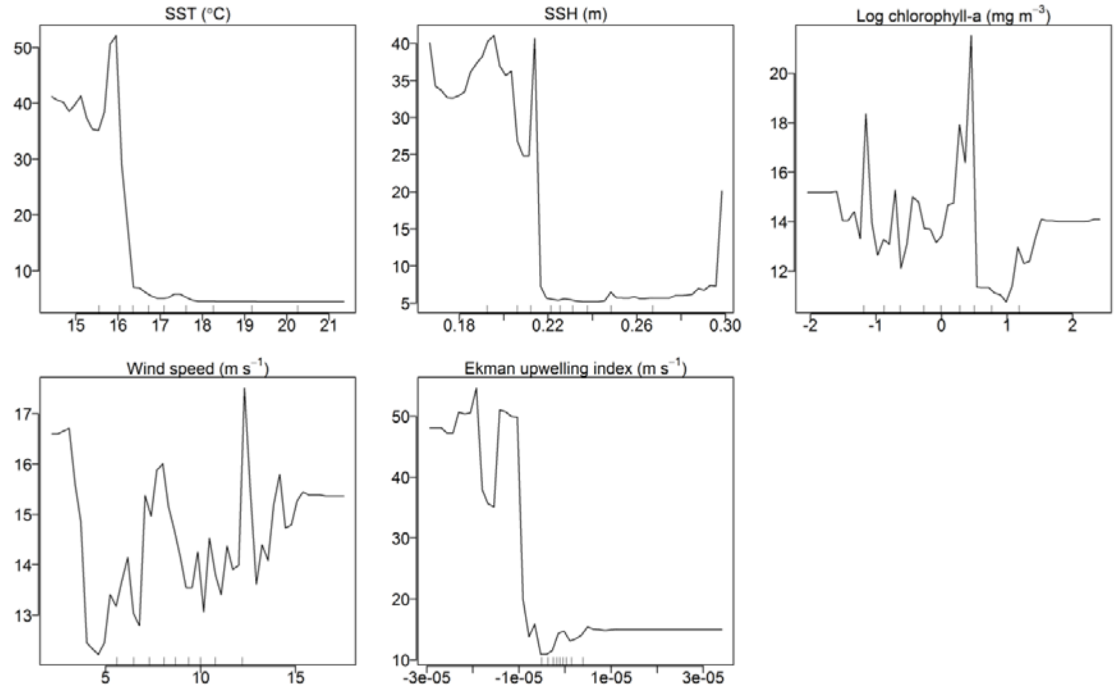
Supplementary Figure S5.3. Marginal effects of different variables on blue whale Z-call rates. Y-axis is the partial effect of each predictor on acoustic behaviour. Barplot is for factor variable (i.e. non-continuous variable).



Supplementary Figure S5.4. Marginal effects of different variables on blue whale D-call rates. Y-axis is the partial effect of each predictor on acoustic behaviour. Barplot is for factor variable (i.e. non-continuous variable).



Supplementary Figure S5.5. Marginal effects of different variables on fin whale call occurrence. Y-axis is the partial effect of each predictor on occurrence (in logit-scale).



Supplementary Figure S5.6. Marginal effects of different variables on fin whale call rates. Y-axis is the partial effect of each predictor on acoustic behaviour.

Chapter 6: Acoustic seasonality and behaviour of Antarctic blue and fin whales off the Maud Rise, eastern Weddell Sea

Shabangu et al. Under review in Polar Biology

Abstract

Vocalisations of Antarctic blue and fin whales were recorded off the Maud Rise in the Southern Ocean between January and September 2014 using an autonomous acoustic recorder. We detected the two kinds of blue whale calls, namely D- and Z-calls, and calls of eastern Antarctic fin whale acoustic population. A random forest model was used to determine the important environmental predictors of blue and fin whale call occurrence (call presence or absence) and call rates (calls detected per hour) between different seasons. Diel call rates of both whale species varied between seasons. Blue whale calls were detected throughout the whole period of our study but peaked in February, suggesting that animals could have asynchronously migrated out of the area with a part of the population remaining in the Antarctic throughout the austral winter. In contrast, fin whale calls were only detected in January and March; suggesting seasonal presence or vocalisation around the Maud Rise. Wind speed and sea surface temperature (SST) were the most important predictors of blue and fin whale call occurrences respectively. Fin whale call rates were largely predicted by the wind speed. The feeding associated D-calls of blue whales were only recorded in autumn; their rates were primarily predicted by wind speed. SST was the most important predictors of Z-call rates. Our work highlights the Maud Rise region as a potentially important habitat of blue and fin whales whilst identifying factors that may influence the presence and behaviour of vocal active whales in the area.

6.1 Introduction

The Southern Ocean is an important habitat for large baleen whales including the Antarctic blue whales *Balaenoptera musculus intermedia* and fin whales *B. physalus* as its productivity supports large biomass of prey such as Antarctic krill *Euphausia superba* (Everson, 2000; Knox, 2007). Modern whaling in the Southern Ocean caught numerous baleen whales (around 360,000 blue whales and 704,000 fin whales) during the austral summer between 1904 and the early 1970s, which reduced whale population to dangerously low numbers (Clapham and Baker, 2002; IWC, 1995; Branch *et al.* 2007). After whales have fed throughout the austral summer in the Southern Ocean (Mackintosh, 1942); most animals migrate to the low latitudes to mate and calve while some overwinter in the Southern Ocean (Širović *et al.* 2004; Thomisch *et al.* 2016). The low abundances of these species post the extensive whaling operations mean that visual surveys are generally not cost effective for monitoring of their population distributions or seasonal abundances and automated acoustic methodologies are increasingly used for monitoring (Branch *et al.* 2007; Thomas and Marques, 2012; Miller *et al.* 2015). However, to date, the environmental drivers that influence the seasonal call rates and occurrences of blue and fin whales in the Southern Ocean are not well understood or described.

Antarctic blue whales are known to produce two types of calls, D- and Z-calls (Ljungblad *et al.* 1998; Rankin *et al.* 2005; Oleson *et al.* 2007a). The D-calls are slightly higher in frequency; are frequency modulated (FM) and downsweeps from 106 to 22 Hz (Rankin *et al.* 2005). D-calls are used for short-range communication, lasts about 2-6 s and are produced by males and females likely during feeding (Oleson *et al.* 2007a). The characteristic Z-calls are low frequency, stereotyped three-unit sequences of tonal sounds that last from 18 s to ~26 s (Ljungblad *et al.* 1998; Rankin *et al.* 2005). The first unit of the Z-call is frequency constant at ~27 Hz followed by a second unit that frequency modulates and downsweeps from ~27 to 20 Hz and third unit slight frequency modulate from 20 to ~18 Hz. Only males supposedly produce Z-calls as a long-distance contact call for sexual advertisement and other social interactions as found in other blue whale populations (McDonald *et al.* 2001, Oleson *et al.* 2007a). The vocalization/tonal frequency of the Z-call song has decreased from ~28 to ~26

Hz over the past 15 years due to a wide variety of suggested reasons including cultural conformity, sex, body size, climate change and many other (McDonald *et al.* 2009; Gavrillov *et al.* 2012; Ward *et al.* 2017).

Fin whale calls consist of short FM downsweeps from ~28 Hz to 15 Hz (also known as the 20 Hz pulse) that last for less than 1 s and a higher frequency pulse (Širović *et al.* 2004). The higher frequency pulse is used to differentiate between the two acoustic populations of fin whales in the Antarctic: the eastern Antarctic population with a secondary frequency peak in the pressure spectrum at 99 Hz and the western Antarctic population with a peak at 89 Hz (Širović *et al.* 2009). Both male blue and fin whales produce calls in repeated sequences at regular intervals, these repeated stereotyped sequences of calls are considered songs (McDonald *et al.* 2001, 2006; Croll *et al.* 2002; Oleson *et al.* 2007b). Songs can last from minutes to hours, days or even weeks with slight breaks between surfacing to breathe (Cummings and Thompson, 1971; McDonald *et al.* 2001, 2006). Fin whales also make an irregular and short (usually under 1 s) pulses that tend to downsweep from 70 to 40 Hz, termed hereafter the 40 Hz pulses. Unlike the 20 Hz pulses, the fin whale 40 Hz pulses are not repeated but irregularly produced like blue whale D-calls, thus the 40 Hz pulse is sometimes confused with D-call as they both cover similar frequency band (Kate Stafford, Personal Communication). However, the D-call is slightly slanted to the right as it downsweeps whereas the 40 Hz pulse downsweeps vertically without slanting.

The Maud Rise is a seamount or plateau centred at 65°S, 2.5°E in the Weddell Sea of the Southern Ocean (Figure 6.1). Its peak rises almost 3,000 m from the seafloor and its summit is positioned just less than 1,000 m beneath the sea surface (Brandt *et al.* 2011). The rise is known to disturb the flow of deep circumpolar waters causing upwelling of warm, nutrient-rich deep waters to the sea surface leading to significant phytoplankton growth (Comiso and Gordon, 1987; Hellmer, 2007). The newly upwelled waters also disintegrate sea-ice cover during winter, which results in the formation of polynyas and initiate the spring melt of sea ice to benefit the biological ecosystem of the area (Comiso and Gordon, 1987; Hellmer, 2007; Gordon, 2011; Martin, 2011). The presence of large swarms of Antarctic krill around the Maud Rise has been associated with the phytoplankton blooms as well as the presence of sea ice due to the propensity of krill to feed off the sea-ice algae (Everson, 2000; Hellmer, 2007). Seasonal changes in sea surface temperatures, sea ice, wind speed and sea surface height drive the seasonal changes in chlorophyll-a concentrations (proxy for the productivity) of the Maud Rise (e.g., Goosse and Zunz, 2014; Swart *et al.* 2015; Thomalla *et al.* 2015). This consequently also drives the seasonal occurrence of marine top-predators such as whales, seabirds, seals, and fish (e.g., Everson, 2000; Širović *et al.* 2004; Knox, 2006).

Whale call occurrences and call rates are important for intraspecific communication over long distances, and importantly, due to their long distance ranges, can be useful indicators of whale presence. Whale calls can thus be useful indicators that can aid in the understanding of the acoustic behaviour and ecology of blue and fin whales. In this study, we present results of Antarctic blue and fin whale call occurrence and rates recorded over an eight-month period off the Maud Rise, eastern Weddell Sea. We estimated the seasonal diel call patterns, call occurrences and call rates of both whale species; and identified predictors that influence these.

6.2 Materials and methods

6.2.1 Acoustic data collection

Passive acoustic recordings of blue and fin whale calls were collected at 65°S; 2.5°E on the Maud Rise in the eastern Weddell Sea of the Southern Ocean (Figure 6.1). An autonomous acoustic recorder (AAR), Autonomous Underwater Recorder for Acoustic Listening-Model 2 version 04.1.3 (Multi-Electronique Inc., Canada), with a 320GB hard drive was used to record acoustic data. The AAR was positioned 250 m below the sea surface, secured on a specially designed mooring fixed at a depth of 1,267 m. The AAR was deployed from 12

January 2014 to 17 January 2015 but stopped recording on 17 September 2014 due to battery depletion and only eight months of acoustic data were recorded. During this time, the AAR sampled the acoustic environment at a rate of 2,048 Hz for 25 minutes per hour throughout the day to preserve the battery life. The proportion of each species occurrence was calculated as the number of call occurrences of each species divided by the total number of samples over unit time (month or season). Mean daily call rates were calculated as average of call rates per day.

We used austral seasons of the year to describe our data where summer is December to February, autumn is March to May, winter is June to August, and spring is September to November. Different light regimes were defined over different seasons according to the altitude of the sun (nautical twilight (dawn and dusk), daytime, and nighttime) based on averages of hourly sun altitudes over austral seasons. We used hourly sun altitudes for each day of the year from the AAR location. Sun altitudes were obtained from the United States Naval Observatory Astronomical Applications Department (http://aa.usno.navy.mil). We defined the nautical dawn hours as periods when the centre of the sun was geometrically 12° below the horizon before sunrise. Daytime hours were between sunrise and sunset, and the nautical dusk hours were between sunset and the evening. Nighttime hours were instants when the geometric centre of the sun was 12° below the horizon in the evening, which is between dusk and dawn.

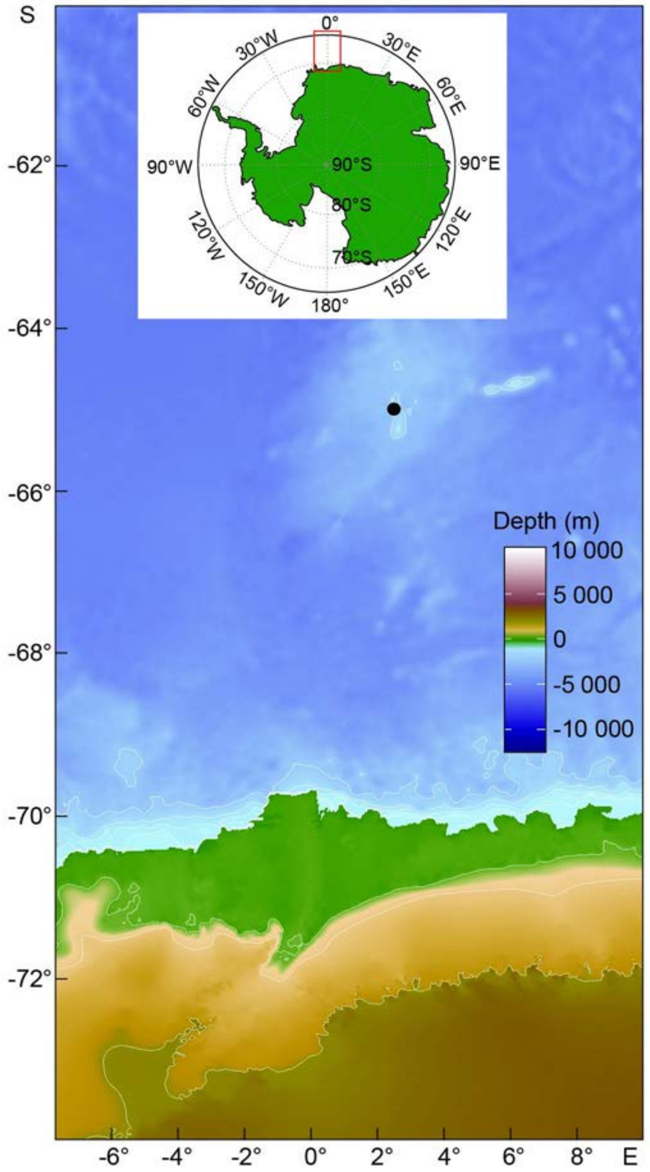


Figure 6.1. The position of the AAR mooring (●) off the Maud Rise in the Weddell Sea. Bathymetry data were obtained from ETOPO1 dataset (Amante and Eakins, 2009).

