UNIVERSITY of OTAGO

SAPERE AUDE

Te Whare Wānanga o Otāgo

NEW ZEALAND

Southern right whales (*Eubalaena australis*): acoustic behaviour and ambient noise

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A thesis submitted for the degree of Doctor of Philosophy

University of Otago, Dunedin, New Zealand

December 2014

Southern right whale (*Eubalaena australis*)
Auckland Islands, sub-Antarctic New Zealand

ABSTRACT

Anthropogenic noise in the ocean is steadily increasing as more industrial and recreational activities occur in coastal and offshore areas. Responses of marine mammals to noise vary widely, ranging from temporary behavioural change to permanent physiological damage.

For studies of responses to noise, passive acoustic monitoring offers the dual benefit of recording the noise, and an individuals' vocal response to it. To be maximally effective, it is first necessary to gather basic information about the whales' acoustic behaviour. Little is known about the vocal behaviour of southern right whales (SRWs, *Eubalaena australis*) in the sub-Antarctic Auckland Islands. This habitat is the major calving ground for this species in New Zealand waters. To describe the vocal repertoire, 4355 calls were classified into ten call types, including a *long tonal low* call (up to 25 s long) which had not been described previously. Random Forest multivariate analysis of 28 measured variables was used to classify calls with a high degree of accuracy (82%). The repertoire encompassed a range of tonal and pulsive sounds similar to those produced by other right whale populations.

For data on right whale presence, vocalisation rate and type, an autonomous recorder was moored at the Auckland Islands for a year. Recordings were made in each month except June, and SRW calls were audible in all months with recordings except January. A total of 35,487 calls was detected, of which *upcalls* were the most common (11,623) in all months and at all times of the day. Call rate was highest in August (288±5.9 [SE] calls/hour) and July (194±8.3). Vocalisation rates were highest at dusk and night, consistent with the idea that *upcalls* function primarily as contact calls. Seasonal variation was more important than diel variation for explaining differences in vocalisation rate. An automated detector designed for North Atlantic right whales (NARWs, *E. glacialis*) detected 80% of *upcalls,* but false detection rates were high, particularly when call rates were low.

To compare the acoustic environments used by NARWs and SRWs, a long-term statistical analysis of ambient noise was carried out at two calving sites in the Atlantic Ocean and one in the Southern Ocean. SRWs at the Auckland Islands were exposed to far lower levels of ambient noise than NARWs on their respective calving grounds. At low frequencies (40 Hz spectrum level) ambient noise was 20 to 30 dB re 1μPa^{2}/Hz higher in the North Atlantic. This may be reflective of high levels of shipping traffic near major ports in the Atlantic or of species differences.

A detailed comparative study of *upcalls* revealed that NARWs use significantly higher maximum, minimum and peak frequencies (40%, 30% and 9%, respectively) than SRWs. NARW calls were also longer, although this difference was less pronounced. *Upcalls* of the two species were easily discriminated via a random generalised linear model, with a very low misclassification rate (<0.01%). The differences in ambient noise levels and *upcall* characteristics support the evidence from the USA that noise has an important influence on the calling behaviour of right whales. Noise pollution could potentially be of consequence for SRWs in New Zealand, especially as they continue to re-colonise the mainland coast where anthropogenic noise is increasing.

ACKNOWLEDGEMENTS

A big thanks to my supervisors and advisors: Steve Dawson, Sofie Van Parijs, Susan Parks and Mike Paulin. I couldn't have done it without you. Steve, you finally wore me down and persuaded me to do a PhD. I'm super grateful and have loved every minute of it. A big thank you for all of your help and support throughout the duration of my research. Thank you Susan for your wise words and helpful tips. Sofie, you have been an amazing adviser, supporter and general cheerleader. Thank you so much for supporting my trips out to the states and generally being awesome.

These generous funders made this project possible - the University of Otago, Foundation for Research Science and Technology, Otago Museum, National Oceanic and Atmospheric Administration, Department of Conservation and the New Zealand Whale and Dolphin Trust. Thanks again to Otago University for my PhD scholarship, without which I would have been unable to do this research. Thanks also to Emma Burns, Ellen Sima, Clare Wilson, Cody Fraser, Robert Morris, Kane Fleury, Ian Griffin and the wider CRE team for supporting my research and being a great team to work with at the museum.

Thanks to the fantastic NOAA staff at my second home in Woods Hole - Danielle Cholewiak, Denise Risch, Sofie, Peter Corkeron, Genevieve Davis, Samara Haver, Keith Hernandez, the aerial survey crew (Tim, Pete and Allison), and everyone else at the office. You were all so welcoming, sharing your lab space and knowledge, giving advice on analysis techniques and general inspiration, and inviting me to parties. Marie Martin you kept me entertained and smiling throughout my time at Woods Hole. A big thanks to Gen for pulling out upcall after upcall, and being a superstar. Thanks to my awesome friend Denise Risch, you are so special to me, thanks for sharing your home and for all of your amazing support and kindness. We have had some super fun times and chatted long into the night on many occasions. Dani you have been an amazing mentor and friend over the last couple of years and it's been a pleasure to work with you and get to know you. And a big thank you to Melissa Soldevilla who kindly let me use the data that she collected off the Florida and Georgia coastline. I'm looking forward to working with you all again in the future!

A huge thank you to Will Rayment who superbly organised and led the expeditions to the Auckland Islands. Without him the trips to the sub-Antarctic would not have happened. You have been a logistical champion, permit king, acoustic assistant extraordinaire and general sorter of all things fieldwork. Thanks to Simon Childerhouse for giving me the opportunity in 2008 to go on an amazing expedition down to the Auckland Islands with an awesome team of people.

The crew of the Polaris (Bill Dickson, Steve Little, Phil Heseltine, Evan Kenton, Steve King, Sophie Fern, Tim Lever and Steve Bradley) worked tirelessly and took us down to the Auckland Islands and got us back safely many times in often testing conditions. Thanks for your support during the field seasons, becoming masters of deployment and recovery and for feeding us all.

Thanks to everyone that helped with the acoustics propagation experiment – Steve, Billy, Tim Lever, Tim "I'm going to get my dickie out" Cole and Ant "s in your panthony" Davidson. I enjoyed sharing the expeditions down to the Auckland Islands with other members of the research team – Helen McConnell, Chris Lalas, Hiltrun Ratz, Dave Buckton, Lucy Rowe, Liz Slooten, Kath Blakemore and Richard Kinsey. Thanks for the encouragement when equipment worked, consolation when didn't, cups of coffee and endless chats - particularly when I was up at all hours of the night.

The Marine Science Department has supported me throughout my time at Otago but thanks especially to Abigail Smith, Chris Fitz, Daryl "Steve" Coup, Pete Russell, Bev Dickson, JA and Gary Wilson. Thanks also to AJ at the research and enterprise office.

Staff at the Department of Conservation have been particularly helpful with permits, quarantine procedures and deploying acoustic recorders, including Pete McLelland, Doug Veint, Gilly Adam, Jo Hiscock, Ros Cole, Kath Blakemore, Rich Kinsey, Pete Young and Hannah Edmonds. David Mann provided advice and assistance with acoustic recorders at all stages and supplied new equipment at short notice when equipment failed. Glen Rowe from Land Information New Zealand provided essential data on nautical twilight, sunrise and sunset times.

Thanks to the research group at the Defence Evaluation and Research Agency in the UK (Tony Heathershaw, Sam Healey, Ed Harland, Peter Ward, Graham Smith, Antoine David, Roland Rogers, Peter Varley, Steve Parvin, John Carney and Liz Clement) for igniting my passion for marine mammals and sound.

Thanks to all my friends near and far – you are all amazing and very special to me. Many of you I see rarely but I think about you often. I'm looking forward to future visits – Stock and Knox, Niff and Polo, the mighty Thomos, Sarah and Alex, Andrea and Kenko, Chaz and Romy, Fabienne, Liz D, Hoot and Niamh, Skip and Baker, Dan and Laino, Greig and Sarah, Sioban, Nina and Liz B. Thanks to Dunedin friends old and new – I can't wait to spend more quality time with you - Sam and Becs, Les and Pablo, Rik and Kel, Lu and Joel, Jo and Karl, Tash and Matt, Katie and Shaun, Lucy and Tim, Derek and Buzzy, Kalinka and Graham, Amy and Arnie, Anna and Mike, Andrew and Brig, Holly and Toby - if I've forgotten you a thousand apologies, it's not because I don't care, but because my thesis ate my brain. The finest marine mammal and marine science research group and possibly the best beer and chip posse in the land – Madda, Liz, Steve, Wilhelm, Olga, Claudia, Mel, Stefan, Tom, Marta, Tracey, Nath, Shaun, Kane, Desmo, Emma, Peri, Jordan, Brenton and Ant. In particular thanks to Olga, Madda, Amy and Katie for going the extra mile, keeping me fed, coffee'd and relatively sane through the final few weeks. And never forget Olga -"the happy fox loves you". Will's family have been hugely supportive and encouraging at all stages of this epic journey and I look forward to seeing you all and celebrating! Bring on the bubbles – "oh go on then"!

And finally Will, I've thanked you a million times already, but you've been amazing and super supportive over a crazy few years. I could not and would not have wanted to do it without you!

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LIST OF ABBREVIATIONS

AIC	Akaike’s Information Criterion
ANN	Artificial Neural Network
BOF	Bay Of Fundy
CART	Classification And Regression Trees
CCB	Cape Cod Bay
dB	deciBel
DFA	Discriminant Function Analysis
DOC	Department Of Conservation (New Zealand)
DSG	Digital SpectroGram
ECDF	Empirical Cumulative Distribution Function
FFT	Fast Fourier Transform
FN	False Negative
FP	False Positive
FPR	False Positive Rate
FRMS	Frequency Root Mean Square
GLM	Generalised Linear Model
GPS	Global Positioning System
Hz	Hertz
IQR	Inter-Quartile Range
kHz	kiloHertz
LINZ	Land Information New Zealand
LOOCV	Leave One Out Cross Validation
MARU	Marine Autonomous Recording Unit
µPa	microPascal
NARW	North Atlantic right whale
NOAA	National Oceanic and Atmospheric Administration (United States of America)
NPRW	North Pacific right whale
NPV	Negative Predictive Value
OOB	Out-of-bag

PAM	Passive Acoustic Monitoring
PCA	Principal Components Analysis
PFC	Peak Frequency Contour
PPV	Positive Predictive Value
RF	Random Forest
RGLM	Random Generalised Linear Model
SD	Standard Deviation
SE	Standard Error
SNR	Signal to Noise Ratio
SRW	Southern Right Whale
SVM	Support Vector Machines
TN	True Negative
TP	True Positive
TPR	True Positive Rate
XBAT	eXtensible BioAcoustic Tool
ZIM	Zero Inflated Model

CHAPTER 1

GENERAL INTRODUCTION

Communication is fundamental for all social animals and forms the basis of any interaction between individuals. Acoustic communication is important across a diverse range of taxa; including birds (Polaki and Kaspryzykowski 2010), insects (Nakano et al. 2006), mammals (McComb et al. 2000; Fenton et al. 2004), amphibians (Shen et al. 2011), reptiles (Manly and Kraus 2010) and fish (Finstad and Nordeide 2004). Communication through tactile methods (e.g. licking, Laister et al. 2011; grooming, Cooper and Bernstein 2000; kicking, Langbauer 2000) and some visual means (e.g. gestures, Pika et al. 2003; facial expressions, Schilder et al. 2010) requires close proximity to be effective. Chemical communication via pheromones (Bauer 2011) and scent marking (Arakawa et al. 2008) and some visual methods, for example bioluminescence (Takatsu et al. 2012), can be successful over greater distances. Sound, however, allows long-distance communication as calls can be detected to ranges of tens or even hundreds of kilometres for some species (Payne and Webb 1971; McComb et al. 2003).

1.1 Vocal communication

Vocal communication is extremely versatile; it can be used day and night and does not require the sender or receiver to be visible. Vocalisations can be learned (Janik and Slater 2000; Beecher and Brenowitz 2005) and are used in a variety of social contexts to fulfil a diverse range of functions, including; group or individual recognition (Dentressangle et al. 2012); coordination and cohesion of group behaviour (Vergne et al. 2009); mate attraction, advertisement or competition (Byers et al. 2009) and predator warning (Zuberbühler 2001). In addition to *intentional communication*, sound can also be used passively via *eavesdropping* - by an individual using sound emitted by others to gather information about conspecifics, prey, predators or competitors (Barclay 1982; Dawson 1991; Naguib et al. 2004; Gregg et al. 2007). Additionally, a remarkable diversity of mammals (odontocetes, bats and shrews) and birds (oilbirds and cave swiftlets) use sound for echolocation which provides key information enabling individuals to navigate accurately and forage (e.g. Price et al. 2004; Jones 2009).