6.2.2 Oceanographic data

Daily sea surface temperature (SST) from the Operational Sea Surface Temperature and Sea Ice Analysis (OSTIA) were used. OSTIA uses satellite data provided by the Group for High Resolution Sea Surface Temperature project (Donlon *et al.* 2007). The daily OSTIA SST data were converted from Kelvin to degree Celsius (°C) by subtracting 273.15. Daily sea surface wind speeds were sourced from ftp://eclipse.ncdc.noaa.gov/pub/seawinds/SI/ (Zhang *et al.* 2006). Daily sea surface height (SSH) was sourced from the Archiving, Validation and Interpretation of Satellite Oceanographic data (http://www.aviso.altimetry.fr/duacs/).

Chlorophyll-a concentrations sourced from GlobColour project (Maritorena *et al.* 2010) were unfortunately not available for the whole study period and could not be included in analyses.

To determine the oceanographic conditions around the AAR mooring, the above variables were averaged by 1° grid and the values of the four 1° blocks adjacent to the AAR mooring were averaged. One degree of latitude and longitude at further than 40° south is approximately 111 km and 85 km respectively. Since the detection range for blue whale calls near Maud Rise is estimated to be around 100 km (Thomisch *et al.* 2016) and 56 km for fin whale calls in the Southern Ocean (Širović *et al.* 2007), all whales from which calls were detected by the AAR would fall within this area making oceanic variables directly comparable. The 111 km grid also falls within the large spatial scale (100-500 km) for foraging baleen whales (Torres, 2017).

Monthly sea ice extensions were downloaded from the G02135 dataset (Fetterer *et al.* 2016) at the National Snow and Ice Data Centre (NSIDC) data pool server: ftp://sidads.colorado.edu/DATASETS/NOAA/G02135/shapefiles/. From the monthly sea extensions, we measured the distance of the nearest sea ice extent to the AAR mooring position. Daily sea ice concentrations (%) were obtained within the 111 km grid using the satellite sea ice concentration product of the Advanced Microwave Scanning Radiometer-2 (AMSR-2) with a 3.125 km grid resolution (Spreen *et al.* 2008; Beitsch *et al.* 2014). The AAR mooring was submerged under sea ice from the beginning of May through mid-September, with sea ice concentrations around 80% at beginning of May to 100% by mid-May through mid-September. Therefore those months when the AAR mooring was submerged under ice were not included in the below modelling due to uncertainty about whale location relative to the AAR mooring but only used for describing the ecology of the whales. From January 12th to April 20th the sea ice concentration was 0% within our 111 km grid but increased to 50% by the end of April. The oceanographic variables were processed and analysed using libraries of Pierce (2015) and Bivand *et al.* (2016) in R statistical software package (R Core Team, 2016).

6.2.3 Autonomous call detections

We performed the passive acoustic data analyses in eXtensible Bio-Acoustic Tool (XBAT) software (Figueroa, 2006) implemented as a MATLAB routine (MathWorks Inc, 2014) with the automatic detection templates of fin whale calls, Z- and D-calls developed and applied in XBAT. The first tonal sound (8 to 12 seconds, ~27 Hz) of the blue whale Z-call (Figure 6.2a) was used as a detection template as our data did not any contain a complete three-unit Z-calls. The short duration ~28-15 Hz tone (Figure 6.2b) of the eastern Antarctic fin whale acoustic population calls; and D-call (Figure 6.2c) downsweeping from 75-40 Hz were used as detection templates because they contained most of the energy of the calls. Individual Z-calls were not discernible in bands of continuous calling (i.e. singing a chorus) when the call rate of the species was indisputably high (Figure 6.2b,c), thus such calling periods were not considered or quantified in this analysis due to complexity of delineating calls.

Noise of earthquakes and other noises (e.g., ice noise) were frequently recorded and these sometimes masked whale sounds. Blue whale continuous calling band between 27 and 18 Hz possibly masked some of the fin whale 20 Hz pulses; however, we did not quantify and account for this random and unknown error during our data analyses. The fin whale 40 Hz pulse was not considered during our analyses due to their absence in our dataset. Calls were recognized from spectrograms by cross-correlating with the template kernel based on a similarity level above the set threshold (i.e. the lowest detectable similarity percentage between a template and call). To estimate the number of false positive (detections that were not real blue and fin whale calls) and false negative (missed true blue and fin whale calls) calls, we visually assessed the whole acoustic dataset (2,499 hours). Visually identified false positive detections were manually excluded from further acoustic analyses. Visually identified false negatives were manually incorporated into the total call number calculations.

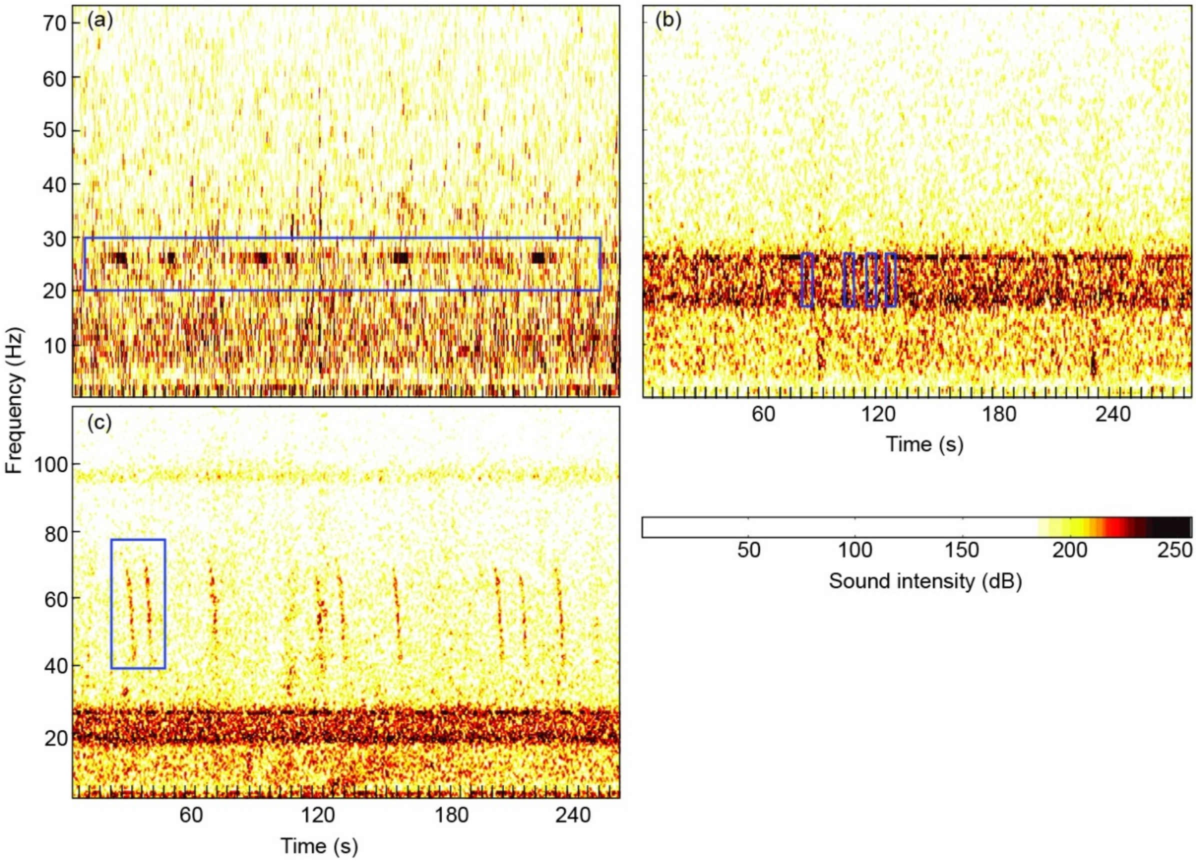


Figure 6.2. Spectrograms showing a sequence of blue whale Z-calls (a), 20 Hz pulse of a fin whale song with an aggregation of songs at ~27 Hz from multiple blue whale singers (b), 75-40 Hz D-calls (in rectangle) and songs at ~27 Hz from multiple blue whale singers (c) recorded off the Maud Rise. Spectrograms parameters: frame size 1.28 s, 25% overlap, FFT size 4,096 points, Hanning window.

Seven different thresholds from 15% to 75% in increments of 10% were tested to determine optimal thresholds for our analyses of blue and fin whale calls (Figure 6.3). The 15% detection threshold was best suited to the detections of fin whale calls; D- and Z-calls as it produced the fewest missed calls compared to other thresholds (Figure 6.3). Thresholds lower than 15% produced high false positives but low false negatives, they were therefore not considered here due to the trade-off of effort required to remove the high number of false positives. Detection templates produced false negative error rates of 17% and 0% for D- and Z-calls respectively; and accuracy rates of 83% and 100% for D- and Z-calls respectively. The fin whale detection template produced 0% false negatives and 100% accuracy rate (Figure 6.3). Smoothed means of the call rates per season were calculated by a locally weighted polynomial regression using the function ‘loess’ (Cleveland *et al.* 1992) in R. The

25-minute recording intervals were converted to recording duration in hours and call rates (i.e. calls per hour) of each sampling interval were calculated for both blue and fin whales.

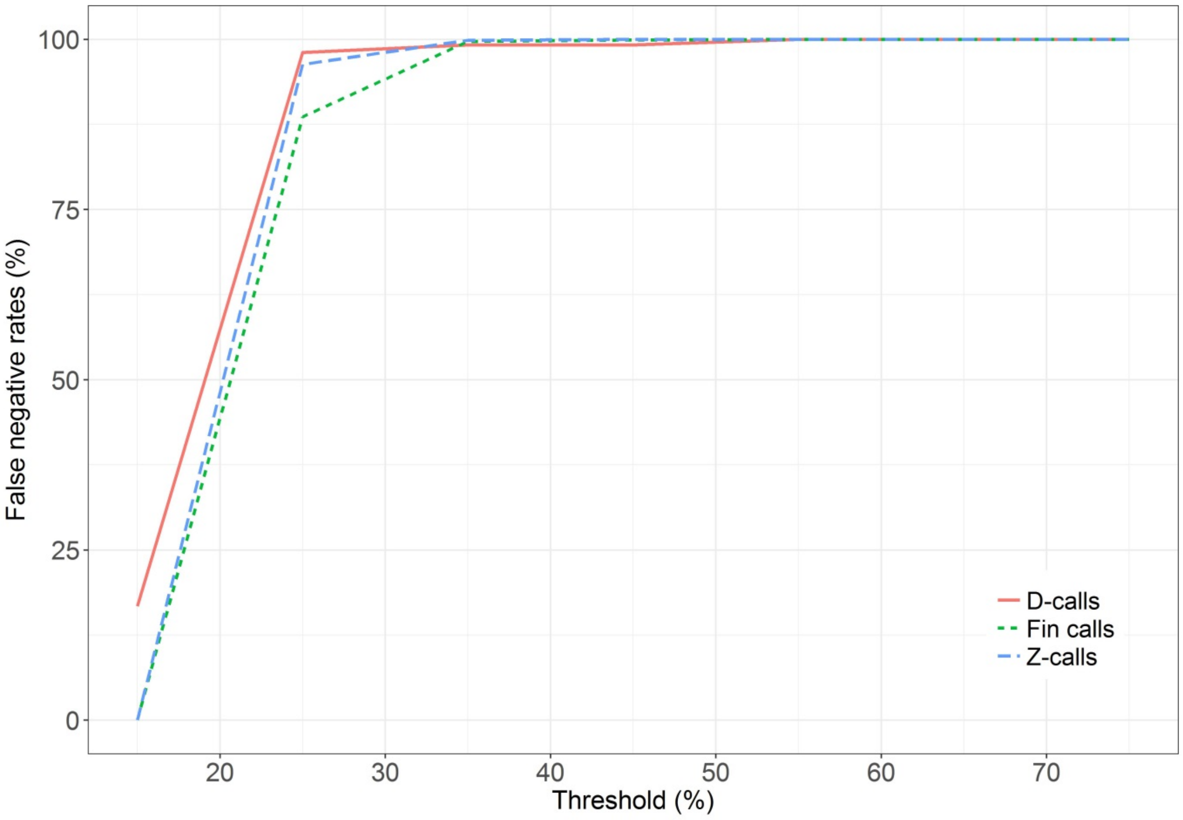


Figure 6.3. False negative rates at different thresholds for the fin whale call, blue whale D- and Z-calls recorded off the Maud Rise.

6.2.4 Modelling occurrence and behaviour

We used a random forest (RF) model (Ho, 1995; Breiman, 2001) to investigate the influence of different environmental variables (time of the day, SSH, distance to sea ice extent, sea ice concentration, SST, wind speed, and months of the year) on the acoustic occurrence (i.e. presence or absence of calls) and behaviour (i.e. call rates) of Antarctic blue and fin whales. RF models are an ensemble modelling approach for classification, regression and other functions with non-parametric inferential properties (Breiman, 2001; Hastie *et al.* 2009). As a machine learning method, RF models provide higher performances and have considerable benefits over standard regression methods such as generalized additive models (GAM; Guisan *et al.* 2002; Elith *et al.* 2008; James *et al.* 2013). RF models have also been found to perform better than GAM and generalised boosted regression models (GBM, Friedman *et al.*

2000) for modelling blue and fin whale occurrence and call rates in the Southern Ocean and Atlantic Ocean (Shabangu *et al.* 2017-Chapter 4, Shabangu *et al.* Under review- Chapter 5).

RF models use a set of unpruned decision trees in the forest that are bootstrapped as they grow with trained sample data, and rely on randomly chosen subsets of the predictor variables as candidate splitting tree nodes (Hastie *et al.* 2009; James *et al.* 2013). Unlike GBMs, RF models do not completely ignore some variables and the candidate split-variable selection process increases the probability of any solitary variable being included (Hastie *et al.* 2009; James *et al.* 2013). RF models are generally built to avoid overfitting of growing trees in the training data (e.g., Hastie *et al.* 2009). Furthermore, RF models are known to be immune to autocorrelation and are also better at dealing with zero-inflated count data (Hastie *et al.* 2009; Mascaro *et al.* 2014).

Before fitting the model, we investigated the correlations between different predictor variables and the existence of multi-collinearity was determined using generalised variance inflation factors (GVIF; Fox and Monette, 1992) implemented through the ‘car’ library (Fox and Weisberg, 2011) in R. Low GVIF values (around one) indicate weak or no correlations, GVIF values around five indicate moderate correlations, and high GVIF values around 10 or more indicate strong correlations (Fox and Monette, 1992; O’Brien, 2007; Hair *et al.* 2009). Our GVIF values were below 7.2 when excluding months of the year but reached a maximum of 14.9 when including months of the year, thus months of the year were eliminated from further analyses as they were highly correlated with SST, SSH and distance to the ice extent. To improve the performance prediction of the RF model, time of the day was removed from fin whale call occurrence modelling because the index of relative importance was negative, indicating that the variables were not important predictors (Perrier, 2015). Time of the day was also eliminated from the RF model of fin whale call rates and Z-call rates due to their negative importance.

After eliminating the highly correlated predictor and insignificant variable, the RF model was fitted to investigate the effects of environmental parameters (i.e. time of the day, SSH, distance to sea ice extent, sea ice concentration, SST, and wind speed) on the seasonal call occurrences and acoustic behaviour of blue and fin whales. The RF model was fitted using the optimal configuration values (i.e. best settings) in Table 6.1. The RF modelling was performed in R statistical software package using the ‘randomForest’ library (Liaw and Wiener, 2002), whilst the optimal parameter configuration values were determined using the ‘ranger’ library as a computational-time-saving method (Wright and Ziegler, 2017) to implement the RF model.