Sound is especially important for communication in many aquatic animals as light rapidly attenuates in water rendering visual signals of limited use (e.g. Southall and Nowacek 2009). In the marine environment communication via sound has been observed in fish (Finstad and Nordeide 2004; Kasumyan 2009), crustaceans (Patek and Caldwell 2006), pinnipeds (Bartholomew and Collias 1962), cetaceans (Payne and McVay 1971; Watkins and Schevill 1977) and sirenians (Schevill and Watkins 1965). Cetaceans are typically extremely vocal (Whitehead and Weilgart 1990; Akamatsu et al. 2005); although vocalisation rates vary with species, behaviour, location and group structure. That sound appears to be of paramount importance in cetacean sensory systems indicates that acoustic research has a valuable role in understanding the behaviour and ecology of whales, dolphins and porpoises.

1.2 Sound in the marine environment

Sound is the primary mode of communication for cetaceans due to the excellent acoustic transmission properties of water. Visibility in seawater is limited to *c.* 100 m in the clearest surface waters, but is typically much less, whilst sound is transmitted extremely effectively, especially at relatively low frequencies (<10 kHz).

The vocalisations used by marine mammals are highly diverse; varying in frequency composition, source level, directionality and duration (Richardson et al. 1995). The detection range of a call is influenced by these variables as well as the physical characteristics of the water and underwater environment (including temperature, salinity, stratification, depth and seabed type). Sound absorption, for example, is highly frequency-dependent and greater losses are evident at higher frequencies. Due to high attenuation losses, high frequency sounds are transmitted over shorter distances (e.g. less than 500 m for ultrasonic sounds, >100 kHz, of Hector's dolphin, *Cephalorhychus hectori,* Rayment et al. 2009). In contrast, the larger baleen whales produce low frequency calls which can be detected over distances of hundreds of kilometres (e.g. infrasonic sounds, <20 Hz, of blue whales, *Balaenoptera musculus,* Širović et al. 2007).

In the ocean, natural ambient noise has many sources (Wenz 1962; Urick 1983), including abiotic noises (e.g. rain, surf, sea ice, lightning strikes) and biological noises (e.g. fish, cetaceans and other marine animals). Noise pollution relates specifically to anthropogenic noise, which can be either intentional (e.g. seismic exploration, geo-physical surveys, sonar) or a by-product of other activities (e.g. shipping, drilling, dredging, pipe-laying, recreation). Anthropogenic noise is of concern both in the water (Nowacek et al. 2007; Weilgart 2007; Clark et al. 2009) and in the air (Patricelli and Blickley 2006; Parris et al. 2009). Noise pollution is gaining attention as its level in the ocean increases (e.g. Andrew et al. 2002; McDonald et al. 2006) and its impacts become increasingly apparent. The impacts of ocean noise have been observed not only in marine mammals (Nowacek et al. 2007), but also fish (Slabbekoorn et al. 2010; Radford et al. 2014) and cephalopods (André et al. 2011). Anthropogenic underwater noise has recently been classified by the European Commission as a pollutant under the Marine Strategy Framework Directive (Law et al. 2010), highlighting it as an area of concern.

1.3 The impact of anthropogenic sound

Anthropogenic noise affects animals in a variety of ways depending on the hearing sensitivity of the species (or individual), received sound exposure level, frequency and type of noise, and the behavioural context at the time of exposure. Acoustic disturbance may result in masking - in which noise conceals the communication signals of individuals (Lohr et al. 2003; Barber et al. 2010). Masking is often difficult to quantify and its effects difficult to assess, but it is increasingly perceived as a threat. In the terrestrial environment, masking due to urban noise has been observed for many species of birds (e.g. Slabbekoorn and Peet 2003), amphibians (e.g. Parris et al. 2009) and insects (Samarra et al. 2009). In the marine environment, masking is increasingly an issue, in particular for baleen whales because of an increase in low frequency shipping noise (Clark et al. 2009).

An individual's physical response to noise typically falls into one (or more) of three categories: behavioural, acoustic or physiological (Nowacek et al. 2007). Sound may evoke a behavioural response including a change in direction, avoidance of a particular area or a change in activity (e.g. Richardson and Würsig 1997). Acoustic reactions may include a change in vocalisation rate, type, amplitude or duration (e.g. Miller et al. 2000). Physiological responses include a temporary or permanent auditory threshold shift, stress, damage to hearing mechanism or tissue shear (Popper 2003; Smith et al. 2004). Chronic noise exposure is associated with increased levels of stress hormones in various taxa including marine and freshwater fish (Sverdrup et al. 1994; Santulli et al. 1999; Wysocki et al. 2006) and giant pandas (*Ailuropoda melanoleuca*), particularly for females during oestrus and lactation (Owen et al. 2004). Responses may also interact, for example a change in diving behaviour (behavioural response) may result in gas bubbles forming in tissue (a physiological response) (Houser et al. 2001; Hooker et al. 2009). The significance of these responses is typically unclear, and it is often difficult to measure the impact of noise on an individual or population (Richardson et al. 1995). This does not imply that important impacts do not occur. Cumulative impacts from repeated noise exposure or combined noise exposure and other stressors further confuse the picture.

1.4 Right whales

Right whales are large, robust mysticetes reaching up to 18 m long and 100 tonnes (Kenney 2009). They are filter feeders, sieving dense aggregations of zooplankton including copepods (*Calanus* sp., *Pseudocalanus* sp., *Centropages* sp.), krill (*Euphausia superba*) and munida (*Munida gregaria*) through fine baleen plates (Matthews 1932; Hamner et al. 1988; Wishner et al. 1988). Genetic research has identified three species of right whale (Rosenbaum 2000); the North Atlantic right whale (NARW, *Eubalaena glacialis*), the North Pacific right whale (NPRW, *Eubalaena japonica*) and the southern right whale (SRW, *Eubalaena australis*). All three species suffered extensive commercial whaling in the 1800s and early 1900s (Dawbin 1986; Scarff 2001; Richards 2009).

Whales in the *Eubalaena* genus were traditionally the "right whale to hunt" (hence the name) as they swim slowly, float when dead, have high oil and whalebone yield and were easily accessible due to their coastal distribution.

NARWs are now limited to coastal waters of the Atlantic coast of the USA and Canada, with very occasional sightings along the coastline of Europe in the eastern Atlantic (Jacobsen et al. 2003). Two remnant populations of NPRWs are thought to exist in the northern Pacific; the eastern population in the Bering Sea and Gulf of Alaska, and the western population in the Sea of Okhotsk (Brownell et al. 2001). SRWs are split into several populations in the southern hemisphere with major breeding centres off South Africa (Best 1990), Argentina (Payne et al. 1990), Brazil (Castello and Pinedo 1979), Australia (Bannister 2001) and the Auckland Islands in sub-Antarctic New Zealand (Richards 2002). There is at least some interchange of individuals among these breeding sites (Best et al. 1993; Pirzl et al. 2009). Right whales occur at temperate and sub-polar latitudes, but all three species migrate annually, moving between separate feeding and calving grounds. The higher-latitude feeding grounds are relatively well known for NARWs (Winn et al. 1986) but poorly known for NPRWs and SRWs.

NARWs are classified as *critically endangered* (IUCN 2012) and are functionally extinct in the eastern north Atlantic (Jacobsen et al. 2003). Only about 400 individuals remain in the west (Kraus and Rolland 2007). Despite their less urgent *endangered* status, it is likely that NPRWs (IUCN 2012) are even rarer than NARWs (Kenney 2009). Abundance estimates for the eastern population in the Bering Sea are extremely low (Photo-ID: n = 31, 95% CI 23-54; genetics: n = 28, 95% CI is 24-42, Wade et al. 2010). The SRW is the most abundant of the three right whale species despite the fact that 150,000 individuals were killed worldwide during the 19th and early 20th centuries (Dawbin 1986; Tormosov et al. 1998). Southern hemisphere populations are now showing strong rates of increase in some locations and consequently their IUCN status has been reviewed and downgraded to *least concern* (Reilly et al. 2008).

Long-term recognition of individual right whales using photo-identification (Payne et al. 1983; Kraus et al. 1986a) has provided much of what is known about migration, age at maturity, inter-calf interval, survival rates, population size and population trajectory (e.g. Payne et al. 1990; Fujiwara and Caswell 2001; Kraus et al. 2001). All three species are very long-lived; the oldest known individual is a NARW of at least 70 years old (Kenney 2009). Mean annual calving interval has been estimated at approximately 3 years and females are thought to reach maturity at eight or nine years old (Best et al. 2001; Kraus and Rolland 2007).

The coastal distribution of right whales means that the overlap with anthropogenic activities is high. Entanglement in fishing gear and collision with ships (Knowlton and Kraus 2001; Parks et al. 2012a) are the major source of a continuing population decline for NARWs (Caswell et al. 1999; Kraus et al. 2005). Nineteen reliably documented ship strike deaths of NARW occurred between 1986 and 2005 (Kraus et al. 2005) and 75% of NARWs alive today bear obvious entanglement scars (Knowlton et al. 2005). Other threats likely have a cumulative impact upon right whales, including noise, (e.g. from oil and gas exploration, mining, military activities, shipping and recreation), habitat degradation and loss, climate change and pollution.

1.5 Southern right whales in New Zealand

The SRW (or Tohorā) was once common around mainland New Zealand but was hunted to the brink of extinction in the early 19th century (Richards 2009). In New Zealand, pelagic offshore whaling was concentrated in areas south-east of the Kermadec Ridge, on the Chatham Rise and around the sub-Antarctic Campbell Island and Auckland Islands (Figure 1.1). The majority of inshore coastal whaling occurred in sheltered bays along the east coast of New Zealand (Figure 1.1). Whalers targeted mothers with young calves in these inshore winter calving areas. Hunting peaked in the 1830s, leading to commercial extinction within two decades (Dawbin 1986). Opportunistic hunting continued for many years until legal protection was introduced in 1935. However, illegal Soviet whaling continued around the Auckland Islands killing a further 294 SRWs in the 1960s (Tormosov et al. 1998; Carroll et al. 2014).

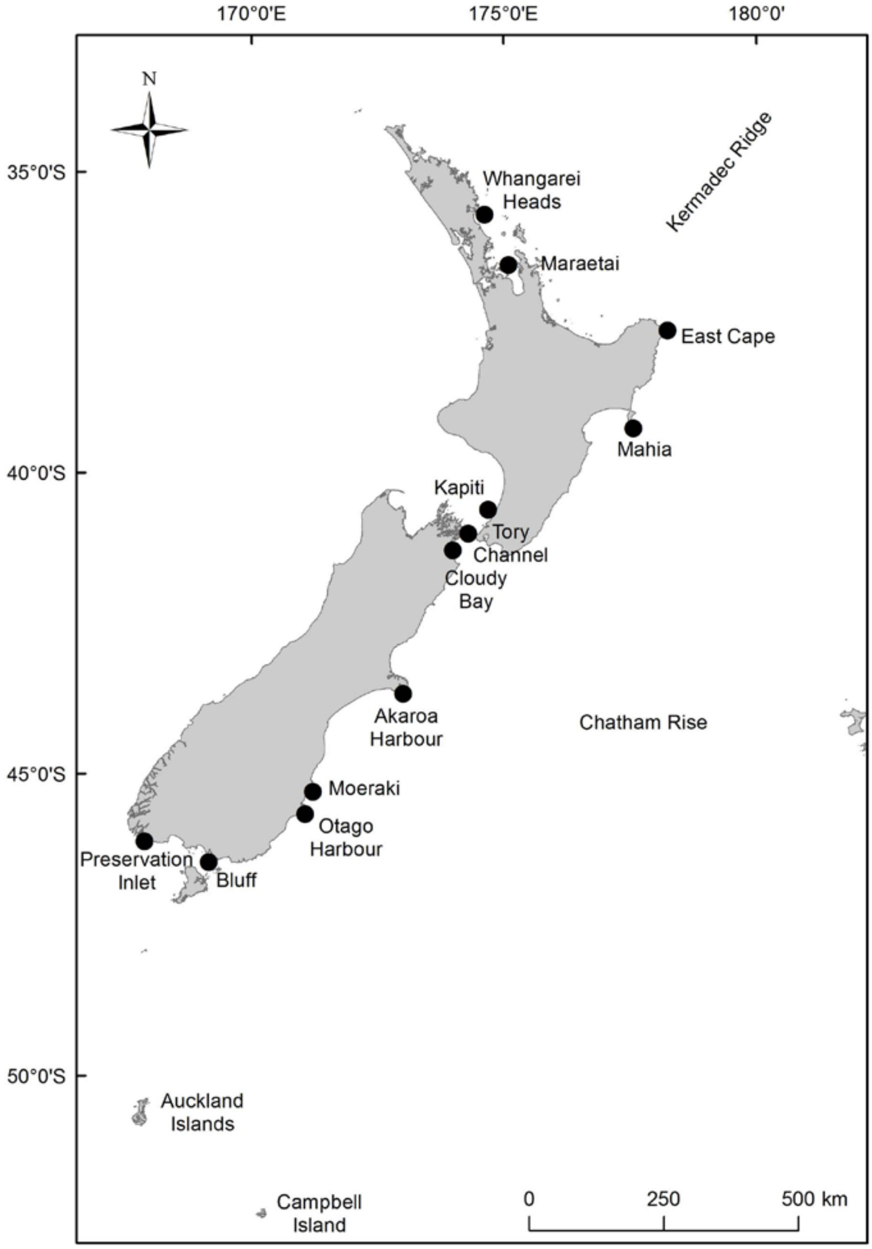


Figure 1.1. Key places in the history of right whales in New Zealand, including major shore whaling stations (Preservation Inlet, Otago, Moeraki, Akaroa, Cloudy Bay, Tory Channel, Kapiti, Mahia and East Cape), pelagic whaling regions (Chatham Rise and Kermadec Ridge), sub-Antarctic Auckland and Campbell Islands and the first four sightings of whales around the mainland after a 36 year gap (Bluff, Tory Channel, Maraetai and Whangarei Heads).