Table 6.1. Optimal parameter configurations used in the RF model. Mtry is the tree node, ntrees is the number of growing trees, nodsize is the splitting minimum size of terminal nodes of trees, Z is Z-calls, D is D-calls, F is fin whale calls, BP is blue whale presence and BF is fin whale presence.

Mtry	Ntrees	NodSize	Group
3	1000	1	Z
4	500	2	D
2	1000	1	F
4	1000	1	BP
1	500	1	FP

The relative importance of predictor variables in the model was assessed by computing the influence of each of the variables on the prediction error of the model. The relative importance of each of the variables in the model was computed by permuting the out of the bag (OOB) on test data or by determining the decrease in node impurity, as measured by the mean sum of squares, resulting from splitting of the variable of interest and averaging over all trees (Hastie *et al.* 2009). For each tree, the prediction error was computed on the OOB data and the permuted data were calculated and averaged across all trees and normalized by the standard deviation of the difference. This normalized index was calculated for each of the variables and used as an index of relative importance.

6.3 Results

Sea surface temperatures around Maud Rise decreased sharply from February to April, whereas SSH was relatively stable throughout the deployment period and wind speed gradually increased from January to April (Figure 6.4). A total of 2,479.17 hours were recorded within the eight months of AAR deployment. Blue whale calls were present in 2,349.17 (i.e. 95 % of the recorded time) hours and were acoustically absent in only 130 hours (5%). Calls of the eastern Antarctic fin whale acoustic population were present in 16.67 hours (0.6%) and absent in 2,462.50 hours (99.4%). We detected a total number of 50,407 blue whale Z-calls, 365 blue whale D-calls, and 5,381 fin whale calls. Antarctic blue whales were acoustically present throughout the whole period of the AAR deployment and the monthly proportion of blue whale call occurrence was above 81% across different months with the highest monthly proportion of 100% in February (Figure 6.5). The monthly proportion of fin whale call occurrences was 2 and 4% during January and March respectively. There was no trend in the diel proportion of call occurrences for both whale species across seasons (Figure 6.6). Mean daily Z-call rates (i.e. calls per day) were higher between January and March but peaked in February whereas D-calls were surprisingly only detected in March and April (Figure 6.7a). Fin whale calls were only detected in January and March (Figure 6.7b). The highest mean daily Z-call rate detected was 76 calls per day recorded in February; the highest mean daily D-call rate was 28 calls per day recorded in March (Figure 6.7a). The highest mean daily fin whale call rate was 314 calls per day recorded in March (Figure 6.7b).

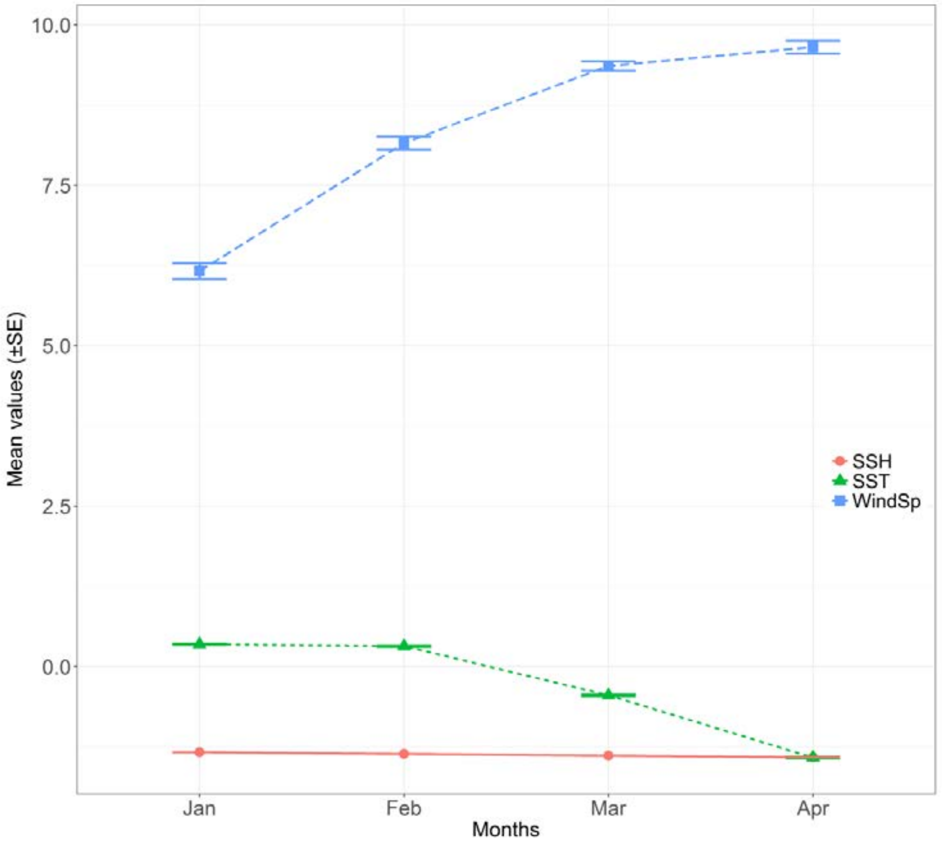


Figure 6.4. Mean (± SE) monthly SSH (m), SST (°C) and wind speed (WindSp, m s^{-1}) off the Maud Rise. SE is standard error of the mean.

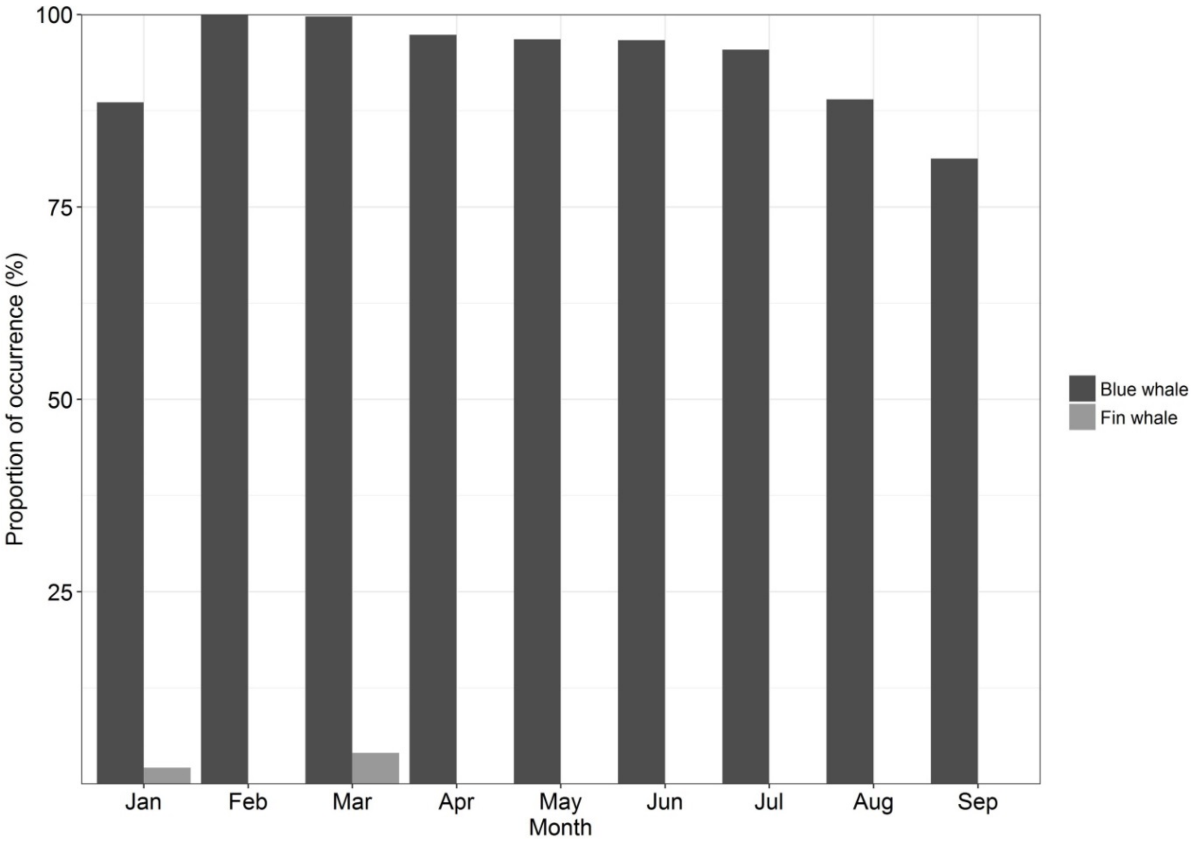


Figure 6.5. The monthly proportion of blue and fin whale call occurrence off the Maud Rise from January to September 2014.

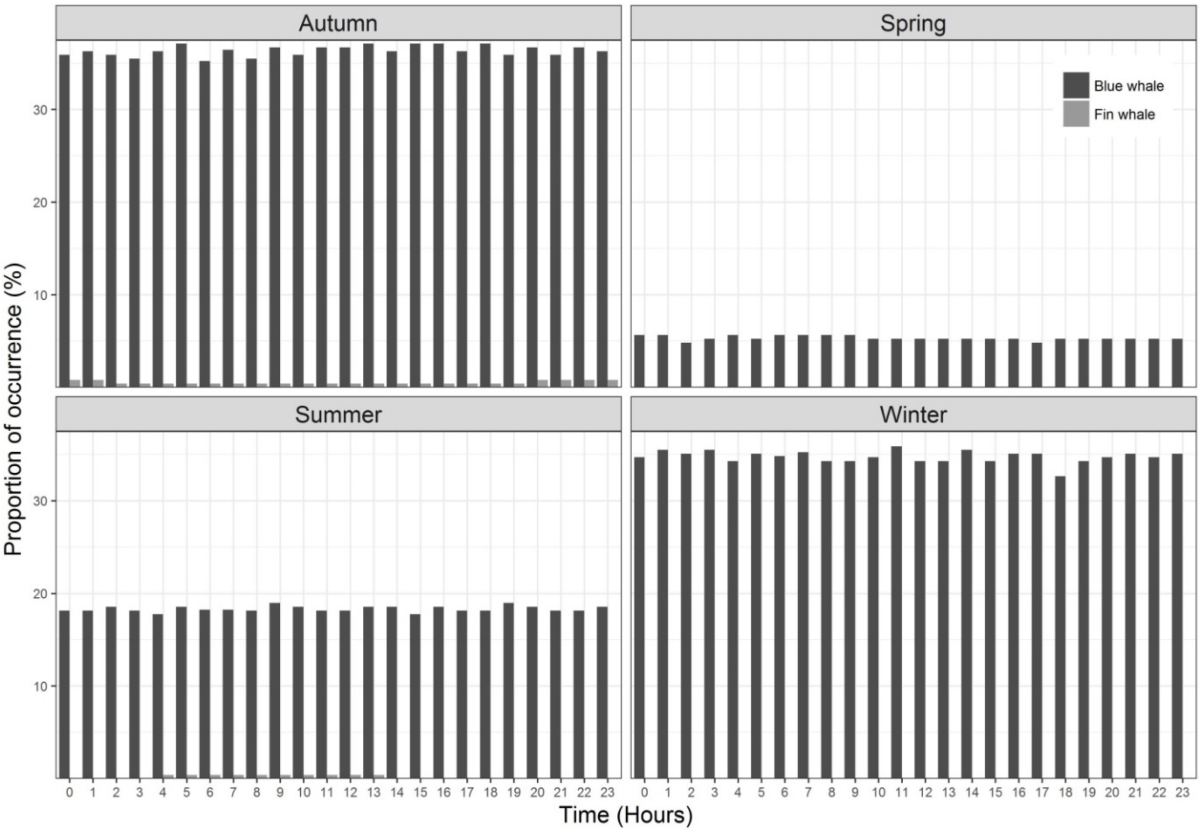


Figure 6.6. Seasonal proportions of diel call occurrences of blue and fin whale off the Maud Rise.

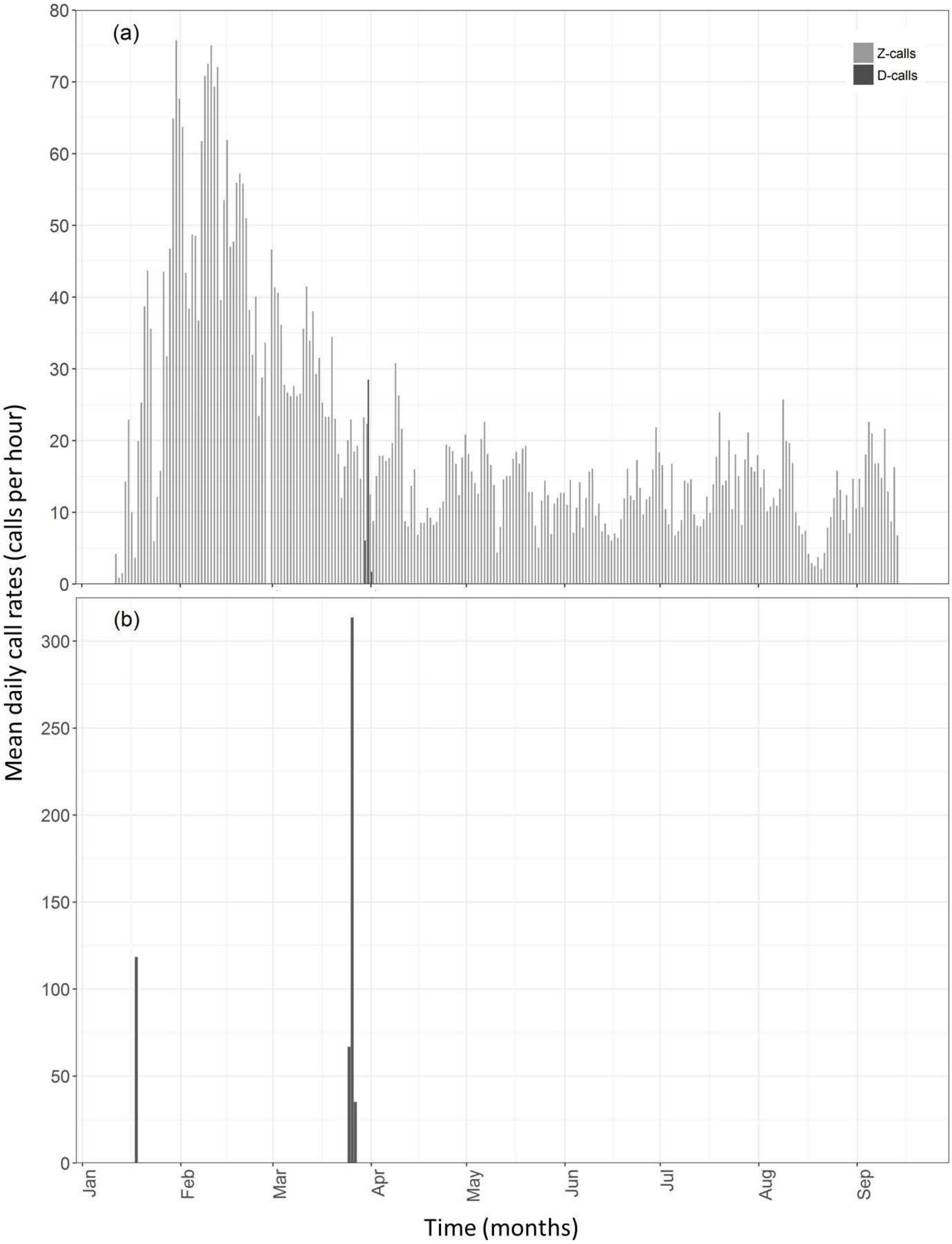


Figure 6.7. Mean daily call rates of blue (a) and fin (b) whales off the Maud Rise in 2014.

There was a sharp decrease in Z-call rates from dawn to dusk during winter but call rates increased immediately after sunset to early morning (Figure 6.8a). In spring, Z-call rates peaked from dawn to 11:00 but slightly decreased from 12:00 to 17:00 and then increased again from 17:00 until midnight (Figure 6.8b). Z-call rates peaked from dawn to 16:00 during autumn (Figure 6.8c) and 09:00 to 18:00 in summer (Figure 6.8d). D-call rates increased dramatically after 11:00 to 23:00 during autumn (Figure 6.8e) and there were no calls recorded during the other seasons. Fin whale call rates also increased from 20:00 to 10:00 in summer (Figure 6.8f), and increased in autumn from 05:00 to 23:00 with a small drop between 11:00 and 14:00 and then sharply decreased from 11:00 until 19:00 (Figure 6.8g). There was no temporal segregation in the peaks of diel call rates of blue and fin whales in autumn but clear temporal segregation in peaks of diel call rates for summer (Figure 6.8).

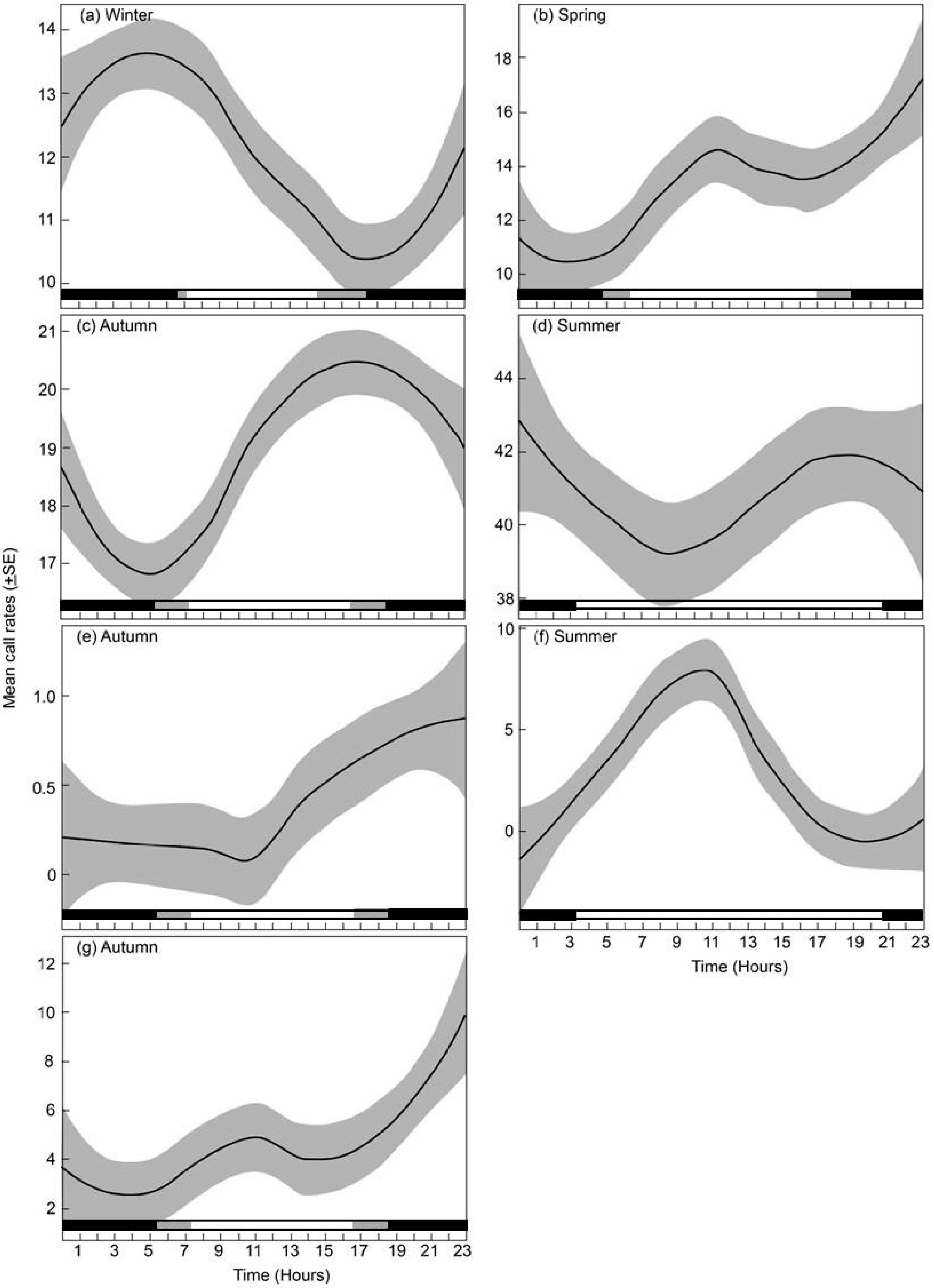


Figure 6.8. Smoothed mean diel call rate patterns of acoustic seasonal behaviour for Antarctic blue and fin whales of the Maud Rise. (a)-(d) Diel Z-call rates in winter, spring, autumn, and summer respectively; (e) diel D-call rate in winter; and (f)-(g) diel fin whale call rates in autumn and spring respectively. Horizontal diel bar shading: black represents average nighttime hours, grey represents average twilight hours and white represents average daytime hours; no dawn and dusk for summer. The above plots demonstrate the patterns of diel call rates over seasons and not a model predicted call rates.

SST was the most important predictor of blue whale call occurrence followed by distance of the sea ice extent from the AAR mooring, SSH and wind speed as moderately important predictors of blue whale call occurrence (Figure 6.9). Time of the day was the least important predictor of blue whale call occurrence (Figure 6.9). Distances of the sea ice extent from AAR mooring position of no farther than 250 km were highly influential on blue whale call occurrences (Supplementary Figure S6.1). Various times of the day, SST between -0.5 and 0.5 °C, SSH below -1.36 m, wind speeds between 6 and 10 m s^{-1} had great influence on blue whale call occurrences (Supplementary Figure S6.1).

Wind speed was the most important predictor, SST was moderately important whereas SSH and distance to the ice extent were the least important predictors of fin whale call occurrence (Figure 6.9). Sea ice extent farther than 250 km from the AAR mooring position, low wind speeds below 3 m s^{-1} and SSTs around -0.75 °C positively influenced the occurrence of fin whale calls (Supplementary Figure S6.2). Effects of SSH were high at -1.39 and -1.33 m (Supplementary Figure S6.2).

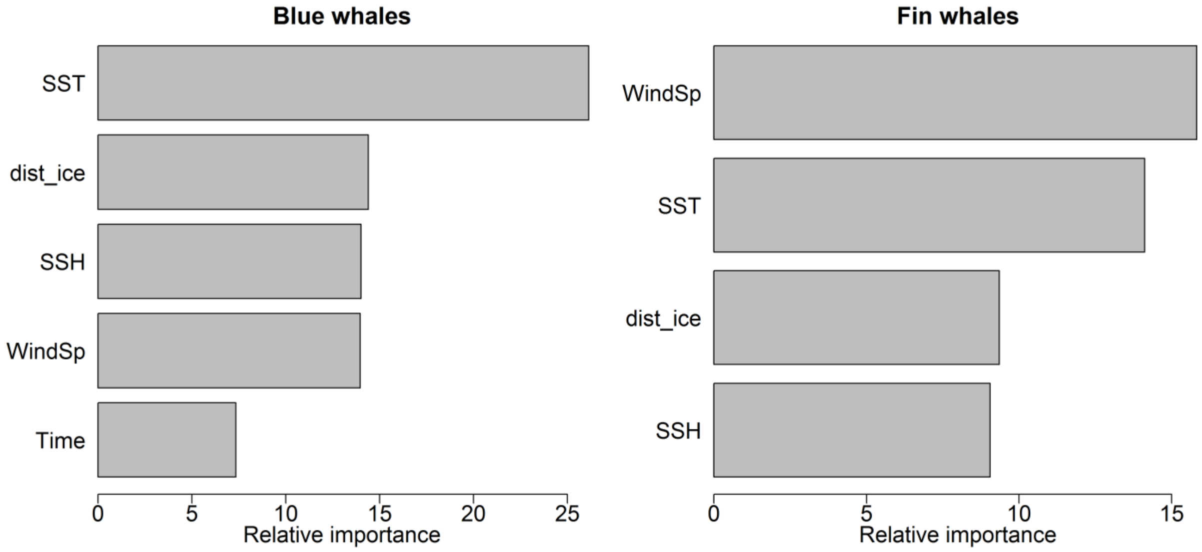


Figure 6.9. Relative importance of predictor variables on the call occurrence of blue whales. WindSp is wind speed and dist_ice is distance to sea ice extent.

Wind speed was the most important predictor of D-call rates whereas SST and time of the day were moderately important predictors; SSH and distance to the sea ice extent were the least important predictors of D-call rates (Figure 6.10). SST was the most important predictors of Z-call rates, followed by wind speed as moderately important predictor; SSH and distance to the ice extent was the least important of Z-call rates (Figure 6.10). Distance to the sea ice extent above 245 km, wind speed above 10 ms^{-1}, SST around -0.6 °C, SSH below -1.38 m and time of the day between 16:00 and 23:00 were highly influential on D-call rates (Supplementary Figure S6.3). Wind speeds below 7 m s^{-1}, SST around 0.5 °C, below -1.36 m, and distances of the sea ice extent no farther than 250 km from the AAR mooring position were the highly influential on Z-call rates (Supplementary Figure S6.4).

Wind speed was the most important predictor, SST was moderately important, distances to the sea ice extent and SSH were the least important predictors of fin whale call rates (Figure 6.10). Wind speed below 3 m s^{-1}, SST around -0.75 °C, distances of the ice extent farther than 250 km from the AAR mooring position and SSH around -1.39 m highly influenced fin whale call rates (Supplementary Figure S6.5).

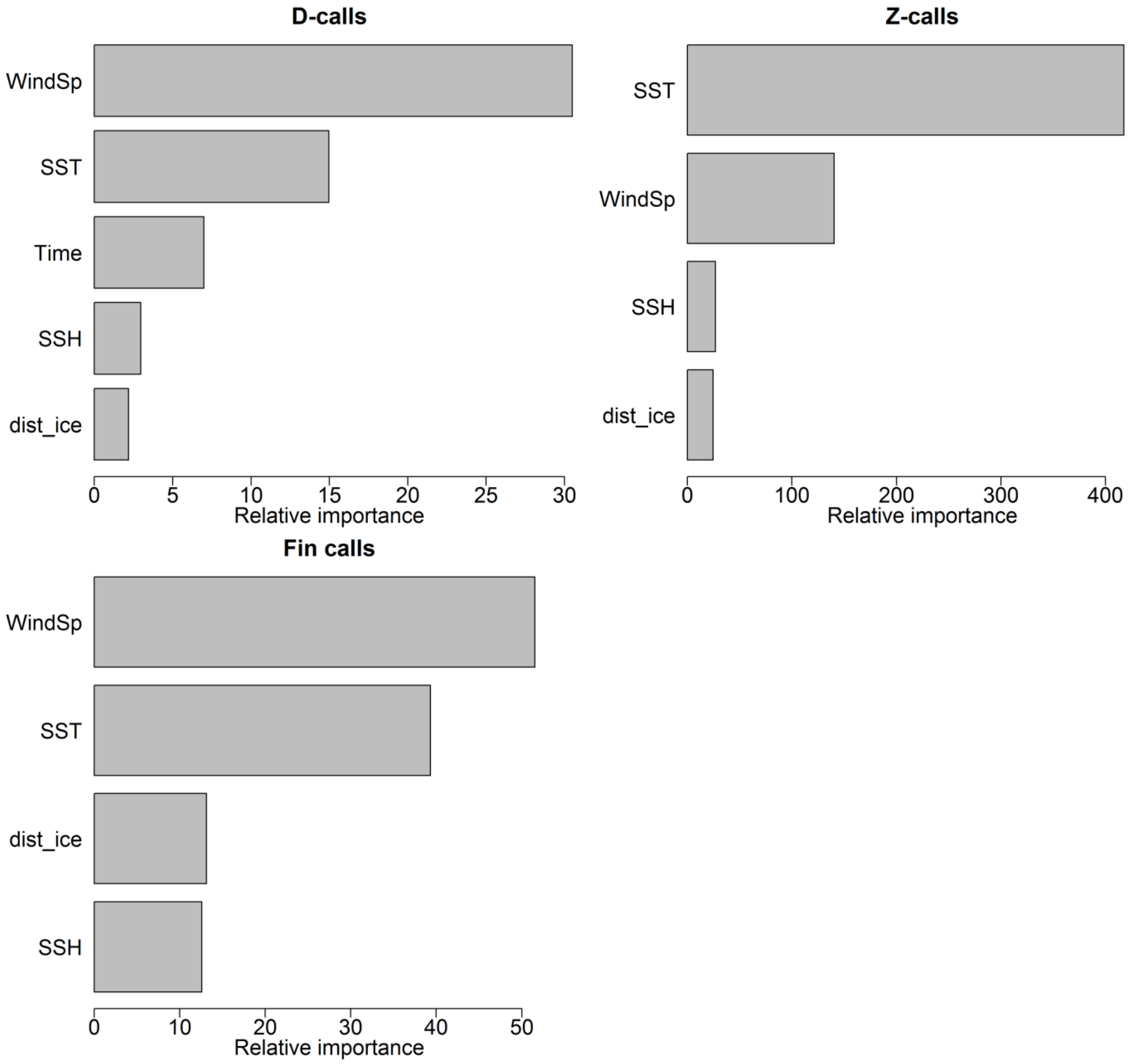


Figure 6.10. Relative importance of predictor variables on the rates of blue whale D- (top left), Z-calls (top right) and fin whale calls (bottom left).

6.4 Discussion

Satellite observations of environmental conditions such as chlorophyll-a levels are not always available in the Southern Ocean due to being obscured by cloud and ice cover during colder months (e.g., Tucker and Sellers, 1986; Corlett *et al.* 2006; Giles *et al.* 2006; Richards and Jia, 2006). This was true for the region assessed around the Maud Rise in this study. Using environmental predictors that would influence biological variables may be useful as proxies to drivers of whale abundance and activity. The marked decrease in SST at the beginning of autumn indicated the influence of the formation of sea ice around the mooring position and the increase in the cloud cover (Knox, 2007; Leahy *et al.* 2013).