Following this extensive period of exploitation, there were no SRW sightings around mainland New Zealand for 36 years (Gaskin 1964). Finally in 1963 there were four sightings; one in Tory Channel (Marlborough Sounds), one near Bluff (Southland), one off Maraetai (near Auckland) and a mother-calf pair seen near Whangarei Heads (Northland) (Gaskin 1964; Figure 1.1). Small numbers of whales continued to be sighted at Campbell Island in Perseverance Harbour and North West Bay; although it is likely that numbers there dwindled to fewer than 20 individuals post-World War 2 (Gaskin 1964). Opportunistic sightings by yachtsmen at the Auckland Islands in the 1980s prompted Royal New Zealand Air Force over-flights of the islands in 1992 and 1993 which resulted in 70 and 42 SRW observations, respectively (Donoghue 1995; Stewart and Todd 2001). Vessel-based research surveys in the 1990s observed that SRWs were wintering at the Auckland Islands (Patenaude et al. 1998).

Using a Bayesian logistic population model incorporating mark-recapture data, estimates of whaling catch, population growth rate estimates from conspecific populations and genetic data, Jackson et al. (2009) estimated the pre-whaling population size of SRWs in New Zealand waters at 27,000 (95% CI 22,000-32,000). The population dropped to a low of fewer than 100 whales in 1925 (Jackson et al. 2009). The most recent abundance estimate for SRWs in New Zealand is 2169 (95% CI: 1836-2563) with population growth rate estimated at approximately 7% (Carroll et al. 2013). This growth rate is similar to rates observed for other conspecific populations (7.1% off South Africa, Best et al. 2001; 7.6% in Argentina, Payne et al. 1990). SRWs are still considered *nationally endangered* under New Zealand’s threat classification system (Hitchmough et al. 2007) although recent sightings around mainland New Zealand suggest that SRWs are slowly recovering (Carroll et al. 2014).

The Auckland Islands lie 460 km south of mainland New Zealand at approximately 50°S (Figure 1.2). SRWs are known to congregate in the austral winter and spring to calve around these islands, particularly in Port Ross, a shallow, sheltered harbour at the northern tip of the Auckland Islands (Patenaude et al. 1998; Figure 1.3). The Auckland Islands are thought to be the primary calving grounds for SRWs in New Zealand waters (Patenaude et al. 1998) and it is likely that this remote location has been fundamental to the whales’ recovery post-whaling. In 2011, surveys along the east and south coasts of Auckland Island confirmed Port Ross as the primary wintering ground, and that no other significant calving habitats exist in the Auckland Islands (Rayment et al. 2012, Appendix A). Recently, genetic and photo-ID research has established links between SRWs around the Auckland Islands and those in coastal waters surrounding mainland New Zealand (Carroll et al. 2011; 2014); and between the sub-Antarctic and Australia (Pirzl et al. 2009).

Figure 1.2. Location of the main calving ground for southern right whales in New Zealand at Port Ross in the sub-Antarctic Auckland Islands.

1.6 Sounds made by right whales

As for most cetaceans, sound is of great importance to right whale communication. Despite this, systematic studies of SRW sounds exist across only part of their range; in

South America (Cummings et al. 1972; Clark 1980, 1982; Clark and Clark 1980) and South Africa (Hofmeyer-Juritz 2010). In comparison, the acoustic behaviour of the critically endangered NARW has been studied across most of its range due in part to the proximity of human population centres and thus researchers (e.g. Matthews et al. 2001; Vanderlaan et al. 2003; Parks et al. 2005; 2007; 2009; Van Parijs et al. 2009; Trygonis et al. 2013). Indeed, a book on NARWs was entitled “The Urban Whale” (Kraus and Rolland 2007). Acoustic studies of NPRWs have also been undertaken (e.g. McDonald and Moore 2002; Mellinger et al. 2004; Munger et al. 2008) because their exceptionally low numbers make surveys via visual observation challenging.

Right whales produce a wide range of pulsive and tonal vocalisations, but categorisation of their call types has been highly variable between studies. Unlike other baleen whales, such as humpback whales (*Megaptera novaeangliae*) (Payne and McVay 1971), fin whales (Croll et al. 2002) and bowhead whales (Stafford et al. 2008), right whales do not produce songs (Tyack and Clark 2000). The most well-known vocalisation is the *upcall*; a short stereotypical call with an upsweep in frequency, produced by males and females of all age-classes (Clark 1983; Parks and Tyack 2005). This call is typically employed for passive acoustic detection of right whales (Gillespie 2004; Urazghildiiev and Clark 2006) and is thought to function as a contact call (Clark 1982). Right whale vocalisations are low in frequency, with the majority of energy below 1 kHz (Clark 1983; Parks and Tyack 2005). Different call types have been associated with various behaviours (Clark 1983; Parks et al. 2005; Parks and Tyack 2005), strongly suggesting they have different meaning. For example, impulsive *gunshot* sounds are thought to be produced by males as a mating advertisement (Parks et al. 2005; 2012b), *screams* are made by females that are the focus of mating attention and *warble* sounds are produced by calves (Parks and Tyack 2005). To date there has been little research on acoustic behaviour of SRWs in New Zealand or indeed Australasian waters.

1.7 Thesis overview

Right whales in the North Atlantic and at the Auckland Islands live in strongly contrasting acoustic environments. The Auckland Islands are remote, uninhabited and are surrounded by a marine reserve; hence it is a comparatively pristine acoustic habitat with little anthropogenic noise. The North Atlantic is in close proximity to major human populations, major ports and major shipping lanes (Halpern et al. 2008; Kaluza et al. 2010) and thus are exposed to high levels of anthropogenic noise. The acoustic behaviour of NARWs is relatively well studied (e.g. Matthews et al. 2001; Vanderlaan et al. 2003; Parks and Tyack 2005; Parks et al. 2005; 2007; Mellinger et al. 2007a; Van Parijs et al. 2009; Parks et al. 2009; 2010; 2011; Morano et al. 2012; Mussoline et al. 2012; Trygonis et al. 2013; Matthews et al. 2014) whilst little is known about the acoustic behaviour of SRWs in New Zealand. NARWs share their habitat with several other baleen whale species and the humpback whale in particular uses similar calls which may be misidentified as right whale calls. No other cetacean species regularly use the Auckland Islands (Baker 1977) and thus vocalisations can be attributed to SRWs with certainty. NARWs have been shown to suffer impacts of anthropogenic noise and have changed the frequency, duration and amplitude of their calls (Parks et al. 2007; 2010) and exhibited elevated levels of stress hormones (Rolland et al. 2012) in response to noise. It is assumed that SRWs are minimally impacted by noise, at least in the vicinity of the Auckland Islands. This remote sub-Antarctic study site therefore offers a unique opportunity for comparative analyses between the NARW and SRW populations.

Currently there is nothing published on right whale vocalisations in New Zealand or wider Australasian waters. In chapter two I aim to quantitatively describe the vocal repertoire used by SRWs at the Auckland Islands. This is a necessary first step in attempting to understand the complexities of communication in any species. SRW vocalisations will be categorised using a multivariate statistical approach based on measured call characteristics.

Passive acoustic monitoring techniques enable cetaceans to be studied 24 hours a day in all weather conditions, and are particularly useful for remote locations which cannot be accessed regularly. Recent technological advances and increased capacity for data storage greatly facilitate long-term acoustic studies. Data from an autonomous bottom mounted recorder are used in chapter three for temporal analyses of acoustic behaviour to provide insights into the habitat use at the remote Auckland Islands.

Temporal variation is examined by looking at seasonal and diel patterns in SRW vocalisation rates and call types. Information pertaining to the acoustic repertoire and temporal changes will be important for future development of passive acoustic monitoring and detection systems.

In chapter four ambient noise is measured on right whale calving grounds in the North Atlantic and the Auckland Islands using calibrated recording systems. The major contributors to environmental noise are quantified and the potential for overlap with SRW vocalisations assessed. I hope that this will provide the perspective needed to understand the differences between a population inhabiting waters with very low levels of acoustic pollution and a population in an area with significant anthropogenic noise.

As outlined above, acoustic pollution is significant for right whales, especially given the observed changes in the vocal characteristics of NARWs due to acoustic pollution (Parks et al. 2007; 2009; 2010). In chapter five I undertake a statistical comparison of the contact call used on the calving grounds by SRWs and NARWs. Multiple call characteristics are measured before attempting to tease apart any differences and categorise the calls by population.

The appendices describe work that was undertaken at the same time and location as fieldwork for the acoustics research. This work underpins the acoustic work and although I am not first author on either paper, it is work that I was involved in. It has been included here to provide key background information about the distribution and habitat preferences of right whales at the Auckland Islands.

In summary, the aim of this thesis is to fully describe the vocal repertoire of southern right whales in New Zealand, including how call use changes with time of day and seasonally. The impacts of ambient noise on right whales and any differences in contact calls are addressed via a statistical comparison of the calls and ambient noise environments of two different calving grounds. I hope that this work complements research undertaken on right whales in other locations and adds to the increasing body of literature on the impact of ambient noise in the marine environment.

CHAPTER 2

QUANTITATIVE ANALYSIS OF THE ACOUSTIC REPERTOIRE OF SOUTHERN RIGHT WHALES

2.1 Introduction

The physical characteristics of water make it a very effective conductor of sound (Urick 1983). For this reason, sound has become the primary mode of communication for marine mammals (e.g. Caldwell and Caldwell 1965; Winn and Winn 1978; Weilgart and Whitehead 1993). Marine mammals produce many types of vocalisations; some are stereotypical sounds which are relatively easy to classify (e.g. sperm whale (*Physeter macrocephalus*) codas, Watkins and Schevill 1977), while others do not fall into well-defined categories. Classifying vocalisations quantitatively is a complex problem with a long history (Winter et al. 1966; Gerhardt 1974; Sparling and Williams 1978). Ensuring that the categories are biologically relevant is a further important challenge (Deecke and Janik 2005). The quantitative process of measuring call features and objectively categorising calls allows further investigation, such as correlating sounds to specific behaviours (Ford 1989; Van Parijs and Corkeron 2001) or comparative studies across geographical regions (Risch et al. 2007).

Classification of a species' repertoire is critical for establishing effective passive acoustic monitoring systems and automated detectors (Van Parijs et al. 2009). Describing the full repertoire of a species is particularly important for detection in areas where visual surveys are not practical due to the remote location or inclement conditions, or where significant conservation problems exist, for example, detecting whales that are prone to ship strike (Knowlton and Kraus 2001). Currently there is no robust standardised way of describing and quantifying sounds produced by right whales (*Eubalaena* sp.). There are also considerable inconsistencies in naming and classification conventions. The majority of acoustic studies on right whales have focussed on detection (Mellinger et al. 2004; Morano et al. 2012), acoustic behaviour (Clark and Clark 1980; Vanderlaan et al. 2003; Parks and Tyack 2005; Mellinger et al. 2007a), and temporal patterns (Munger et al. 2008; Mussoline et al. 2012; Matthews et al.

2014). Studies that have attempted to document the full acoustic repertoire of different right whale populations (Clark 1982, Parks and Tyack 2005, Hofmeyer-Juritz 2010, Trygonis et al. 2013) have often done so within very specific contexts (e.g. social interactions within surface active groups; Parks and Tyack 2005; Trygonis et al. 2013), restricting their generality.

Right whales are known to produce a wide range of sounds. In all cases the majority of the energy is below 1 kHz (Clark 1983; Parks and Tyack 2005). Qualitatively there are similarities in the vocal repertoire of right whales between regions (Table 2.1). The most well-known vocalisation, documented across the majority of studies (Clark 1982; McDonald and Moore 2002; Vanderlaan et al. 2003; Parks and Tyack 2005), is the *upcall*, a simple low-frequency tonal upsweep, thought to be used as a contact call (Clark 1982). *Gunshots,* referred to as *underwater slaps* by Clark (1982), are impulsive broadband sounds thought to be used by males to advertise to females and/or as an agonistic display to other males (Parks et al. 2005). These two vocalisations are consistently described across the literature (Clark 1982; Matthews et al. 2001; Parks et al. 2005; Rone et al. 2012) for all three species of right whale. The other calls made by right whales, however, have proven notoriously difficult to classify and are often combined into large groups for ease of analysis (e.g. Matthews et al. 2001; Parks et al. 2005). Similar problems have been encountered when categorising other mysticete calls (e.g. Clark and Johnson 1984; McDonald et al. 2005). Hence, the acoustic repertoire of right whales has often been described as a continuum of sounds (Payne and Payne 1971; Clark 1982).

Quantitative analysis of a species' vocal repertoire typically involves measurement of common acoustic characteristics based on frequency, duration and intensity (e.g. Winter et al. 1966). Multivariate statistical techniques, or more recently machine-learning, can then be employed to classify vocalisations into types based on relationships among the measured variables (e.g. Armitage and Ober 2010, Shamir et al. 2014). Classification is a complex task but efforts to describe and quantify repertoire are extremely valuable. A vast suite of techniques has been applied to acoustic classification including: Principal Component Analysis (PCA, e.g. Clark 1982), discriminant function analysis (DFA, Sparling and Williams 1978), cluster analysis (Rendell and Whitehead, 2003), artificial neural networks (ANN, e.g. Deecke et al. 1999), classification and regression trees (CART, e.g. Risch et al. 2007), and support vector machines (SVM, Armitage and Ober 2010). Random forest (RF) analysis (Breiman 2001) is a relatively new technique popular in medical and, in particular, genetic research (Shi et al. 2005; Díaz-Uriarte and Alvarez De Andres 2006; Ward et al. 2006). The technique has recently been employed to identify species using their acoustic signals (Briggs et al. 2012; Hannay et al. 2013), classify behaviour (Henderson et al. 2011) and to describe vocal repertoire (Risch et al. 2013). Comparisons of classification techniques have favoured RF over SVM, DFA, NN and ANN for its sensitivity, specificity, predictive power and its ability to train quickly and measure variable importance (Breiman 2001; Liaw and Wiener 2002; Armitage and Ober 2010). RF is a powerful machine-learning method which has the ability to model complex interactions among variables and measure error rate (Cutler et al. 2007). The model creates a series of classification trees which are not influenced by one another when constructed and are robust to over-fitting (Breiman 2001). CART models, a precursor to RF, have been used previously to classify North Atlantic right whale (NARW; *Eubalaena glacialis*) vocalisations (Trygonis et al. 2013). RF models provide additional benefits of unbiased error estimates, better stability and higher classification accuracy (Sirosky 2009).

Species	Location	Number of call types	Call types	Reference
North Atlantic right whale	Great South Channel, Cape Cod and Bay of Fundy	3	*Moan*, *gunshot*, *low frequency*	Matthews et al. 2001
	Bay of Fundy	4	*Upsweep*, *downsweep*, *lower frequency*, *higher frequency*	Vanderlaan et al. 2003
	Bay of Fundy	6	*Scream*, *gunshot*, *blow*, *upcall*, *warble*, *downcall*	Parks and Tyack 2005
	Bay of Fundy	4	*Upcall*, *exhalation*, *gunshot*, *variable tonal*	Parks et al. 2011
	Off Florida and Georgia, USA	9	*Upcall*, *downcall*, *upcall high*, *tonal low*, *constant*, *modulated*, *pulsive*, *hybrid*, *gunshot*. In addition a *foghorn* call (n=4) described but not analysed	Trygonis et al. 2013
North Pacific right whale	North Bering Sea	5	*Up*, *down-up*, *down*, *constant*, unclassified	McDonald and Moore 2002
	Gulf of Alaska	2	*Up* and *down*	Mellinger et al. 2004
Southern right whale	Argentina		A continuum of sounds	Payne and Payne 1971
	Argentina	5	*Belch*, *simple moan*, *complex moan*, *pulse*, miscellaneous phonations	Cummings et al. 1972
	Argentina	8	*Upcall*, *downcall*, *constant call*, *high call*, *hybrid call*, *pulsive call*, *blow*, *slap*.	Clark 1982, Clark 1983
	South Africa	14	*Up* (low, medium or high), *down* (low, medium or high), *flat* (low, medium or high), *variable* (low, medium or high), *gunshot* or *blow*. *Blow* later excluded	Hofmeyer-Juritz 2010

Table 2.1 Classification of vocalisations from various studies of right whale call repertoire.

The major objective of this study was to quantitatively describe the entire acoustic repertoire of southern right whales (SRWs; *Eubalaena australis*) at the Auckland Islands, sub-Antarctic New Zealand. To date, there has been no published research on the vocal repertoire of right whales from New Zealand waters or the wider Australasian region. These islands constitute a major calving ground for right whales where mother-calf pairs, other adults and juveniles are found together in one area during the austral winter (Patenaude et al. 1998). The

Auckland Islands are an ideal location for the acoustic study of right whales; they are the only cetacean species typically present (Baker 1977), so vocalisations can be readily assigned without fear of misidentification. Further, anthropogenic noise is minimal, so the acoustic environment is near pristine. The characterisation of SRW signals will enable classification of the vocal repertoire and provide essential information for developing passive acoustic monitoring and detection systems.

2.2 Methods

Data collection

Acoustic recordings were made at the sub-Antarctic Auckland Islands approximately 460 km south of mainland New Zealand (50°42'S, 166°6'E, Figure 2.1). During seasonal visits in July and August (austral winter) SRWs are at peak abundance (Patenaude 2000). To ensure that a large sample of individuals were recorded, data were collected at various times of the day/night during a 17 day period in 2010 (30 July to 16 August), 19 days in 2011 (21 July to 9 August) and 21 days in 2012 (26 July to 16 August) (Appendix C). Recordings were made whenever acoustic conditions were favourable (i.e. low wind and rain noise and minimal generator or engine noise). Recordings were made in areas where SRW densities were high, in sheltered locations throughout Port Ross, a large relatively shallow harbour at the northern end of main Auckland Island (Patenaude et al. 1998; Rayment et al. 2012, Appendix A). Specific recording locations within Port Ross included Erebus Cove, Laurie Harbour, Terror Cove, Deas Head, Sandy Bay and off Shoe Island (Figure 2.1).

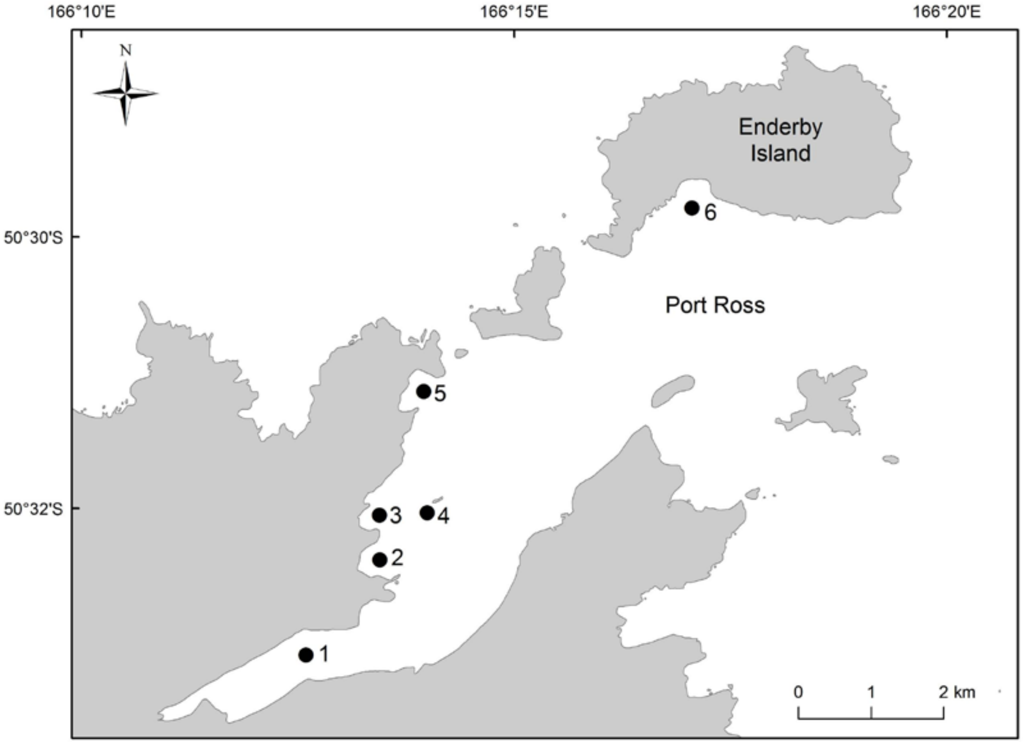


Figure 2.1: Approximate locations (marked with a numbered black dot) for recordings of southern right whale vocalisations in Port Ross, sub-Antarctic Auckland Islands. 1 = Laurie Harbour, 2 = Erebus Cove, 3 = Terror Cove, 4 = Shoe Island, 5 = Deas Head, 6 = Sandy Bay.

Acoustic recordings were made with calibrated hydrophones suspended about 4 m beneath a stationary vessel. In 2010, a Sonatech 8178 hydrophone was used (sensitivity: -173 dB re 1V/µPa; frequency response: 30 Hz – 10 kHz ± 3 dB), and in 2011 and 2012 a Reson TC-4032 was used (sensitivity: -164.7 dB re 1V/µPa, frequency response: 15 Hz – 40 kHz ± 2 dB). Vocalisations were recorded onto an Edirol-R4 digital recorder (16 bit, 40 Gb hard-drive) at a sampling rate of 48 kHz.

Measurement of vocalisations

Right whale vocalisations were examined using the sound analysis software Raven Pro version 1.5 (Bioacoustics Research Program, Cornell University, www.birds.cornell.edu) and Osprey (Mellinger 1994), a freely available Matlab (The MathWorks Inc., Natick, MA) toolbox for spectrographic analysis of bio-acoustic signals. Sounds were analysed at the original sampling rate of 48 kHz via Fast Fourier Transform (FFT: 2048 points, Hamming window, 75% overlap) producing a spectrogram with 5.86 Hz frequency resolution and 10.7 ms time resolution. No filters were applied to the acoustic data.

Recordings were browsed manually in Raven and individual vocalisations were selected by drawing a border around the fundamental frequency. Any vocalisations that were not clearly visible on the spectrogram or that overlapped with calls from other individuals were excluded from the analysis. I measured 28 different call features relating to the frequency, duration and entropy of each vocalisation (Table 2.2). All of the variables except four were standard output parameters within Raven software (Charif et al. 2010) and were automatically extracted. The four additional measurements (start frequency f_1, end frequency f_2, start minus end frequency $f_1 - f_2$ and maximum harmonic f_{harm}) were calculated and added as annotations within Raven (Table 2.2). To calculate start and end frequencies for pulsive sounds, frequencies were measured from the peak frequency contour in Raven at the start and end of the call. Maximum harmonic (f_{harm}) was measured across the full spectrum of the call. The other measurements focused on the fundamental frequency.

Parameter	Units	Description
High frequency (f_{max})	Hz	The upper frequency limit of the annotation box.
Low frequency (f_{min})	Hz	The lower frequency limit of the annotation box.
Start (f_1) and end frequency (f_2) *	Hz	The frequency measurement at the start and end of the call.
Start minus end frequency (f_1- f_2)*	Hz	Total bandwidth, calculated by start frequency minus end frequency.
Delta frequency (Δf)	Hz	Total bandwidth, calculated by high frequency (f_{max}) minus low frequency (f_{min}) as defined by the limits of the annotation box.
Delta time (Δt)	s	Total duration, calculated by end time (t_{max}) minus start time (t_{min}).
Peak frequency (f_{peak})	Hz	The frequency at which peak power occurs within the selection.
Centre frequency (f_c)	Hz	Frequency that divides the selection into two frequency intervals of equal energy.
1st quartile ($f_{25\%}$), and 3rd quartile frequencies ($f_{75\%}$)	Hz	The frequencies that divides the selection into two frequency intervals containing 25% and 75% of the energy in the selection, where the summed energy exceeds 25% and 75% of the total energy, respectively.
Inter-quartile bandwidth (B_{IQR})	Hz	The difference between $f_{25\%}$ and $f_{75\%}$.
Inter-quartile duration (t_{IQR})	s	The difference between the two points in time that divide the selection into two time intervals containing 75% (t_{75}) and 25% (t_{25}) of the energy in the selection, i.e. t_{75} minus $t_{25.}$
Frequency 5% ($f_{5\%}$), frequency 95% ($f_{95\%}$)	Hz	The frequency that divides the selection into two frequency intervals containing 5% and 95% of the energy in the selection.
Bandwidth 90% ($B_{90\%}$)	Hz	The difference between $f_{5\%}$ and $f_{95\%}$.
Duration 90% (t_{90})	s	The difference between the two points in time that divide the selection into intervals containing 95% (t_{95}) and 5% (t_5) of the energy, i.e. t_{95} minus $t_{5.}$
Aggregate entropy (h_{agg})	bits	The *disorder* in a sound, calculated from the energy distribution, higher entropy values correspond to broadband pulsive sounds while zero entropy would be a pure tone.
Average entropy (h_{avg})	bits	The *disorder* for a typical spectrum, calculated by averaging the entropy for each time bin over the total duration of the call Δt.
Maximum entropy (h_{max})	bits	The maximum amount of disorder within a vocalisation.
Minimum entropy (h_{min})	bits	The minimum amount of disorder within a vocalisation.
PFC max frequency, PFC min frequency	Hz	A measurement of frequency taken directly from the peak frequency contour (PFC) that traces the peak frequency throughout the selected call.
PFC: max slope, min slope, average slope	Hz/ms	A measurement taken from the PFC where the slope is at its maximum, minimum and averaged throughout the call.
PFC inflection points	none	The number of inflection points from the PFC that traces the peak frequency against time throughout the selected call.
Max ceiling frequency (f_h)*	Hz	The maximum ceiling frequency across the full spectrum of the vocalisation; for tonal calls the maximum harmonic.