The exclusion of periods with intense calling in our automated call detection method due to the difficulty of delineating individual Z-calls from the chorus potentially induced a negative bias in the total number of detected blue whale calls in our data during those periods. Thomisch *et al.* (2016) used the Blue Whale Index (BWI) to quantify the proportion of time when the chorus had higher energy levels than ambient noise, and Leroy *et al.* (2016) used a similar technique but termed it the Chorus to Noise-without-chorus Ratio (CNR). The BWI and CNR time series generally followed the same trend as the seasonal variations of call numbers (Leroy *et al.* 2016; Thomisch *et al.* 2016). Consequently, the automated template detector method routinely underestimated the Z-call numbers during chorus singing (Thomisch *et al.* 2016) but were effective for assessing and providing indication of whale call occurrence and behaviour (Širović *et al.* 2004, 2009; Shabangu *et al.* 2017- Chapter 4).

The recent increase in the recording of the blue whale chorus could be indicative of an increase in the blue whale population since the chorus consisted of songs from multiple whales. For example, there were no choruses recorded during the circumpolar cruises conducted by the Southern Ocean Whale and Ecosystem Research programme of the International Whaling Commission (IWC SOWER) between 1996 and 2009 (Shabangu *et al.* 2017- Chapter 4). Furthermore, this chorus is nowadays commonly recorded in the low latitudes such as the Indian Ocean (e.g., Leroy *et al.* 2016).

Blue whale calls were recorded for the whole period of our AAR deployment off the Maud Rise, indicating that whales are acoustical present in the eastern Antarctica year-round as found by Širović *et al.* (2004, 2009) and Thomisch *et al.* (2016). This almost year-round presence of blue whales observed here could indicate that the Maud Rise has year-round favourable environmental conditions and prey availability for blue whales. The Maud Rise is known to have recurring large polynyas (generally referred to as the Weddell Polynya) over the deep ocean during the winter (Comiso and Gordon, 1987; Hellmer, 2007), providing suitable habitats for blue whales. It is unlikely that polynyas were present around Maud Rise during late autumn through spring as distance to the sea ice extent was far off the AAR location and we also observed 100% ice concentration. This detection of blue whale Z-calls in months when the AAR was fully submerged under sea ice may reflect the long distances (just over a 1,000 km) travelled by these low frequency calls produced by whales in open waters free of sea ice (Cummings and Thompson, 1971; Stafford *et al.* 1998; Širović *et al.* 2007; Samaran *et al.* 2010; Miller *et al.* 2010).

February and March had the highest proportion of blue whale call occurrence and rates, suggesting that the most animals were more vocal active during those months and most migratory whales had arrived in the eastern Antarctica from their overwintering grounds after most of the sea ice extent had retracted (Mackintosh and Wheeler, 1929; Širović *et al.* 2004). February and March also corresponds to the farthest distance of the sea ice extent from our AAR location and to high krill biomass at the end of summer (Hewitt *et al.* 2004). On the other hand, fin whale calls were only recorded in January and March; a phenomenon that was unexpected as fin whales usually occurs simultaneously and sympatrically with blue whales (Širović *et al.* 2004, 2009). Only calls of the eastern Antarctic fin whale acoustic population were detected off the Maud Rise, suggesting some isolation between the western Antarctica fin whale population and the eastern Antarctic fin whale acoustic population in the Southern Ocean (Širović *et al.* 2009) and off the South African west coast (Shabangu *et al.* Under review- Chapter 5).

The higher blue whale call rates recorded between January and March could also indicate an increase in the numbers of vocal active blue whale in the area and the retraction of the ice extent from the AAR mooring location. March had the highest fin whale call rates, close to peaks observed by Širović *et al.* (2004, 2009); however, it is concerning that fin whales were not detected in other months of the year. Since no 40 Hz pulses of fin whales were found in this study, it can be suggested that fin whales off the Maud Rise do not synchronous change their song over seasons. However, Oleson *et al.* (2014) observed a synchronous seasonal change in the fin whale song in the North Pacific. Surprisingly, D-calls were only detected in March and April but not as expected for blue whales to feed throughout the summer season (Mackintosh, 1942). For example, an average of 847 D-calls in three months (from 9,315 calls in 11 years) were recorded in summer during the IWC SOWER cruises (Shabangu *et al.* Accepted- Chapter 3). This low D-call occurrence could be because blue whales rarely produce this call type, thus, there are generally low sample sizes of this call (e.g., Oleson *et al.* 2007a). Furthermore, blue whales could have been feeding further to the south of the Maud Rise at the ice edge as observed during the circumpolar IWC SOWER cruises (Shabangu *et al.* 2017- Chapter 4).

Seasonal variations in diel Z-call rates of blue whales suggest that these animals adjusted their behaviour in response to different light regimes and environmental conditions of the Antarctica. Blue whale call rates in summer and autumn trended similarly since those seasons are closer to each other whereas winter call rates were the opposite of summer and autumn. Spring blue whale call rates were slight similar to summer and autumn call rates as these seasons might have similar environmental conditions. There was a clear difference in fin whale diel call rates between autumn and summer; this is possibly due to low sample size of fin whale calls from our study to depict reliable and accurate diel call behaviour. The absence of temporal segregation between the peaks of diel call rates of blue and fin whales in autumn shows that blue and fin whales do not vocally compete but vocalise at the similar times as found in the Benguela ecosystem (Shabangu *et al.* Under Review- Chapter 5). Interestingly, there was a strong temporal segregation in summer that might have been induced by the low sample size of fin whale diel call rates under consideration from one day in summer.

Blue whale call occurrence peaked between 05:00 and 17:00, confirming that most blue whale vocal social activity occurs during the day (Shabangu and Findlay, 2014- Chapter 2;

Leroy *et al.* 2016; Shabangu *et al.* 2017- Chapter 4). In contrast, Tripovich *et al.* (2015) found Antarctic blue whales off Australia to be more vocal active during nighttime to avoid vocal competition with pygmy blue whales. SST was the most important predictor of blue whale call occurrence in the eastern Antarctica demonstrating the importance of environmental conditions on call occurrence and prey availability (Shabangu *et al.* 2017- Chapter 4). The seasonal changes in environmental conditions of wind speed and sea ice extent around Maud Rise probably limited the number of whales that could inhabit the region. Although call occurrences peaked at different times of the day, time of the day was the least important predictor of call occurrences. Wind speed and SST were respectively the most and moderately important predictors of fin whale call occurrence, again highlighting the importance of environmental conditions on whale occurrence. Distance of the sea ice extent from the AAR mooring position and SSH were the least important predictors of fin whale call occurrence, indicating that more calls were recorded when the area around the AAR was ice free and suitable for feeding (Širović *et al.* 2004, 2009).

Wind speed was the most important predictor of blue whale D-call rates, an indication that oceanographic conditions are potentially vital in the feeding ecology of whales and that wind speed affected call detectability. Colder SST was moderately important predictors of D-call rates, indicating a link between potential blue whale feeding and temperatures by Antarctic krill (e.g., Atkinson *et al.* 2006), blue whale major prey. Midday to night-time (15:00 to 23:00) was important for the D-call rates, suggesting that blue whales could be feeding at night on ascending krill (Piakowski, 1985; Gaten *et al.* 2008). The high influence of SST on Z-call rates verifies the importance of these environmental conditions on whale behaviour. Colder SSTs were also observed to positively influence blue whale Z-call rates in the low latitudes, off the west coast of South Africa (Shabangu *et al.* Under review- Chapter 5). Wind speed was a moderately important predictor for Z-call rates suggesting detectability of calls was impacted by wind and also increased productivity around the area.

Distances of the sea ice extent to AAR position and SSH were the least important predictors of Z-call rates reflecting that blue whales socialise closer to the ice extent where there are calm waves and abundant krill. The faint ~27 Hz tonal unit of the Z-calls recorded here could be indicative of animals calling farther from AAR location. Wind speed and SST were respectively the most and moderately important predictors of fin whale call rates, also emphasizing the importance of environmental on whale acoustic behaviour. Distance to the sea ice extent and SSH were the least important predictors of fin whale call rates, probably indicating that fin whales are not very dependent on the sea ice and calm sea state conditions for socialising and foraging. The disassociation of fin whales with the edge of the ice extent suggests that they might have avoided prey competition with blue whales and maximised energy gain by feeding on areas less preferred by blue whales as found elsewhere by Friedlander *et al.* (2015).

Antarctic blue whale sounds recorded in our study could be from each population of the three Antarctic blue whales that are genetically distinct but acoustically indifferent found between 0° and 20° E (Attard *et al.* 2016). This study shows the benefits of using passive acoustic monitoring to study marine mammals in remote, harsh, challenging and sometimes inaccessible area such as the Antarctica. The deployment of AARs on oceanographic moorings could be a cost-effective way to collect more passive acoustic data in the Southern Ocean. Our current efforts to identify diel call patterns in behaviour and to describe seasonal call occurrence of Antarctic blue and fin whales relative to environmental conditions in the Southern Ocean provide a powerful tool for a better description of the feeding and distributional ecology of these species.

6.5 Acknowledgements

We are grateful to the National Research Foundation and the South African National Antarctic Programme (Grant No. SNA 2011112500003) for financially supporting the South African Blue Whale Project. We thank Meredith Thornton, Kirsty Venter, Ian Thompson, and

Ove Fabriciussen for their kind assistance with the deployment of the AAR. We would like to give special thanks to Sinekhaya Bilana, Jarred Voorneveld and Jethan d'Hotman for their outstanding and expert technical assistance with the acoustic transponder releases of the AAR mooring during recovery. Many heartfelt thanks to captains and crew of the RV *SA Agulhas II* for their great assistance with the AAR deployment and recovery. Marcel van den Berg is thanked for his invaluable advices and guidance with the procedure for the AAR mooring deployment and recovery. MetOcean Services are thanked for the loan of a satellite transponder, while Mr Bruce Spolander of MetOcean Services is thanked for providing satellite positions of the AAR during the recovery at late hours of the day. Cathy Boucher is acknowledged for graphic assistance. Dr Taryn Morris is thanked for her invaluable comments and suggestions on the earlier draft of this manuscript.

6.6 References

Amante, C. and Eakins, B.W. 2009. ETOPO1 1 Arc-Minute Global Relief Model: Procedures, Data Sources and Analysis. NOAA Technical Memorandum NESDIS NGDC-24. National Geophysical Data Center, NOAA.

Atkinson, A., Shreeve, R.S., Hirst, A.G., Rothery, P., Tarling, G.A., Pond, D.W., Korb, R., Murphy, E.J., and Watkins, J. 2006. Natural growth rates in Antarctic krill (*Euphausia superba*): II. Predictive models based on food, temperature, body length, sex, and maturity stage. Limnol Oceanogr 51(2): 973–987.

Attard, C.R.M., Beheregaray, L.B., and Möller, L.M. 2016. Towards population-level conservation in the critically endangered Antarctic blue whale: the number and distribution of their populations. Scientific Reports 6: 22291.

Beitsch, A., Kaleschke, L., and Kern, S. 2014. Investigating high resolution AMSR2 sea ice concentrations during the February 2013 fracture event in the Beaufort Sea. Remote Sensing 6: 3841–3856.

Bivand. R., Keitt, T., Rowlingson, B., Pebesma, E., Sumner, M., Hijmans, R., and Rouault, E. 2015. Package ‘rgdal’. (Bindings for the Geospatial Data Abstraction Library.) https://cran.rproject.org/web/packages/rgdal/. Accessed 13 October 2016.

Branch, T.A., Stafford, K.M., Palacios, D.M., Allison, C., Bannister, J.L., Burton, C.L.K., Cabrera, E., Carlson, C.A., Vernazzani, B.G., Gill, P.C., Hucke-Gaete, R., Jenner, K.C.S., Jenner, M.N.M., Matsuoka, K., Mikhalev, Y.A., Miyashita, T., Morrice, M.G., Nishiwaki, S., Sturrock, V.J., Tormosov, D., Anderson, R.C., Baker, A.N., Best, P.B., Borsa, P., Brownell, R.L., Childerhouse, S., Findlay, K.P., Gerrodette, T., Ilangakoon, A.D., Joergensen, M., Kahn, B., Ljungblad, D.K., Maughan, B., McCauley, R.D., McKay, S., Norris, T.F., Whale, O., Rankin, S., Samaran, F., Thiele, D., Van Waerebeek, K., and Warneke, R.M. 2007. Past and present distribution, densities and movements of blue whales (*Balaenoptera musculus*) in the Southern Hemisphere and northern Indian Ocean. Mammal Review 37(2): 116–175.

Brandt, A., Bathmann, U., Brix, S., Cisewski, B., Flores, H., Gocke, C., Janussen, D., Kragefsky, S., Kruse, S., Leach, H., Linse, K., Pakhomov, E., Peeken, I., Riehl, T., Sauter, E., Sachs, O., Schuller, M., Schrodl, M., Schwabe, E., Strass, V., van Franeker, J.A., and Wilmsen, E. 2011. Maud Rise–a snapshot through the water column. Deep-Sea Research II 58: 1962–1982.

Breiman, L. 2001. Random forests. Machine Learning 45: 5−32.

Clapham, P.J., and Baker, C.S. 2002. Modern whaling. In: Perrin, W.F., Würsig, B., and Thewissen, J.G.M. (eds) Encyclopedia of Marine Mammals. Academic Press, New York. p. 1328–1332

Cleveland, W.S., Grosse, E., and Shyu, W.M. 1992. Local regression models. In: Chambers, J.M., and Hastie, T.J. (eds) Statistical Models in S. Wadsworth and Brooks, Cole. p. 309–376.

Comiso, J.C., and Gordon, A.L. 1987. Recurring polynyas over the Cosmonaut Sea and the Maud Rise. Journal of Geophysical Research 92(C3): 2819–2833.

Corlett, G.K., Barton, I.J., Donlan, C.J., Edwards, M.C., Good, S.A., Horrocks, L.A., Llewellyn-Jones, D.T., Merchant, C.J., Minnett, P.J., Nightingale, T.J., Noyes, E.J., O'carroll, A.G., Remedios, J.J., Robinson, I.S., Saunders, R.W., and Watts, J.G. 2006. The accuracy of SST retrievals from AATSR: An initial assessment through geophysical validation against in situ radiometers, buoys and other SST data sets. Advances in Space Research 37(4): 764–769.

Croll, D.A., Clark, C.W., Acevedo, A., Tershy, B., Flores, S., Gedamke, J., and Urban, J. 2002. Only male fin whales sing loud songs. Nature 417: 809–811.

Cummings, W.C., and Thompson, P.O. 1971. Underwater sounds from the blue whale, *Balaenoptera musculus*. Journal of the Acoustical Society of America 50: 1193–1198.

Donlon, C., Robinson. I., Casey, K.S., Vazquez-Cuervo, J., Armstrong, E., Arino, O., Gentemann, C., May, D., Leborgne, P., Piollé, J., Barton, I., Beggs, H., Poulter, D.J.S., Merchant, C.J., Bingham, A., Heinz, S., Harris, A., Wick, G., Emery, B., Minnett, P., Evans, R., Llewellyn-Jones, D., Mutlow, C., Reynolds, R.W., Kawamura, H., and Rayner, N. 2007. The Global Ocean Data Assimilation Experiment High-resolution Sea Surface Temperature Pilot Project. Bulletin of the American Meteorological Society 88(8): 1197–1213.

Elith, J., Leathwick, J.R., and Hastie, T. 2008. A working guide to boosted regression trees. Journal of Animal Ecology 77(4): 802–813.

Everson, I. 2000. Krill: Biology, ecology and fisheries. Blackwell Sciences Ltd, Malden, MA.

Fetterer, F., Knowles, K., Meier, W., and Savoie, M. 2016. Sea Ice Index, Version 2. Boulder, Colorado USA. NSIDC: National Snow and Ice Data Center, http://dx.doi.org/10.7265/N5736NV7. Accessed: 28 August 2016.

Figueroa, H.K. 2006. XBAT: Extensible BioAcoustic Tool. Available: http://xbat.org. Accessed: 22 June 2015.

Fox, J. and Monette, G. 1992. Generalized collinearity diagnostics. Journal of the American Statistical Association 87: 178–183.

Fox, J. and Weisberg, S. 2011. An R companion to applied regression, 2nd edn. SAGE Publications Inc, Thousand Oaks, CA.

Friedlaender, A.S., Goldbogen, J.A., Hazen, E.L., Calambokidis, J., and Southall, B.L. 2015. Feeding performance by sympatric blue and fin whales exploiting a common prey resource. Marine Mammal Science 31(1): 345–354.

Friedman, J.H., Hastie, T., and Tibshirani, R. 2000. Additive logistic regression: a statistical view of boosting. Annals of Statistics 28: 337−407.

Gaten, E., Tarling, G., Dowse, H., Kyriacou, C., and Rosato, E. 2008. Is vertical migration in Antarctic krill (*Euphausia superba*) influenced by an underlying circadian rhythm? Journal of Genetics 87:473–483.

Gavrilov, A.N., McCauley, R., and Gedamke, J. 2012. Steady inter and intra-annual decrease in the vocalization frequency of Antarctic blue whales. Journal of the Acoustical Society of America 131: 4476–4480.

Giles, K.A., Laxon, S.W., and Worby, T. 2006. Validating satellite radar altimetry estimates of Antarctic sea ice thickness using the ASPeCt data set. Proceedings of 2006 American Geophysical Union Fall Meeting.

Goosse, H. and Zunz, V. 2014. Decadal trends in the Antarctic sea ice edge ultimately controlled by ice–ocean feedback. The Cryosphere 8: 453–470.

Gordon, A.L. 2011. Bottom water formation. In: Steele, J.H., Thorpe, S.A., and Turekian, K.K. (eds) Encyclopedia of ocean sciences, 2nd edn, 4 vol. Academic Press, London. p. 415–421.

Guisan, A., Edwards, T.C., and Hastie, T. 2002. Generalized linear and generalized additive models in studies of species distributions: setting the scene. Ecological Modelling 157: 89−100.

Hair, J.F., Black, W.C., Babin, B.J., and Anderson, R.E. 2009. Multivariate data analysis, 7th edn. Pearson Education, Upper Saddle River, NJ.

Hastie, T.J., Tibshirani, R., and Friedman, J. 2009. The elements of statistical learning. Springer, New York.

Hellmer, H. 2007. Oceanography of Weddell Sea. In: Riffenburgh, B. (ed) Encyclopedia of the Antarctic. Routledge, New York. p. 1053–1056.

Hewitt, R.P., Kim, S., Naganobu, M., Gutierrez, M., Kang, D., Takao, Y., Quinones, Y., Lee, Y.-H., Shing, H.-C., Kawaguchi, S., Emery, J.H., Demer, D.A., and Loeb, V.J. 2004. Variation in the biomass density and demography of Antarctic krill in the vicinity of the South Shetland Islands during the 1999/2000 austral summer. Deep-Sea Research II 51: 1411–1419.

Ho TK (1995) Random Decision Forests. Proceedings of the 3rd International Conference on Document Analysis and Recognition, Montreal, QC, 14–16 August 1995. p. 278–282.

IWC, 1995. Report of the scientific committee. Report of International Whaling Commission 45: 53–221.

James, G., Witten, D., and Hastie, T. 2013. An introduction to statistical learning: with applications in R. Taylor and Francis Group, New York.

Knox, G.A. 2006. Biology of the Southern Ocean, 2nd edn. Taylor and Francis Group, New York.

Leahy, S.M., Kingsford, M.J., and Steinberg, C.R. 2013. Do clouds save the Great Barrier Reef? Satellite imagery elucidates the cloud-SST relationship at the local scale. PLoS ONE 8(7): e70400.

Leroy, E.C., Samaran, F., Bonnel, J., and Royer, J.-Y. 2016. Seasonal and diel vocalization patterns of Antarctic blue whale (*Balaenoptera musculus intermedia*) in the Southern Indian Ocean: A multi-year and multi-site study. PLoS ONE 11(11): e0163587.

Liaw, A., and Wiener, M. 2002. Classification and Regression by randomForest. R News 2(3): 18–22.

Ljungblad, D.K., Clark, C.W., and Shimada, H. 1998. A comparison of sounds attributed to pygmy blue whales (*Balaenoptera musculus brevicauda*) recorded south of the

Madagascar Plateau and those attributed to ‘true’ blue whales (*Balaenoptera musculus*) recorded of Antarctica. Report of International Whaling Commission 48: 439–442.

Mackintosh, N.A. 1942. The southern stocks of whalebone whales. Discovery Reports 22: 197–300.

Mackintosh, N.A. and Wheeler, J.F.G. 1929. Southern blue and fin whales. Discovery Reports I: 259–540.

Maritorena, S., Fanton d’Andon, O.H., Mangin, A., and Siegel, D.A. 2010. Merged satellite ocean color data products using a bio-optical model: Characteristics, benefits and issues. Remote Sensing of Environment 114: 1791–1804.

Martin, W.R. 2011. Polynyas. In: Steele, J.H., Thorpe, S.A., and Turekian, K.K. (eds) Encyclopedia of ocean sciences, 2nd edn, 4 vol. Academic Press, London. p. 540–545.

Mascaro, J., Asner, G.P., Knapp, D.E., Kennedy-Bowdoin, T., Martin, R.E., Anderson, C., Higgins, M., and Chadwick, K.D. 2014. A tale of two ‘‘forests’’: Random forest machine learning aids tropical forest carbon mapping. PLoS ONE 9(1): e85993.

Matworks Inc, 2014. MATLAB R2014a version 8.3.0.532. The MathWorks, Inc., Natick, Massachusetts, United States.

McDonald, M.A., Calambokidis, J., Teranishi, A.M., and Hildebrand, J.A. 2001. The acoustic calls of blue whales off California with gender data. Journal of the Acoustical Society of America 109(4): 1728–1735.

McDonald, M.A., Hildebrand, J.A., and Mesnick, S.L. 2006. Biogeographic characterization of blue whale song worldwide: using song to identify populations. Journal of Cetacean Research and Management 8: 55–65.

McDonald, M.A., Hildebrand, J.A., and Mesnick, S.L. 2009. Worldwide decline in tonal frequencies of blue whale songs. Endangered Species Research 9: 13–21.

Miller, B.S., Barlow, J., Calderan, S., Collins, K., Leaper, R., Kelly, N., Peel, D., Olson, P., Ensor, P., and Double, M.C. 2013. Long-range acoustic tracking of Antarctic blue whales. Paper submitted for consideration by the IWC Scientific Committee, SC/65/SH18.

Miller, B.S., Barlow, J., Calderan, S., Collins, K., Leaper, R., Olson, P., Ensor, P., Peel, D., Donnelly, D., Andrews-Goff, V., Olavarria, C., Owen, K., Rekdahl, M., Schmitt, N., Wadley, V., Gedamke, J., Gales, N., and Double, M.C. 2015. Validating the reliability of passive acoustic localisation: a novel method for encountering rare and remote Antarctic blue whales. Endangered Species Research 26: 257–269.

O’Brien, R.M. 2007. A caution regarding rules of thumb for variance inflation factors. Quality Quantity 41:673–690

Oleson, E.M., Calambokidis, J., Barlow, J., and Hildebrand, J.A. 2007a. Blue whales visual and acoustic encounter rates in the Southern California Bight. Marine Mammal Science 23(3): 574–597.

Oleson, E.M., Calambokidis, J., Burgess, W.C., McDonald, M.A., LeDuc, C.A., and Hildebrand, J.A. 2007b. Behavioral context of call production by eastern North Pacific blue whales. Marine Ecological Progress Series 330: 269–284.

Oleson, E.M., Širović, A., Bayless, A.R., and Hildebrand, J.A. 2014. Synchronous seasonal change in fin whale song in the North Pacific. PLoS ONE 9(12): e115678.

Perrier, A. 2015. Feature importance in random forests. http://alexperrier.github.io/jekyll/update/2015/08/27/feature-importance-random-forests-gini-accuracy.html. Accessed: 15 May 2017.

Piakowski, U. 1985. Distribution, abundance and diurnal migration of macrozooplankton in Antarctic surface waters. Meeresforschung 20: 264–279.

Pierce D (2015) ncdf4: Interface to Unidata netCDF (Version 4 or Earlier) Format Data Files. R package version 1.15. https://CRAN.R-project.org/package=ncdf4. Accessed: 11 June 2016.

R Core Team, 2016. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. http://www.R-project.org/. Accessed 06 July 2015.

Rankin, S., Ljungblad, D., Clark, C.W., and 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, Antarctica. Journal of Cetacean Research and Management 7: 13–20.

Richards, J.A. and Jia, X. 2006. Remote sensing digital image analysis: An introduction, 4th edn. Springer-Verlag, Berlin, Heidelberg.

Samaran, F., Adam, O., and Guinet, C. 2010. Discovery of a mid-latitude sympatric area for two Southern Hemisphere blue whale subspecies. Endangered Species Research 12: 157–165.

Shabangu, F.W., and Findlay, K. 2014. Passive acoustic monitoring of marine mammals in South Africa, with special reference to Antarctic blue whales. In: Funke, N., Claassen, M., Meissner, R. and Nortje, K. (eds) Reflections on the state of research and development in the marine and maritime sectors in South Africa. Council for Scientific and Industrial Research, Pretoria. p 153–173.

Shabangu, F.W., Yemane, D., Stafford, K.M., Ensor, P., and Findlay, K.P. 2017. Modelling the effects of environmental conditions on the acoustic occurrence and behaviour of Antarctic blue whales. PLoS ONE: e0172705.

Širović, A., Hildebrand, J.A., Wiggins, S.M., McDonald, M.A., Moore, S.E., and Thiele, D. (2004) Seasonality of blue and fin whale calls and the influence of sea ice in the Western Antarctic Peninsula. Deep-Sea Research II 51: 2327–2344.

Širović, A., Hildebrand, J.A., and Wiggins, S.M. 2007. Blue and fin whale call source levels and propagation range in the Southern Ocean. Journal of Acoustical Society of America 122(2): 1208–1215.

Širović, A., Hildebrand, J.A., Wiggins, S.M., and Thiele, D. 2009. Blue and fin whale acoustic presence around Antarctica during 2003 and 2004. Marine Mammal Science 25(1): 125–136.

Spreen, G., Kaleschke, L., and Heygster, G. 2008. Sea ice remote sensing using AMSR-E 89-GHz channels. Journal of Geophysical Research - Oceans 113: C2S03. DOI:10.1029/2005JC003384.

Stafford, K.M., Fox, C.G., and Clark, D.S. 1998. Long-range acoustic detection and localization of blue whale calls in the northeast Pacific Ocean. Journal of the Acoustical Society of America 104: 3616–3625.

Swart, S., Thomalla, S.J., and Monteiro, P.M.S. 2015. The seasonal cycle of mixed layer dynamics and phytoplankton biomass in the Sub-Antarctic Zone: a high-resolution glider experiment. Journal of Marine Systems 147: 103–115.

Thomalla, S.J., Racault, M.-F., Swart, S., and Monteiro, P.M.S. 2015. High-resolution view of the spring bloom initiation and net community production in the Subantarctic Southern Ocean using glider data. ICES Journal of Marine Science 72(6): 1999–2020.

Thomas, L. and Marques, T.A. 2012. Passive acoustic monitoring for estimating animal density. Acoustics Today 18(3): 35–44.

Thomisch, K., Boebel, O., Clark, C.W., Hagen, W., Spiesecke, S., Zitterbart, D.P., and Van Opzeeland, I. 2016. Spatio-temporal patterns in acoustic presence and distribution of Antarctic blue whales *Balaenoptera musculus intermedia* in the Weddell Sea. Endangered Species Research 30: 239–253.

Torres, L.G. 2017. A sense of scale: Foraging cetaceans' use of scale-dependent multimodal sensory systems. Marine Mammal Science 33(4): 1170–1193.

Tripovich, J.S., Klinck, H., Nieukirk, S.L., Adams, T., Mellinger, D.K., Balcazar, N.E., Klinck, K., Hall, E.J.S., and Rogers, T.L. 2015. Temporal segregation of the Australian and Antarctic blue whale call types (*Balaenoptera musculus* spp.). Journal of Mammalogy 96: 603–610.

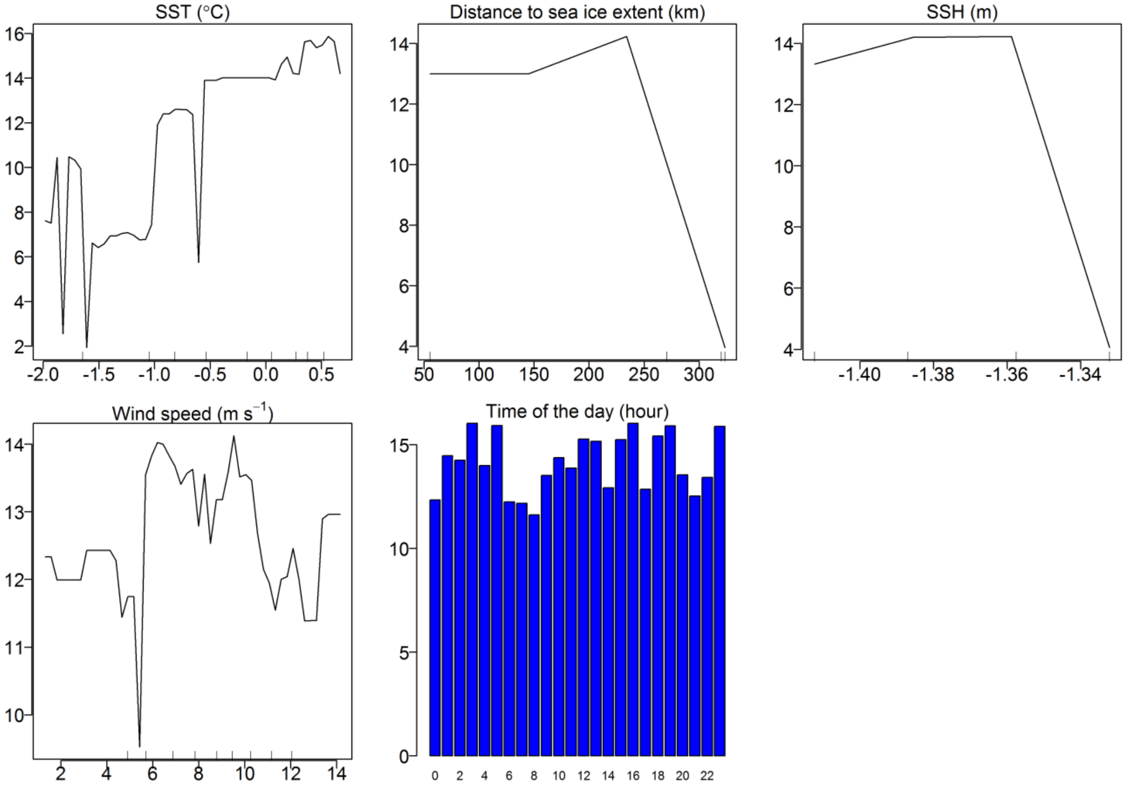
Tucker CJ, Sellers PJ (1986) Satellite remote sensing of primary production. International Journal of Remote Sensing 7(11): 1395–1416.