Table 2.2 The parameters used to measure southern right whale vocalisations at the Auckland Islands. All parameters except those marked (*) are standard Raven Pro measurements.

The frequency (f_{min} and f_{max}) and time bounds (t_{min} and t_{max}) for each vocalisation were entered into Osprey to calculate the signal to noise ratio (SNR, Mellinger and Bradbury 2007). Only signals with a SNR greater than 10 dB, the limit commonly used in cetacean studies (e.g. Parks et al. 2011; Baumann-Pickering et al. 2013), were included in subsequent analyses. Call types were based on the classification system used for SRWs in Argentina by Clark (1982), in which calls were categorised based on acoustic similarity and association with biologically meaningful, simultaneously observed behaviours. Modified versions of this system have formed the basis of subsequent studies of NARW calls (e.g. Parks and Tyack 2005; Trygonis et al. 2013). Call types were assigned based on their similarity to the description and spectrograms depicted in Clark (1982), largely derived from features relating to the frequency, duration and harmonic structure of the vocalisations, and added as an annotation in Raven. An example spectrogram image for each of the defined call types was produced using the Seewave package in R (Sueur et al. 2008).

Classification of vocalisations

After the vocalisations had been measured and assigned an initial call type, the classification scheme was examined further using a random forest analysis. All classification analyses were conducted in program R version 3.0.2 (R Development Core Team 2004, www.R-project.org) using the *randomForest()* function in the Random Forest package (Liaw and Wiener 2002).

The overall aim of the RF model was to produce a repeatable and objective method of classifying the vocal repertoire of right whales, and hence validate, or not, the subjective classification described above. One third of the data was set aside completely for use at the end of the modelling process. Of the remaining vocalisation measurement data, two thirds (e.g. Shamir et al. 2014) were used to train the supervised RF model. Call type was used as the response variable and each of the variables (Table 2.2) were included as predictor variables. The training data were bootstrapped, with the model randomly selecting predictor variables at each node and choosing the best split (Sirosky 2009). Two parameters in the RF model are defined by the user - the number of predictor variables to be searched at each node (*mtry*) and the number of trees to grow (*ntree*). The number of *mtry* was defined as $\sqrt{p}$, where p is the number of predictor variables (Cutler et al. 2007; Strobl et al. 2009). A sufficiently large *ntree* value was chosen which provided robust and stable results (Strobl et al. 2009). The parameters for this particular model were set at 2000 *ntree* and 5 *mtry*.

An estimate of classification error rate was based on the third of the training observations that were not used in each bootstrapped iteration. These test observations are referred to as *out-of-bag* (*OOB*) observations, and call classifications based on the *OOB data* were aggregated and used to calculate an *OOB error rate*. A test was conducted to ensure that error had stabilised by plotting *OOB error* against the number of trees in the model.

The mean *decrease in accuracy* measure (or permutation accuracy) was implemented to determine which of the predictor variables (call features) best described the classification in the RF model. The model was initially created using all of the defined predictor variables (n = 28). For each tree in the forest, the prediction error is calculated on the *OOB data*, then for each variable, the same calculation is performed using a random permutation of the value of that variable. Finally, for each variable, the differences in prediction errors are averaged over all trees (Liaw and Wiener 2002). Measures of mean decrease in accuracy were also computed for each vocalisation type. An alternate method for assessing variable importance, the *Gini index*, was also calculated. This metric is based on a weighted mean of the improvement of individual trees based on the inclusion of each variable as a predictor (Breiman 2001). These indices were used to rank the variables considered important for the classification; a higher number indicates a more important variable (Shih 2011). Preference was given to permutation accuracy as the *Gini index* is known to have some biases, in particular a positive bias towards correlated variables (Strobl et al. 2007). In contrast, the permutation accuracy measure spreads the importance more uniformly across variables (Hastie et al. 2009). Variables were considered informative and important if their index was above the absolute value of the lowest negative scoring variable or above zero if there were no negative values (Shih 2011).

Classification prediction

The final step was to test the predictive power of the RF model and assess whether the vocalisation type could be effectively predicted from standardised call measurements. A third of the original dataset was randomly selected and set aside, before the analysis was carried out, for use as the prediction dataset. These data were not involved in the training of the model. The call types previously assigned by a human analyst were removed from the prediction dataset so that the test was conducted blind. Predictions were made using the *predict()* function in the Random Forest package (Liaw and Wiener 2002). This function classified the data based on the complex relationships among the predictor variables as determined by the RF model. The *predict()* function assigned an expected vocalisation type to each set of variable measurements and these predictions were then compared to the call categories assigned by a human analyst.

2.3 Results

Acoustic recordings totalling 50 h 13 mins were used to analyse the vocal repertoire of SRW at the Auckland Islands (Table 2.3). Of the individual vocalisations identified for analysis, 4358 calls (99.4%) were above the 10 dB SNR threshold. Vocalisations were typically clustered in time, consisting of call bouts interspersed with periods of silence. The vocal repertoire included a diverse mix of tonal, pulsive or combined tonal/pulsive vocalisations. All vocalisations, including noisy exhalations (or *blows*), were included in the analysis. The mean duration (Δt) of calls was 1.1 s (SE ± 0.01, range: 0.1 - 15.5 s). The mean peak frequency of all vocalisations was 264 Hz (SE ± 5, range: 43 - 3984 Hz). When the entire spectrum of each call (including harmonics) was incorporated, the mean maximum frequency was 3201 Hz (SE ± 63, range: 104 - 24000 Hz). The majority of *gunshot* vocalisations (97%) exceeded the full frequency range of the recorded spectrum (> 24 kHz), but the maximum frequency of all other vocalisations was within the recorded frequency range.

Year	Total number of calls	Mean number of calls per recording	Total recording length (mins)	Mean recording length (mins)
2010	1631	68 (± 15)	1265	53 (± 4)
2011	1155	92 (± 39)	734	56 (± 8)
2012	1563	74 (± 21)	943	45 (± 7)

Table 2.3 Summary of acoustic vocalisation recordings made between 2010 and 2012 (± SE) at the Auckland Islands.

Description and measurement of vocalisation types

Vocalisations were assigned to ten different call types (Figure 2.2). Six classes of tonal vocalisations were observed: *tonal low*, *upcall*, *downcall*, *high*, *very high* and *long tonal low*.

Typically, all had clear harmonic structure. The most commonly observed call type (17.4% of all calls), were *tonal low* vocalisations. *Upcalls* were low-frequency, tonal sounds ending with a frequency-modulated upsweep at a mean peak frequency of 121 Hz (SE ± 1). *Upcalls* were the third most common call type observed, contributing to 16.1% of all calls. *Downcalls,* a low-frequency tonal sound ending with an FM downsweep, were less frequently observed (4.4% of all vocalisations). They were typically shorter in duration and higher in mean peak frequency than *upcalls*. *High* calls typically had a clear harmonic structure and consisted of a high frequency tone with a peak frequency of 336 Hz (SE ± 5). *High* calls were uniformly tonal, frequency modulated, or included an upsweep or downsweep as part of the vocalisation; they accounted for 10% of all calls. *Very high* frequency tonal sounds accounted for only 4.3% of vocalisations and had a peak frequency of 749 Hz (SE ± 11). The *long tonal low* call was frequency modulated, had a peak frequency of 110 Hz (SE ± 5) and was the least frequently observed call type (1.5% of all calls).

Three classes of non-tonal vocalisations were observed: *gunshot*, *pulsive* and *blow*; plus an additional class which contained a combination of tonal and pulsive elements, *hybrid* calls. *Pulsive* calls were the second most common type overall, contributing to 16.6% of all calls. *Pulsive* calls were harsh growl type sounds, with no strong harmonic structure but with complex amplitude and frequency modulation. *Blows* have been excluded from measurements of vocal repertoire in previous studies of right whales (Parks and Tyack 2005; Trygonis et al. 2013), but have been included here for completeness, as they made up 14.3% of all vocalisations. Three sub-types of blow were evident: *simple*, *tonal* and *rumble* (Figure 2.3); but they were treated as one class of vocalisation for RF analysis. *Blows* had little harmonic structure and the mean peak frequency was highly variable. *Rumbles* were more frequent during periods of high vocal activity and often sounded similar to a machine gun. *Gunshots* were intense, short-duration broadband vocalisations which sounded (unsurprisingly) like a gunshot. *Gunshots* accounted for 2.7% of the total calls recorded, had the shortest duration and typically extended across the full frequency spectrum. *Hybrid* calls were often heard as an urgent trumpet-type sound and had very high maximum frequencies up to 18 kHz. Each *hybrid* vocalisation contained tonal sections with a strong harmonic structure and pulsive sections where the harmonic structure broke down.

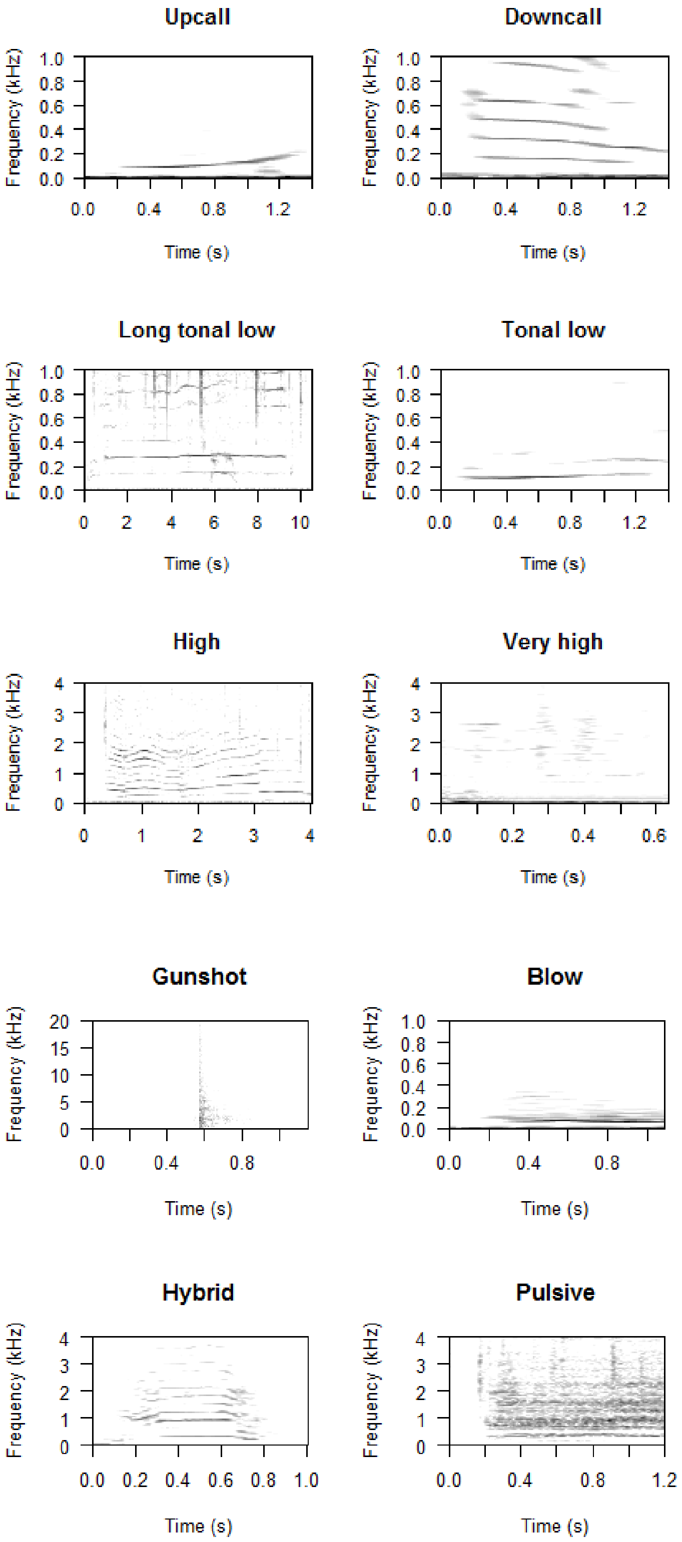


Figure 2.2 Spectrograms of ten vocalisation types assigned to southern right whales during the winter calving season at the Auckland Islands. N.B.: time and frequency scales differ for some spectrograms.