Ward, R., Gavrilov, A.N., and McCauley, R.D. 2017. “Spot” call: A common sound from an unidentified great whale in Australian temperate waters. Journal of the Acoustical Society of America 142(2): EL231– EL236.

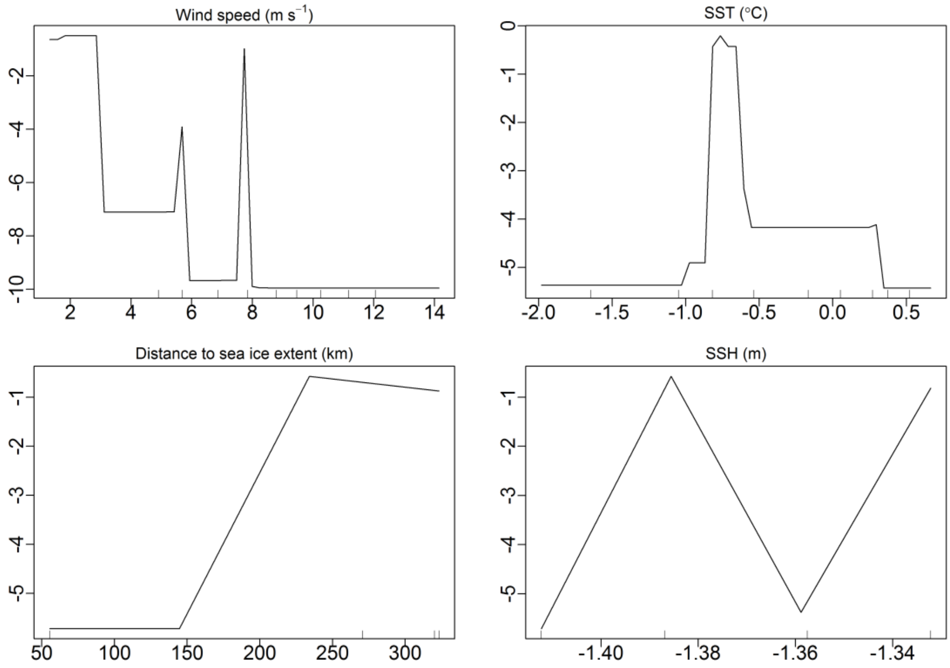
Wright, M.N. and Ziegler, A. 2017. ranger: A Fast Implementation of Random Forests for High Dimensional Data in C++ and R. Journal of Statistical Software 77(1): 1–17.

Zhang, H.-M., Reynolds, R.W., and Bates, J.J. 2006. Blended and gridded high resolution global sea surface wind speed and climatology from multiple satellites: 1987–present. In: Proceedings of the American Meteorological Society 2006 Annual Meeting, Atlanta, GA, January 29- February; P2.23.

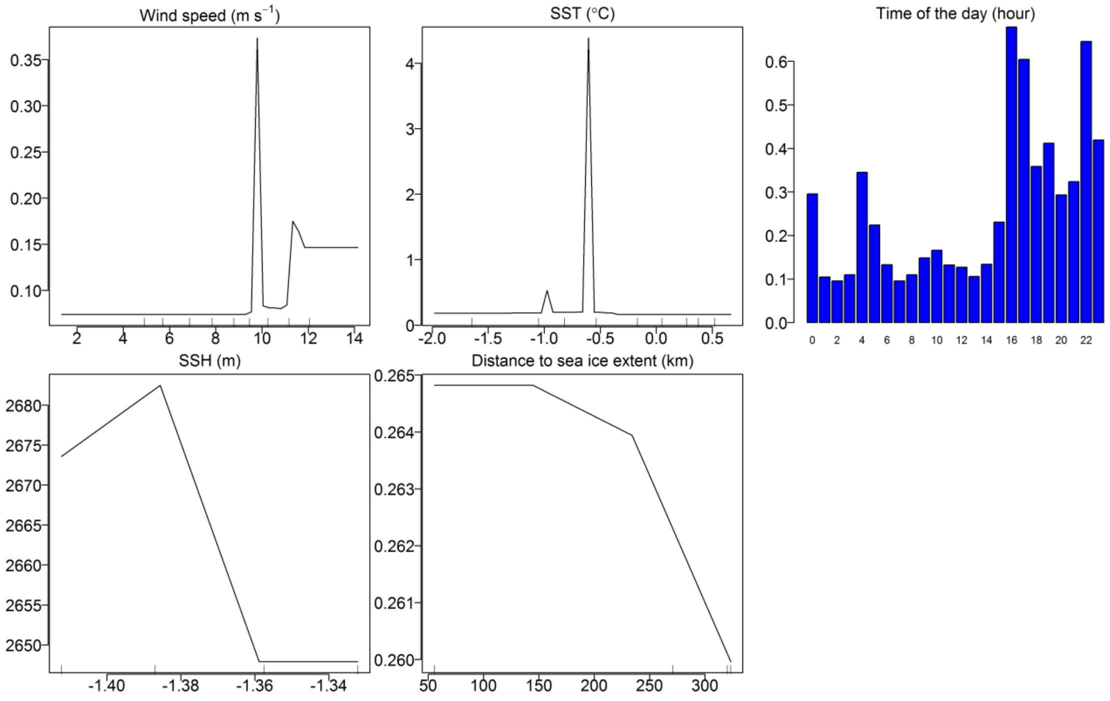
6.7. Supplementary material



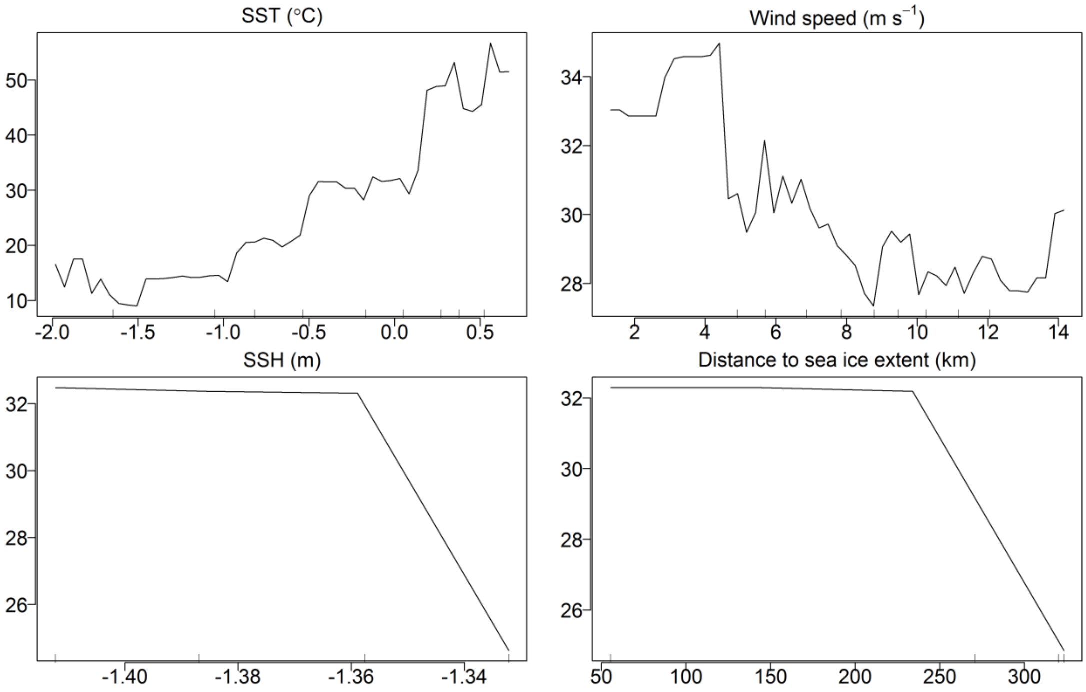
Supplementary Figure S6.1. Partial effects of predictor variables on the blue whale call occurrence.



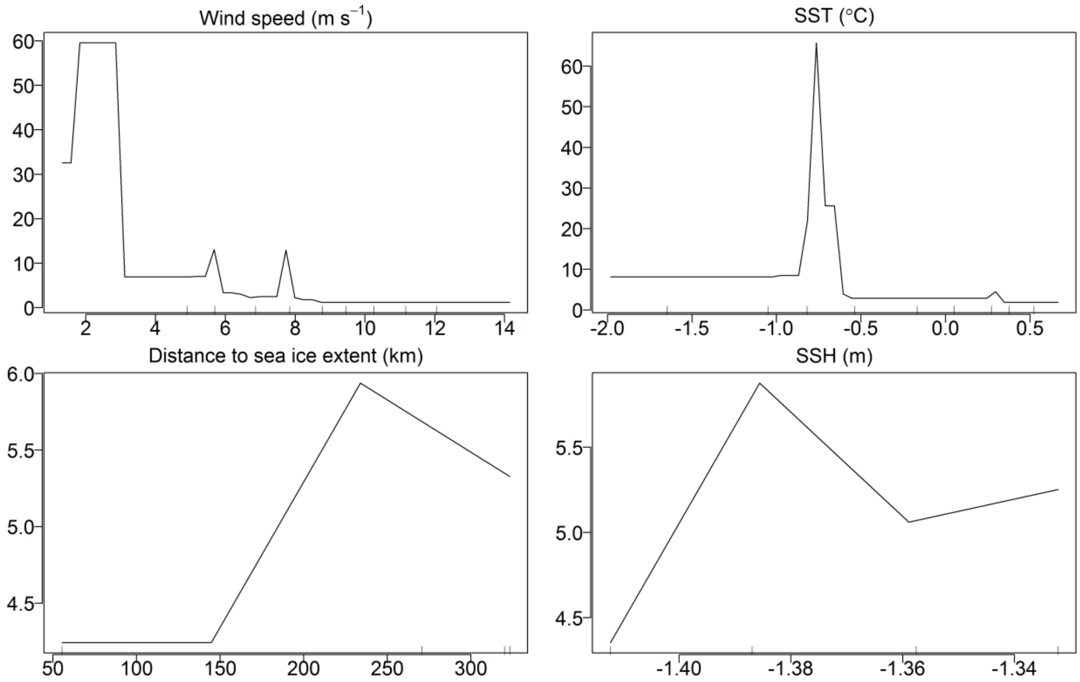
Supplementary Figure S6.2. Partial effects of predictor variables on the fin whale call occurrence.



Supplementary Figure S6.3. Partial influences of predictor variables on the D-call detection rates.



Supplementary Figure S6.4. Partial influences of predictor variables on the Z-call detection rates.



Supplementary Figure S6.5. Partial influences of predictor variables on fin whale call detection rates.

Chapter 7: General conclusions

7.1 Major findings

Overall, this thesis demonstrates the feasibility of using ship-based acoustic recorders and mooring-based autonomous acoustic recorders to monitor the call occurrence and diel calling behaviour of Antarctic blue and fin whales in the low and high latitudes.

The first two main chapters introduce the fundamental concepts of passive acoustics monitoring and acoustic data management. The last three chapters document the seasonal distribution at different latitudes and the effects of environmental conditions on the call occurrence and acoustic behaviour of Antarctic blue whales; whilst the effects of environmental conditions on fin whale call occurrence and acoustic behaviour were documented in the last two chapters. The acoustic autonomous recorders have allowed the first identification and recording of Antarctic blue and fin whale calls in the Benguela ecosystem, and sounds of other whale species such as humpback and minke whales can also be assessed from these datasets. This work demonstrates that applying the random forest (RF) model output in combination with satellite-derived and *in situ* environmental observations advances our understanding of the acoustic occurrence and behaviour of Antarctic blue and fin whales in the low and high latitudes.

The major findings of this work are both methodological and ecological in nature, since this work consisted of a combination of the assessment of the ship-based recordings, mooring-based autonomous acoustic recordings, automated template detections, template accuracy to allow for interrogation of large datasets and development of a time-series within the IWC SOWER acoustic dataset; and the assessment of the acoustic interactions of Antarctic blue and fin whales with their environment.

7.1.1 Methodological implications

Passive acoustic monitoring is demonstrated to be effective at detecting the calls of the vocally active Antarctic blue and fin whales over long distances. The recovery of blue whale and other baleen whales are currently difficult to monitor using sighting surveys due to their low populations. Chapter Two demonstrates that passive acoustic monitoring has considerable potential for application to large offshore marine mammals that occur in South African waters, including blue and fin whales. Challenges of passive acoustic monitoring are identified showing that the method is still nascent and a number of challenges need to be tackled before it reaches the same maturity level as sighting surveys in South Africa and elsewhere.

Chapter Three provides an overview of passive acoustic data collected during the International Whaling Commission’s Southern Whale and Ecosystem Research (IWC SOWER) circumpolar cruises from 1997 to 2009, these surveys were conducted within a considerable temporal and spatial scale. Challenges in sourcing the acoustic data collected during the IWC SOWER cruises resulted in 37% of the data being unavailable, it is recommended that these data be sourced and archived along with data from future acoustic surveys and be managed in a centralised domain to increase access by interested parties.

Chapters Four to Six identify that the automatic template detection method works well for whale vocalizations collected within similar times as they have similar start and end frequencies. However, in Chapter Four the accuracy results of the template detector assessment identified that the blue whale calls are changing over time (i.e. within years). In particular, it is recommended to use a detection template recorded within a similar time frame and from an overlapping region as the collected data being analysed and not to use templates from other years or locations. The overall accuracy of the detection threshold used for automatic detection method changes with the quality of the collected acoustic data and it is recommended that no standard threshold be used for Antarctic blue whales and that the threshold must be determined for each study. The application of the automatic template detection method significantly accelerated the acoustic data processing.

Chapters Five and Six demonstrates the feasibility of using autonomous acoustic instrumentation to monitor the seasonal occurrence and diel calling behaviour of Antarctic blue and fin whales in the low and high latitudes. The acoustic detections of the rarely sighted Antarctic blue and fin whales off the west coast of South Africa in Chapter Five demonstrates the advantage of using passive acoustic technology over sighting surveys for monitoring heavily depleted whale species. It is also confirmed that passive acoustic monitoring is a promising, reliable and cost-effective method for studying marine mammals over a wide temporal scale. Attaching acoustic recorders to existing oceanographic moorings further reduces the costs for collecting passive acoustic data.