Call type	**Peak frequency f_{peak} (Hz)**	**Start frequency f_1 (Hz)**	**End frequency f_2 (Hz)**	**Max ceiling frequency f_h (Hz)**	**Duration Δt (s)**	**Call type in Clark (1982)**
Blow (*n* = 621)	312 (± 17) Range: 47 - 2555	495 (± 27) Range: 32 - 4852	341 (± 19) Range: 32 - 3281	2170 (± 83) Range: 174 - 12164	1.1 (± 0.02) Range: 0.3 – 4.6	*Blow*
Downcall (*n* = 181)	151 (± 3) Range: 35 - 398	203 (± 4) Range: 117 - 387	128 (± 3) Range: 43 - 261	2673 (± 115) Range: 238 - 8432	0.7 (± 0.01) Range: 0.3 – 1.5	*Down call*
Long tonal low (*n* = 60)	110 (± 5) Range: 70 - 270	109 (± 7) Range: 47 - 223	110 (± 5) Range: 47 - 211	1330 (± 113) Range: 160 - 4064	4.6 (± 0.28) Range: 2.7 – 15.5	Not described
Gunshot (*n* = 116)	795 (± 65) Range: 118 - 3984	1520 (± 156) Range: 597 - 8379	807 (± 72) Range: 59 - 3246	23687 (± 166) Range: 9813 - 24000	0.2 (± 0.01) Range: 0.1 – 0.4	*Slap* (but excluded from analyses)
High (*n* = 429)	335 (± 5) Range: 164 - 1131	332 (± 7) Range: 32 - 1087	334 (± 6) Range: 117 - 1206	3648 (± 111) Range: 147 - 21570	1.2 (± 0.03) Range: 0.2 – 3.8	*High* and *constant* (> ~200 Hz)
Hybrid (*n* = 576)	243 (± 6) Range: 54 - 902	226 (± 6) Range: 32 - 879	245 (± 6) Range: 32 - 949	6181 (± 135) Range: 339 - 18171	1.4 (± 0.02) Range: 0.3 – 2.7	*Hybrid*
Tonal low (*n* = 764)	133 (± 1) Range: 43 -281	117 (± 2) Range: 32 - 375	140 (± 5) Range: 32 - 323	2087 (± 50) Range: 104 - 8513	1.2 (± 0.02) Range: 0.2 – 3.7	*Constant* (< ~200 Hz)
Pulsive (*n* = 725)	302 (±14) Range: 43 - 2906	547 (± 24) Range: 32 - 3258	323 (± 14) Range: 32 - 2613	1672 (± 46) Range: 117 - 8758	1.0 (± 0.02) Range: 0.2 – 6.3	*Pulsive*
Upcall (*n* = 701)	121 (± 1) Range: 43 - 281	87 (± 1) Range: 32 - 293	143 (± 2) Range: 35 - 293	1197 (± 30) Range: 119 - 6594	0.9 (± 0.01) Range: 0.3 – 2.7	*Up call*
Very high (*n* = 185)	749 (± 11) Range: 355 -1348	748 (± 12) Range: 312 - 1378	743 (± 12) Range: 340 - 1418	2869 (± 107) Range: 846 - 8446	0.7 (± 0.02) Range: 0.2 – 2.0	Not described

Table 2.4 Summary measurements of frequency and duration parameters for each vocalisation type assigned to southern right whales at the Auckland Islands. The mean measurement (± SE) and range are given for each call type.

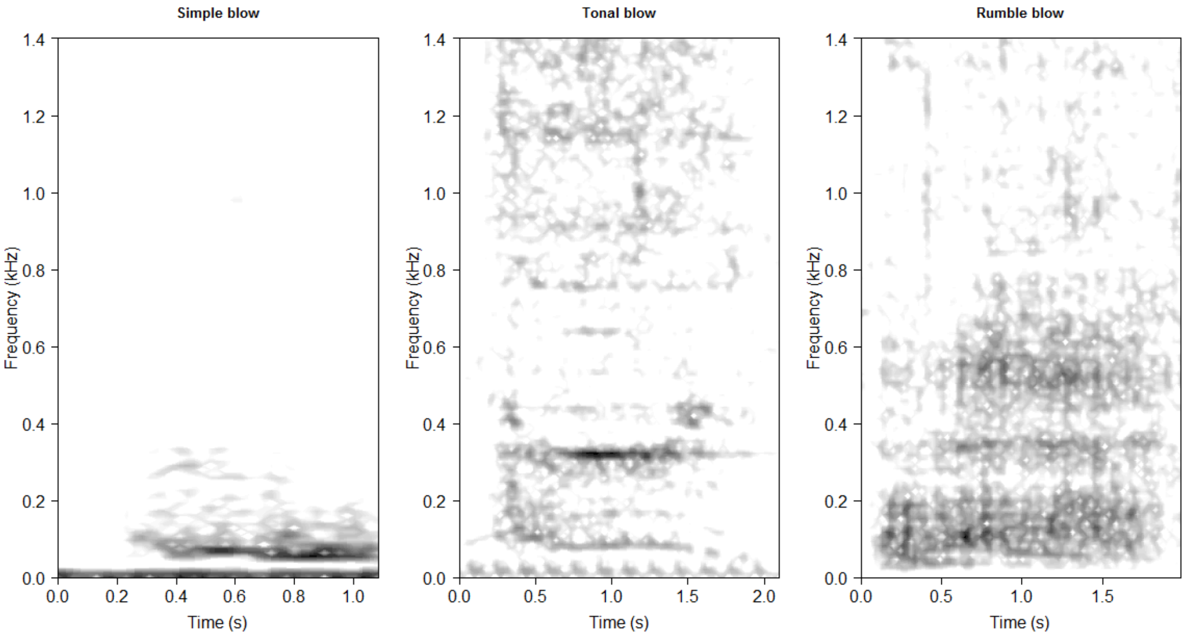


Figure 2.3 Spectrograms of three different blow vocalisation sub-types, *simple*, *tonal* and *rumble* observed for southern right whales during the winter calving season at the Auckland Islands. N.B. the time scale differs across the spectrograms.

Classification analysis

A RF analysis was performed to classify the calls from the acoustic measurements, assess the variability within each call type and identify the parameters that best described the classification. A plot of *OOB error* against number of trees showed that error stabilised when 500 or more trees were used in the model. Reducing the number of variables in the model from twenty eight to fourteen of the highest ranked variables had no discernible effect on the *OOB error rate*. Beyond this point *OOB error rate* increased sharply. Hence, fourteen variables was considered to be optimum (Table 2.5). The overall classification error was 24.4% for the RF model using the top predictor variables. The same top fourteen variables were selected using the *Gini index*, but the ranking within these top variables differed (Table 2.5). While all fourteen variables were considered important for the overall classification, some were unimportant for describing one or more of the call types. In particular, start frequency and delta frequency were unimportant for classifying *blows* and the number of inflection points was not valuable for explaining *pulsive* calls (Table 2.5).

Call types:	*Blow*	*Down*	*Long tonal low*	*Gunshot*	*High*	*Hybrid*	*Tonal low*	*Pulsive*	*Up*	*Very high*	***Mean decrease accuracy***	***Mean decrease Gini***
Maximum ceiling frequency	58.0	11.5	10.1	38.9	12.3	140.0	20.0	41.5	65.1	18.5	141.3	249.4
PFC inflection points	77.5	22.6	34.5	10.5	5.4	39.3	18.1	-7.2	44.2	32.8	96.6	149.4
Delta time	14.5	55.9	74.8	13.9	7.2	28.5	34.9	12.5	53.1	16.9	95.1	177.3
Start-end frequency	17.9	80.1	2.9	-0.3	8.4	13.9	22.9	28.6	80.1	11.4	93.2	152.7
Delta frequency	64.5	28.2	31.9	52.9	29.6	51.6	42.1	73.1	33.7	40.0	75.9	323.9
Low frequency	14.1	16.1	6.7	10.2	69.4	8.3	12.0	30.4	30.3	45.3	71.9	180.0
High frequency	49.4	37.7	43.1	44.4	43.1	53.9	48.8	43.3	47.8	44.3	71.3	335.0
Frequency 5%	32.8	22.9	20.9	4.9	46.4	9.8	19.4	18.5	56.9	33.6	70.1	173.9
Start frequency	-9.7	52.1	4.5	4.4	20.8	15.4	25.1	21.0	43.9	14.5	65.0	114.2
Average entropy	58.3	34.1	26.3	32.6	39.5	50.9	28.3	25.8	55.4	20.6	64.2	246.3
End frequency	11.8	38.8	13.4	2.3	22.8	20.3	31.9	0.7	27.5	14.9	61.0	104.7
First quartile frequency	20.6	26.7	20.5	8.5	42.3	18.4	25.5	24.8	38.0	45.3	58.7	169.5
Aggregate entropy	28.3	11.1	16.4	17.1	8.6	31.6	81.9	3.6	3.2	15.2	56.4	163.8
Duration 90%	1.6	26.8	44.7	16.8	8.1	8.3	13.5	16.3	36.9	14.7	56.1	92.7

Table 2.5 The top fourteen variables used to classify southern right whale calls using a random forest model, as ranked by the mean decrease accuracy. *Gini indices* are given for comparison. Variable importance is also scored separately for each call type. Score metrics are relative with higher numbers showing greater importance.

The confusion matrix (Table 2.6) shows the number of calls that were misclassified using the test data set in the RF model. Tonal calls were typically well classified by the model, although *downcalls* had a relatively high classification error rate (30.7%). *Downcalls*, however, did have a relatively small sample size (*n* = 181) when compared with other tonal calls (*high*, *n* = 434; *tonal low*, *n* = 756; *upcall*, *n* = 701). *Long tonal low* calls (*n* = 60) and *very high* calls (*n* = 185), however, also had relatively small sample sizes but had low classification error rates.

These two call types were at the extremes of the peak frequency spectrum with the lowest and highest peak frequencies for tonal calls, respectively. *Gunshots* were well classified by the model (1.2% error rate) and there was minimal confusion with only one other class (*pulsive*). The confusion matrix shows that the highest misclassification rate was for *blows* (38.2%) and *pulsive* calls (31.8%). These rates were higher than for tonal vocalisations and most of the confusion was between *blow* and *pulsive* calls. *Hybrid* vocalisations (a mix of pulsive and tonal elements) had a misclassification rate of 25.3%, slightly lower than the *pulsive* categories but higher than most tonal calls.

Predicted: **Observed:**	*Blow*	*Downcall*	*Long tonal low*	*Gunshot*	*High*	*Hybrid*	*Tonal low*	*Pulsive*	*Upcall*	*Very high*	**Classification error (%)**
Blow	**268**	1	0	0	1	3	0	161	0	0	38.2
Downcall	0	**88**	0	0	5	9	23	2	0	0	30.7
Long tonal low	0	0	**36**	0	0	0	6	0	0	0	14.3
Gunshot	0	0	0	**81**	0	0	0	1	0	0	1.2
High	0	1	0	0	**237**	55	4	1	0	6	22.0
Hybrid	1	6	0	0	46	**298**	33	5	1	9	25.3
Tonal low	0	22	5	0	4	16	**408**	2	73	0	23.0
Pulsive	126	3	0	1	0	8	16	**347**	8	0	31.8
Upcall	0	1	0	0	0	1	66	3	**420**	0	14.5
Very high	0	0	0	0	7	1	0	0	0	**122**	6.2

Table 2.6. Confusion matrix and classification error outputs from the random forest model used to classify southern right whale calls. The numbers in bold show the number of calls that were classified correctly. The non-bold numbers represent the calls that were misclassified by the model. The classification error shows the total percentage of vocalisations that were misclassified for each call type.