This research in Chapter Six also demonstrates the effectiveness of passive acoustic for monitoring the ecology of marine mammals in remote, harsh and inaccessible environments such as Antarctic waters. However, the cold environment of Antarctica presented a challenge to the battery duration of the autonomous acoustic recorders and engineering efforts should be dedicated to resolve the effects of temperature on battery duration. Passive acoustic monitoring of marine mammals has further benefits including the collection of secondary data such as data on ambient and anthropogenic noises; but due to on-going development of the method it remains rarely used. In South Africa particularly, autonomous acoustic monitoring remains in its infancy, yet its use could potentially provide important data for ocean management including the use of the associated biophysical and anthropogenic noise data to manage the ocean space.

The combination of sighting surveys and passive acoustic monitoring is recommended for the two methods to complement each method’s limitations (Miller *et al.* 2015; Jacobson *et al.*

2017). The high temporal but low spatial resolution of data collected using autonomous acoustic recorders is very efficient at describing seasonal call occurrence and diel calling behaviour of whales. Whereas data collected using sonobuoys from ships on the IWC SOWER cruises has higher spatial and low temporal resolution which enabled the estimation of the distributional trends and acoustic behaviour together with information on Antarctic blue whale social aggregations from sighting surveys. Autonomous acoustic recorders are furthermore cost effective at collecting passive acoustic data as they are re-useable and the cost of deploying and recovering them is relatively low compared to the more costly ship-based towed hydrophone/sonobuoy recordings of the IWC SOWER dataset that are associated with difficult logistical research operations. For example, the cost of purchasing one autonomous acoustic recorder is equivalent to four times the daily at-sea running cost of a small research vessel (e.g., South African RV *Algoa*: 52 m). And autonomous acoustic recorder price is equivalent to eight times the daily at-sea running cost of a large polar supply and research vessel (e.g., South African RV *SA Agulhas II*: 134 m).

The statistical method used in Chapters Four - Six to quantify the importance of different environmental conditions on the call occurrence and calling behaviour of blue and fin whales are simple and have recognisable value, yet their use in marine mammalogy remains rare. The ensemble model, RF, enabled the explicit interpretation of the multifaceted relationships between Antarctic blue and fin whales and their environment. RF model performed well for modelling occurrence and behaviour of whales, and it holds perhaps the greatest potential for acoustic behaviour and occurrence modelling due to its wide versatility that allows it to assume simpler, faster and more interpretable forms with incorporable automatic predictor selection.

7.1.2 Ecological implications

The acoustic component of IWC SOWER cruises was found to be valuable in describing the distributional and behavioural ecology of Antarctic blue whales in the Southern Ocean (e.g., Rankin *et al.* 2005; this study). The recently described southeastern Pacific 2 song (Buchan *et al.* 2014) of the Chilean pygmy blue whale was also found from the acoustic data of the 1997 Chilean IWC SOWER blue whale cruise (Chapter Three), showing that precious and important ecological information can be derived from archived acoustic recordings.

Furthermore, the RF model shows clear environmental preference patterns, spatial occurrence and acoustic behaviour of Antarctic blue whales from the IWC SOWER cruise dataset (Chapter Four). Distance to the southern boundary of the Antarctic Circumpolar Current, latitude, longitude and distance from the nearest Antarctic ice-edge are the main geographic predictors of blue whale call occurrence and behaviour. Satellite-derived sea surface height, sea surface temperature, productivity (chlorophyll-a), wind stress, wind direction, wind speed, and water depth are the important environmental conditions predicting the acoustic occurrence and behaviour of blue whales.

Social parameters such as whale group numbers and number of whales in an area influence Antarctic blue whale behaviour (Chapter Four), confirming that the vocal activity of these whales is essential for close range social interactions. Months, time of the day, and acoustic station duration are valuable at depicting the temporal variability of Antarctic blue whale occurrence and behaviour. The significant variability of blue whale call occurrence and call behaviour in response to inter-annual and long term variability of environmental conditions highlight potential suitable habitats and preferred socialising environments. Furthermore, such responses suggest that Antarctic blue whales through their acoustic behaviour might be vulnerable to environmental variability, and climate change may exert additional pressure on this recovering whale species. Future studies can consider acoustic occurrence and behaviour of other whale species present in the datasets of IWC SOWER and autonomous acoustic recorders including humpback, sperm and minke whales.

In the low latitudes (Chapter Five), off the west coast of South Africa, migratory Antarctic blue whales and eastern Antarctic fin whale acoustic population are present between May and August with some fin whales present until November of 2014 and 2015. These acoustic detections of Antarctic blue and fin whales provide first recordings of these in South African waters and qualify the Benguela ecosystem as the overwintering ground of blue and fin whales as hypothesized from whale catches by Best (1998). They further identify the value of mooring-based AAR in areas where ship-based surveys are limited by cost or sighting conditions. Both whale species vary their diel call in response to changing seasons, an adaptation to changes in light and prey depth regimes. RF model demonstrated that wind speed, sea surface height, sea surface temperature, Ekman upwelling index, and chlorophyll-a are important environmental parameters influencing the occurrence and behaviour of Antarctic blue and fin whales in the Benguela ecosystem.

Although there is some uncertainty around the context of D-calls, the detection of the feeding associated call for blue whales in the Benguela ecosystem; provides new evidence that whales do not necessarily fast during overwintering in the low latitude as they potentially feed on opportunistically available prey items. This work provides preliminary information on which to concentrate further research effort to investigate abundance, distribution and seasonality of these whale populations in the Benguela ecosystem. The importance of monitoring Antarctic top-consumer baleen whales in the low latitudes is clearly highlighted by this work.

The year-round recording off the Maud Rise, Antarctica, indicates that blue whales are present almost year-round (with call numbers peaking in February) and not all blue whales migrated to low latitudes but some animals overwinter in Antarctica (Chapter Six). On the other hand, fin whale calls are present seasonally off the Maud Rise, and only detected in January and March. Both whale species vary their diel call behaviour as an adaptation to changes in light and prey depth regimes. Surprisingly, calls associated with Antarctic blue whale feeding were only recorded in autumn and not in mid-summer when whales are expected to feed maximally on their return to the feeding ground. However, it is possible that the D-calls of whales feeding further south at the ice edge at this time of year were not detected. Wind speed, time of the day, distance to the sea ice extent, sea ice concentration, time of the day, sea surface height and sea surface temperature were influential predictors of Antarctic blue and fin whale behaviour and occurrence. This work highlights the Maud Rise as a potential important habitat of blue and fin whales.

The understanding of Antarctic blue and fin whale *in situ* seasonal occurrence and acoustic behaviour provides essential information on species distributional range, migration, seasonality, area use, and response to environmental change. For the highly migratory Antarctic blue and fin whale species, such information is very important for monitoring the recovery of these species and for protecting their important habitats. The emergent knowledge produced in this entire thesis on the acoustic behaviour, environmental and habitat preferences of Antarctic blue and fin whales is pivotal in improving the management and conservation of these highly-depleted species.

7.2 Future work

Work presented herein showcases the advantages of using passive acoustic monitoring in conjunction with environmental data to model the effects of environmental variability on Antarctic blue and fin whale ecology in the Antarctic and South Africa. Long term collection of acoustic data at multi-decadal scale in the low and high latitudes will enable the tracking of the vocalising frequency evolution of these whales in relation to the forecasted climate change (Gavrilov *et al.* 2012; Širović, 2016; Chapter Four). Recording of acoustic data in an array series of moorings is recommended for tracking individual whales and to identify whale migration corridors; such information will also identify preferred whale habitats and also allow for the estimation of whale density/abundance (Kyhn *et al.* 2012; Thomas and Marques, 2012; Jacobson *et al.* 2017). Continuation of passive data recording in the low latitude off the South African coast is critical in producing more knowledge about these whales' migration, overwintering, mating and calving behaviours as those are poorly understood due to lack of research effort. Performing simultaneous sighting surveys at acoustic stations could also generate knowledge about the behaviour of both vocally active and inactive whales (Kyhn *et al.* 2012), although these are costly and weather condition dependent.

The demultiplexing of the DIFAR signals from the IWC SOWER acoustic data will consequently enable the tracking of individual whales relative to the research vessel for density estimation and furthermore the acoustic response of whales to vessel presence can be described (Rankin *et al.* 2005; Miller *et al.* 2016). After such demultiplexing, detection ranges of Antarctic blue and fin whales to the recorder can be estimated (Miller *et al.* 2013). Information on environmental conditions of the whole water column measured by instruments on oceanographic moorings where passive acoustic recorders are attached can be essential in quantifying the effects of environmental conditions on the propagation of whale sound. The effects of anthropogenic noise on the call behaviour of Antarctic blue and fin whales remain to be quantified, especially in the low latitudes where ship traffic and other human acoustics uses such as seismic surveys of oil and gas deposits are high (e.g., Monaco *et al.* 2016; Schreier *et al.* 2007). The extent of anthropogenic noise increase in the preferred areas of Antarctic blue and fin whales can be determined from historical acoustic data.

Passive acoustic monitoring can be extended to studies on other marine mammals occurring in South African waters including humpback whales, southern right whales, Bryde's whales, and dolphins. In particular, passive acoustic monitoring on shipboard surveys, moorings, or autonomous underwater vehicles such as gliders and sail drones can greatly enhance our understanding of the biology and ecology of these species. Used in conjunction with other new technologies such as remote sensing, satellite tagging, dive telemetry, video and digital acoustic recording tags (DTAGs), can be instrumental in producing new knowledge about responses of Antarctic blue and fin whales to environment related challenges and threats (e.g., Iwakami *et al.* 2002; Doksæter *et al.* 2009; Hodgson *et al.* 2013; Baumgartner *et al.* 2014; McKenna *et al.* 2015; Citta *et al.* 2017; Goldbogen *et al.* 2017). This thesis advances the methodology of passive acoustic monitoring from autonomous acoustic recorders on moorings; a methodology that can be extended from Antarctic blue and fin whales to other baleen whales in South Africa and elsewhere.

7.3 References

Baumgartner, M.F., Stafford, K.M., Winsor, P., Statscewich, H., and Fratantoni, D.M. 2014. Glider-Based Passive Acoustic Monitoring in the Arctic. Marine Technology Society Journal 48(5): 40–51.

Best, P.B. 1998. Blue whales off Namibia - a possible wintering ground for the Antarctic population. Paper SC/50/CAWS14 presented to the IWC Scientific Committee, April 1998, Muscat, Oman, p 10.

Buchan, S.J., Hucke-Gaete, R., Rendell, L. and Stafford, K. 2014. A new song recorded from blue whales in the Corcovado Gulf, Southern Chile, and an acoustic link to the Eastern Tropical Pacific. Endangered Species Research 23: 241–252.

Citta, J.J., Richard, P., Lowry, L.F., O'Corry-Crowe, G., Marcoux, M., Suydam, R., Quakenbush, L.T., Hobbs, R.C., Litovka, D.I., Frost, K.J., Gray, T., Orr, J., Tinker, B., Aderman, H., and Druckenmiller, M.L. 2017. Satellite telemetry reveals population specific winter ranges of beluga whales in the Bering Sea. Marine Mammal Science 33: 236–250. doi: 10.1111/mms.12357.

Doksæter, L., Godø, O. R., Olsen, E., Nøttestad, L., and Patel, R. 2009. Ecological studies of marine mammals using a seabed-mounted echosounder. ICES Journal of Marine Science, 66: 1029–1036.

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

Goldbogen, J.A., Cade, D., Calambokidis, J., Friedlaender, A.S., Potvin, J., Segre, P.S., and Werth, A.J. 2017. How baleen whales feed: The biomechanics of engulfment and filtration. Annual Review of Marine Science 9:11.1–11.20.

Hodgson, A., Kelly, N., and Peel, D. 2013. Unmanned Aerial Vehicles (UAVs) for Surveying Marine Fauna: A Dugong Case Study. PLoS ONE 8(11): e79556. doi:10.1371/journal.pone.0079556.

Iwakami, H., Ura, T., Asakawa, K., Fujii, T., Nose, Y., Kojima, J., Shirasaki, Y., Asai, T., Uchida, S., Higashi, N., Fukuchi, T. 2002. Approaching whales by autonomous underwater vehicle. Marine Technology Society Journal 36(1): 80–85.

Jacobson, E.K., Forney, K.A., and Barlow, J. 2017. Using paired visual and passive acoustic surveys to estimate passive acoustic detection parameters for harbor porpoise abundance estimates. Journal of the Acoustical Society of America 141 (1): 219–230.

Kyhn, L.A., Tougaard, J., Thomas, L., Duve, L.R., Steinback, J., Amundin, M., Desportes, G. and Teilmann, J. 2012. From echolocation clicks to animal density – Acoustic sampling of harbour porpoises with static dataloggers. The Journal of the Acoustical Society of America 131: 550–560.

McKenna, M.F., Calambokidis, J., Oleson, E.M., Laist, D.W., and Goldbogen, J.A. 2015. Simultaneous tracking of blue whales and large ships demonstrates limited behavioral responses for avoiding collision. Endangered Species Research 27: 219–232.

Miller, B.S., Barlow, J., Calderan, S., Collins, K., Leaper, R., Kelly, N., Peel, D., Olson, P., Ensor, P., and Double, M.C. 2013. Long-range acoustic tracking of Antarctic blue whales. Paper submitted for consideration by the IWC Scientific Committee SC/65/SH18.

Miller, B.S., Barlow, J., Calderan, S., Collins, K., Leaper, R., Olson, P., Ensor, P., Peel, D., Donnelly, D., Andrews-Goff, V., Olavarria, C., Owen, K., Rekdahl, M., Schmitt, N., Wadley, V., Gedamke, J., Gales, N., Double, M.C. 2015. Validating the reliability of passive acoustic localisation: a novel method for encountering rare and remote Antarctic blue whales. Endangered Species Research 26: 257–269.

Miller, B.S., Calderan, S., Gillespie, D., Weatherup, G., Leaper, R., Collins, K. and Double, M.C. 2016. Software for real-time localization of baleen whale calls using directional sonobuoys: A case study on Antarctic blue whales. Journal of the Acoustical Society of America 139(3): EL83–89.

Monaco, C., Ibáñez, J.M., Carrión, F., Tringali, L.M. 2016. Cetacean behavioral responses to noise exposure generated by seismic surveys: how to mitigate better? Annals of Geophysics 59(4): S0436. DOI:10.4401/ag-7089.

Rankin, S., Ljungblad, D., Clark, C., and Kato, H., 2005. Vocalizations of Antarctic blue whales, *Balaenoptera musculus intermedia*, recorded during the 2001/2002 and 2002/2003 IWC/SOWER circumpolar cruises, Area V, Antarctica. Journal of Cetacean Research and Management 7: 13–20.

Schreier, M., Mannstein, H., Eyring, V. and Bovensmann, H. 2007. Global ship track distribution and radiative forcing from 1 year of AATSR data. Geophysical Research Letters 34: L17814, doi:10.1029/2007GL030664.

Širović A. 2016. Variability in the performance of the spectrogram correlation detector for North-east Pacific blue whale calls. Bioacoustics 25(2): 145–160.

Thomas, L. and Marques, T.A. 2012. Passive acoustic monitoring for estimating animal density. Acoustics Today l8(3): 35–44.