Vocalisation type predictions

The RF model was applied to the third of the original dataset which had not been used to train the model, to predict vocalisation types based on the standard measurements taken from each call (Table 2.2). Predictions were determined for 1301 vocalisations (Table 2.7). Of these

81.5% were predicted correctly when compared to the classifications attributed by a human analyst. All of the classifications (excluding *high* and *very high* call categories) performed better for the prediction data than for the training data. *High* and *very high* categories exhibited slightly more error but only by 4.9% and 1.1%, respectively. There was no prediction error associated with *gunshots* or *long tonal low* call types. The highest error rate was for *blow* (33.3%) and *pulsive* (30.7%) categories, with the majority of the misclassifications occurring between these two call types.

Observed: **Predicted:**	*Blow*	*Downcall*	*Long tonal low*	*Gunshot*	*High*	*Hybrid*	*Tonal low*	*Pulsive*	*Upcall*	*Very high*	**Prediction error (%)**
Blow	**124**	0	0	0	2	0	1	59	0	0	33.3
Downcall	0	**38**	0	0	2	0	13	1	0	0	29.6
Long tonal low	0	0	**18**	0	0	0	0	0	0	0	0.0
Gunshot	0	0	0	**34**	0	0	0	0	0	0	0.0
High	1	0	0	0	**95**	0	29	0	0	5	26.9
Hybrid	1	2	0	0	15	**134**	11	2	0	6	21.6
Tonal low	0	11	0	0	2	7	**176**	0	30	0	22.1
Pulsive	59	0	0	0	1	3	3	**151**	1	0	30.7
Upcall	0	1	0	0	0	0	26	0	**182**	0	12.9
Very high	0	0	0	0	2	1	0	1	0	**51**	7.3

Table 2.7. Prediction matrix and prediction error outputs from the random forest model. The prediction matrix shows the number of calls that were misclassified by the model and where the misclassifications arose. The prediction error shows the total percentage of vocalisations that were misclassified for each call type.

2.4 Discussion

This study provides the first quantitative classification of the vocal repertoire of right whales from New Zealand waters. Right whales have an extensive acoustic repertoire encompassing a wide range of pulsive and tonal sounds. Calls do not always fall into obvious categories; hence the repertoire has been described as a continuum of sounds (Payne and Payne 1971), or classifications have included broad categories for ease of analysis (e.g. Matthews et al. 2001; Parks and Tyack 2005). Right whale vocalisations recorded at the Auckland Islands during three winter calving seasons were classified into ten call categories in an attempt to fully describe the repertoire. Calls were classified based on their specific characteristics, referenced to previous research on the behavioural context of vocalisations (Clark 1982; Parks and Tyack 2005; Trygonis et al. 2013). Call features were used to describe and measure the vocalisations and a supervised random forest model successfully predicted call types in 82% of cases.

Call repertoire and comparisons with other studies

Vocalisations from the Auckland Islands were split into six tonal, three pulsive and one combination category. This classification scheme is broadly similar to those of other studies of right whales in the North Atlantic (Parks and Tyack 2005; Trygonis et al. 2013) and in the southern hemisphere (Clark 1982). *Upcalls* were first described by Clark (1982) and have since been observed in the majority of studies of right whale vocalisations (e.g. Vanderlaan et al. 2003; Parks and Tyack 2005; Van Parijs et al. 2009; Trygonis et al. 2013). *Upcalls* at the Auckland Islands appear to be lower in frequency and slightly shorter in duration than *upcalls* recorded for NARWs (Parks and Tyack 2005; Trygonis et al. 2013). This may reflect the different ambient noise environments of the Atlantic Ocean, which features high levels of anthropogenic noise (Parks et al. 2007; 2010; 2011), and New Zealand's sub-Antarctic Islands, where the soundscape is largely natural. The relative proportion of *upcalls* recorded at the Auckland Islands (16%) was far higher than recorded for NARWs (6%, Parks and Tyack 2005; 5%, Trygonis et al. 2013). This is likely to be because both of the NARW studies concentrated on recording in social contexts, in which *upcalls* are known to be produced at a lower rate (Clark 1983). *Upcalls* were the most common call type for SRWs off Argentina and were typically associated with travelling whales or low level behavioural activity (Clark 1983). At the Auckland Islands, *upcalls*, *tonal low* and *pulsive* sounds were the most prevalent vocalisations and occurred in similar proportions.

Long tonal low calls have not previously been described in the literature for any right whale population. They are similar in duration to *foghorn* sounds made by NARWs (Trygonis et al. 2013); but are somewhat higher in frequency. Trygonis et al. (2013) observed that these calls were made consecutively by one adult at the surface, and appeared to result in the cessation of surface activity. No similar behaviour was observed at the Auckland Islands. *Long* *tonal low* sounds of up to 15 s duration were recorded during this study, but calls up to 25 s duration have been recorded on an autonomous recorder at the same location (Webster *pers. obs.*). It is possible that these sounds are simply long duration *tonal low* calls.

The *high* and *hybrid* calls described here are similar to *screams* produced by focal females in surface active groups (Parks and Tyack 2005). Trygonis et al. (2013) had a far higher proportion of *high* calls (58%, described separately as *downcall*, *constant*, *modulated* and *upcall high*), than was noted at the Auckland Islands (10%). *Gunshots* are also associated with social behaviour (Parks et al. 2005) and again there was a much higher incidence of *gunshots* (13%, Trygonis et al. 2013) than in this study (3%). My study attempted to encompass a wide range of behaviour states and hence had a different focus to these NARW studies. Trygonis et al. (2013), for example, concentrated entirely on four surface-active groups are unlikely to represent the entire vocal repertoire.

Very high vocalisations have not been previously described for right whales and are potentially produced by calves. The Auckland Islands is a calving ground with births known to occur in July and August (Patenaude 2000). Calves were often in the vicinity when these vocalisations were recorded. These calls are not the same as the warble sounds described by Parks and Tyack (2005), which were produced by older calves (approximately six months old), but are more consistent with the calls made infrequently by calves less than four months old (Parks pers comm.).

Blows have largely been excluded from previous analyses of right whale acoustic repertoire (e.g. Parks and Tyack 2005; Trygonis et al. 2013), likely because they are difficult to classify and it is unclear whether *blow*s function in communication or whether they are incidental to breathing. Right whales are known to make forceful exhalations during social activity (Parks and Clark 2007); potentially these sounds are reflective of intense activity or exertion. It has been suggested that *blows* that are loud, tonal or pulsive in nature may serve a communicative purpose (Clark 1983). Even if incidental, they communicate an individual’s presence to any listening whale within earshot. In any case, *blows* in this study accounted for 14.3% of all calls and were included for completeness in order to describe the entire vocal repertoire.

Classification of vocalisations

Classifying a species' vocal repertoire into biologically relevant categories is a common difficulty across acoustic studies (Deecke and Janik 2005). Classification of the vocal repertoire of right whales at the Auckland Islands using a RF model showed great potential as classification accuracy was high (82%) and the model was consistently good at predicting call types, especially for tonal calls and *gunshots*. The overall aim was to find a consistent, robust method that can be replicated easily and which successfully predicts call categories from parameter measurements. This model approach was successful on both counts. In a similar study, Trygonis et al. (2013) also achieved a high prediction accuracy of 81% for classifying NARW vocalisations using a classification and regression tree (CART) analysis, from which RF analysis was derived (Breiman et al. 1984). Their study used data from only four surface active groups containing a maximum of 18 individuals and hence was likely to include less call variation. My study used a much larger dataset but achieved a comparably high prediction accuracy, reinforcing the validity of using RF analysis in this application.

The error rates associated with classification of the vocalisations via RF analysis varied across call categories, being highest for *blow* and *pulsive* call types and lowest for *gunshots*, *very high* calls, *long tonal low* and *upcalls*. Similarly, NARW tonal calls were easier to classify, and calls with pulsive sections had the highest errors and were the most difficult to classify (Trygonis et al. 2013). There appears to be greater variation and less definition associated with *blows* and *pulsive* calls. Similarly, *high*, *hybrid* and *pulsive* calls were found to be highly variable for SRWs off Argentina (Clark 1982).

Measures of variable importance are valuable for choosing the best predictor variables to include in algorithms for detecting and classifying vocalisations. The RF model highlighted maximum ceiling frequency, number of inflection points, duration (Δt), the difference between the start and end frequency, and the total bandwidth (Δf) as the top predictors for classifying right whale calls. Start minus end frequency was good for categorising tonal vocalisations, in particular, discriminating *down*- and *upcalls* from other categories. Ceiling frequency was critical for discerning and classifying *hybrid*, *high* and *gunshot* vocalisations. The highest ranking parameters for classifying NARW vocalisations (Trygonis et al. 2013) were all included in the top 14 predictor variables here, showing broad agreement between the two methods.

To document the entire repertoire of a species, the ideal scenario is to incorporate many different individuals in a variety of behavioural contexts at different locations. Port Ross at the Auckland Islands are thought to be the primary calving grounds for SRWs in New Zealand waters (Patenaude et al. 1998) and surveys have confirmed that no other significant calving habitats exist in the Auckland Islands (Rayment et al. 2012, Appendix A). Sightings of SRWs elsewhere in New Zealand are somewhat opportunistic at present (Carroll et al. 2011), and hence Port Ross was chosen as the best location to begin a study on the acoustic repertoire of SRWs in New Zealand. There is a high turnover of SRWs within a calving season (~370 individuals each year) and photo-identification surveys (2010-2013) show that individuals are very unlikely to be observed in consecutive years at Port Ross (Rayment, unpublished data). Acoustic recordings made during the same time period over several years, will therefore capture calls from many different individuals. Ideally, behavioural observations would be conducted at the same time as acoustic recordings (e.g. Clark 1983; Parks and Tyack 2005) to provide context. While behavioural states were recorded, no detailed behavioural observations were made during the acoustic recordings in this study, for two reasons. First, I lacked the ability to localise the vocalising individual in real time, and without this it was impossible to know which behaviours to record due to the numbers of whales present. Second, many acoustic recordings were made at night, when behavioural observations were not possible. By recording at different times of day, over several years, a representative range of behavioural contexts is likely to have been sampled. At the Auckland Islands in winter the predominant behaviours are socialising (between cow-calf pairs or groups of mixed individuals), resting or travel; feeding behaviours are not typically observed (Patenaude et al. 1998). The makeup of the acoustic repertoire at the Auckland Islands was found to be more similar to that observed by Clark (1982; 1983) rather than acoustic recordings of NARW populations (e.g. Parks and Tyack 2005; Trygonis et al. 2013). This could be because these recordings (Clark 1982; 1983) were also of SRWs, but additionally it could have been because the recordings were made over a wider range of behavioural contexts.

Classifying vocalisations via their aural or spectrographic similarity using human analysts is highly subjective (Baumgartner and Mussoline 2011). Humans do not necessarily distinguish calls in the way that animals do; although some mammals have been shown to perceive communication sounds in a similar way to humans (e.g. mice, *Mus domesticus*, Ehret and Riecke 2002) the same was not true for birds (e.g. Brown et al. 1988). Using statistical measures of similarity to classify sounds avoids these problems, and is objective and repeatable with transparent decision rules (Deecke et al. 1999; Baumgartner and Mussoline 2011). This approach also facilitates comparative studies of sounds from different habitats and geographical areas. The weakness of the statistical approach is that without information on behavioural context, the resulting call classification might not be meaningful, since only the physical properties of the signals are assessed (Deecke et al. 1999). Here we attempted to give some biological significance to the acoustic classification by basing our categories on those from other studies in which the calling individual was localised (Clark 1983; Parks and Tyack 2005). This method too has its drawbacks, as the biological significance of a call may vary across different geographical regions. Distinct vocalisation types, for example, are evident in two separate groups of blue whale in the northern Pacific (Stafford et al. 2001). For right whales, the rate at which they vocalise and the proportions in which various call types are used appears to be linked to behaviour (Van Parijs et al. 2009; Jaquet and Webster, unpublished data). While call parameters are known to vary across regions, the call types are consistent (Parks et al. 2009), although several different naming conventions have been used.

Large volumes of acoustic data make manual analysis a laborious task; but by choosing call parameters that are automatically extractable from Raven, and using these in a multivariate model, I hope to speed up the process of classification and make it more repeatable. Recent research has shown that the identification of killer whale (*Orcinus orca*) and pilot whale (*Globicephala melas*) sounds from large acoustic datasets using machine learning was more accurate than by crowd-sourcing (Shamir et al. 2014).

Implications for automated detection

Automated detection systems look for specific signal attributes and for this reason tend to focus on signals that are highly stereotypical (Mellinger and Clark 1997). *Upcalls* are most commonly used for passive acoustic detection of right whales (Gillespie 2004; Mellinger 2004;

Clark et al. 2007; Urazghildiiev et al. 2009). They vary little (Van Parijs et al. 2009), are used by both sexes and all age classes, and in a range of behavioural contexts (Parks et al. 2011). *Upcalls* are frequently heard at the Auckland Islands and, in this analysis, they were correctly categorised over 85% of the time and are thus a good candidate for automated detection of right whale presence. Many other call types are used at the Auckland Islands, however, and incorporating these into acoustic detectors (such as the automated pitch-tracking systems currently being developed, e.g. Baumgartner and Mussoline 2011) would increase chances of detection. Reliable, repeatable measurements of call characteristics are crucial for developing passive monitoring systems and call detection algorithms.

Detection and classification of right whale calls in the North Atlantic is complicated by the presence of humpback whales, which make some similar sounds, are more numerous, and vocalise more often and more loudly than right whales (Gillespie 2004). The situation at the Auckland Islands is ideal because of the lack of other large cetaceans (Baker 1977), thus the vocalisations recorded can be assigned to right whales. Knowing which sounds can be confidently attributed to right whales is vital in developing effective call detectors.

In high latitude, remote areas such as the sub-Antarctic and Antarctic, passive acoustic approaches to documenting whale presence hold special promise, because they are less affected by weather and light conditions than visual systems (e.g. Kimura et al. 2009). Describing the acoustic repertoire of SRWs is a crucial step towards an efficient, automated call detector for these whales. Such a tool would be an invaluable aid to understanding habitat use, recovery from whaling, and management of potential threats.

CHAPTER 3

TEMPORAL VARIATION IN THE VOCALISATIONS OF SOUTHERN RIGHT WHALES

3.1 Introduction

Animals vary their behaviour in response to a wide range of factors, including changes in light levels (Valdimarsson et al. 1997), availability of prey (Backwell et al. 1998), predation pressure (Lima and Dill 1990; Noë and Bshary 1997), anthropogenic activities (Cornelius et al. 2001), and weather conditions (Paige 1995; Pellegrino et al. 2013). For example, the vertical migration of many marine animals from deeper mesopelagic waters to epipelagic regions at night to feed on phytoplankton before returning to depth at dawn to escape visual predators is a well-known phenomenon (Lampert 1989). At a larger scale, many taxa make extensive seasonal migrations, often related to feeding and breeding opportunities. The sooty shearwater (*Puffinus griseus*), for example, migrates 64,000 km across the Pacific Ocean to feed off California, Alaska or Japan but returns to New Zealand to breed each year (Shaffer et al. 2006). Whilst temporal variation in behaviour can typically be explained by natural events, anthropogenic activities may also have an impact; for example, black bears (*Ursus americanus*) change their daily routine in response to the presence of human garbage (Beckmann and Berger 2003).

The *vocal* behaviour of many animals also changes temporally. Some terrestrial species, such as wolves (*Canis lupus*), exhibit higher levels of vocal activity during the late evening and dawn (Gazzola et al. 2002). The dawn chorus of many temperate and tropical bird species involves an increase in song rate, chorus period and song complexity which reach maximum levels shortly before sunrise (Burt and Vehrencamp 2005). The calling activity of various frogs can be correlated with precipitation and temperature (Ospina et al. 2013), as is the vocal activity of some insects (Fonseca and Revez 2002; Jacot et al. 2008). The reasons behind such temporal variation in vocal behaviour are often difficult to determine, but may relate to ambient noise and propagation conditions (Patricelli and Blickley 2006), energy reserves (Schwarz et al. 1995), predation risk (Mougeot and Bretagnolle 2000) or social motivations (Burt and Vehrencamp 2005).

Marine mammals in general, and cetaceans in particular, are highly vocal, relying on sound for communication (Smolker et al. 1993; Janik and Slater 1998), navigation (Au 1997) and feeding (Nowacek 2005). The occurrence of species-specific vocalisations reveal patterns of a species' presence. In the Gulf of Alaska, *usual* clicks made by sperm whales (*Physeter macrocephalus*) are heard more often in summer than in winter, consistent with a known seasonal migration of reproductive males from highly productive waters in high latitudes in summer, to the lower latitudes favoured by breeding females in winter (Mellinger et al. 2004). Vocalisation types and rates can change over short timescales (hours/days) or longer monthly or seasonal timescales. Bryde's whales (*Balaenoptera brydei*) show seasonal changes in vocalisation type; alternating tonal phrases are more often recorded from August through February than in the remainder of the year (Heimlich et al. 2005). Diel changes in acoustic behaviour have been observed in both mysticetes (Stafford et al. 2005; Baumgartner and Fratantoni 2008) and odontocetes (Carlström 2005; Au et al. 2013; Wang et al. 2014). Sound pressure levels of vocalisations of wintering humpback whales (*Megaptera novaeangliae*) off Maui increase at sunset, remain relatively high through the night and progressively decrease from sunrise (Au et al. 2000). Vocal behaviour can be used to infer the level and type of activity that an animal is engaged in. Higher echolocation rates and buzzes (associated with foraging) suggest that several odontocete species forage primarily at night, including harbour porpoise (*Phocoena phocoena*, Carlström 2005), finless porpoise (*Neophocoena asiaorientalis*, Wang et al. 2014) and Risso's dolphin (*Grampus griseus*, Au et al. 2013).

Passive acoustic monitoring (PAM) has become an increasingly important area of research (Mellinger et al. 2007b). PAM has proven extremely successful for determining the seasonal presence of marine mammals (Mellinger et al. 2004; Heimlich et al. 2005) and documenting temporal changes in vocal behaviour (Stafford et al. 2005). Autonomous recording systems, along with automated detection of stereotypical calls, have been fundamental in the monitoring and protection of North Atlantic right whales (NARWs, *Eubalaena glacialis*), particularly in and around shipping lanes (Clark et al. 2007). Typically, passive acoustic detection and localisation of right whales uses *upcalls* (Gillespie 2004; Mellinger 2004; Urazghildiiev and Clark 2006; 2007; Urazghildiiev et al. 2009; Dugan 2010a; 2010b) which are the most common call type under many scenarios (Clark 1982; McDonald and Moore 2002; Parks et al. 2011) and are produced by both males and females (Clark 1983; Parks and Tyack 2005). Passive acoustic methods are increasingly used to monitor right whales, particularly in remote regions or those with inhospitable weather conditions (e.g. Stafford et al. 1999; Širović et al. 2004; Mellinger et al. 2007a). Detailed knowledge of a species' call repertoire is essential for improving the algorithms and software to enable successful call-detection (Charif and Pitzrick 2008; Digby et al. 2013).

Most of the current knowledge of southern right whales (SRWs, *Eubalaena australis*) in New Zealand waters comes from visual observations and surveys at the Auckland Islands (Patenaude et al. 1998; Patenaude 2000; Rayment et al. 2012, Appendix A). Right whales are the only cetacean species known to be regularly present in Auckland Islands waters (Baker 1977) and arrive there each winter to calve (Patenaude et al. 1998). Practical constraints restrict the duration of research expeditions to the sub-Antarctic Auckland Islands; beyond a wintertime window of up to eight weeks (Patenaude 2000) little is known about the presence or behaviour of right whales at these islands. The vocal repertoire of SRWs at the Auckland Islands has received attention recently (Chapter 2), but little is known about habitat use by right whales or variation in their calling behaviour throughout the year. Given the limitations of the remote location and inclement weather conditions in the sub-Antarctic, autonomous acoustic recorders (e.g. Van Parijs et al. 2009) provide an excellent tool to gather data on this species, over extended periods.

The main aim of this research was to document diel and seasonal patterns in vocal behaviour of right whales at the Auckland Islands. In addition, an automated *upcall* detector developed for NARWs (Urazghildiiev and Clark 2006) was tested to assess its effectiveness and sensitivity for this population of SRWs.

3.2 Methods

Data collection

Recordings were made using a DSG-Ocean autonomous recorder (Loggerhead Instruments, USA, www.loggerhead.com) moored in Laurie Harbour in Port Ross, a large, sheltered harbour of at the northern end of the Auckland Islands (Figure 3.1). Systematic line-transect surveys along the entire east coast and in Carnley Harbour, the large southern harbour of the Auckland Islands, have confirmed Port Ross as the area where SRWs are most concentrated (Rayment et al. 2012, Appendix A) and hence an ideal location for a moored acoustic recorder. The deployment location, in the upper reaches of Port Ross (50°33.4'S, 166°12.3'E) was chosen for its physical characteristics: shallow depth (<20 m), flat and sandy seabed, shelter from prevailing swells and minimal risk of fouling due to vessels anchoring.

The DSG-Ocean acoustic recording system comprised a single HTI-96-MIN hydrophone (sensitivity: –185.6 dBV/µPa, frequency response: 20 Hz - 50 kHz ± 3dB) with a fully programmable sampling rate and recording schedule. DSG-Ocean recorders have been used extensively for acoustic studies on fish (e.g. Parmentier et al. 2010; Nelson et al. 2011; Andersson et al. 2012; Rowell et al. 2012; Schärer et al. 2012) and are increasingly being used for marine mammal research (e.g. Wells et al. 2013).

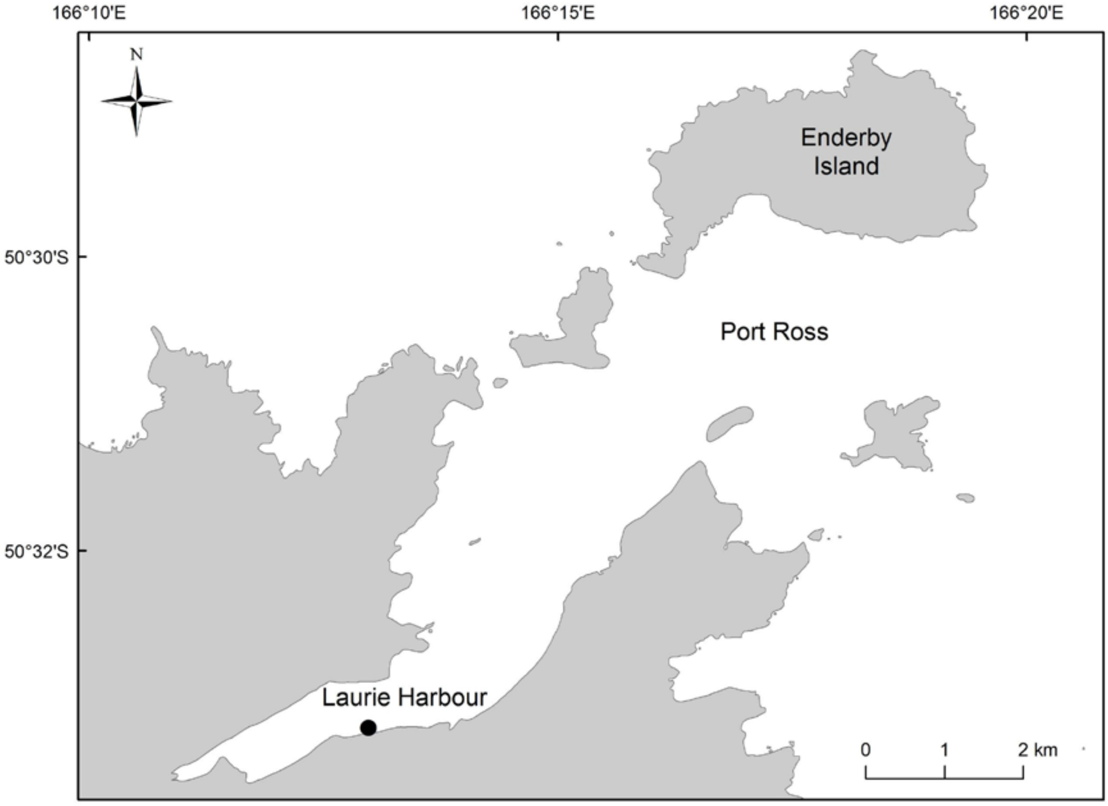


Figure 3.1 Location of the DSG-Ocean recorder for southern right whale vocalisations in Laurie Harbour, Port Ross, sub-Antarctic Auckland Islands.

A compromise between sampling rate and recording schedule was required to maximise data quantity, given limited battery power, over an extended deployment period. A trial deployment was made between 22 July 2011 and 1 August 2011 to check the recorder settings and the practicality of the mooring system. During the testing period the DSG-Ocean recorded at a default sampling rate of 50 kHz for a duty cycle of 2.5 min every 30 min. The DSG-Ocean was successfully retrieved and downloaded after the trial. The first long-term deployment was on 6 August 2011 and the recorder was subsequently recovered and downloaded on 27 July 2012. The recorder was set to a sampling rate of 4 kHz recording for 3.75 min every 30 min.

The mooring system was designed without surface buoys or trailing lines to minimise entanglement risk. The DSG recorder was attached via a 1 m length of 5 mm nylon line (designed to break in an entanglement) to a steel mooring weight. A second mooring weight was attached to the first with 40 m of negatively buoyant 16 mm nylon rope. The weights were deployed so that the rope was stretched taut along the seabed. A flotation collar was attached to the top of the PVC housing of the recorder to ensure that the hydrophone remained upright during deployment. The recorder was retrieved by snagging the line between the two moorings with a grapnel and winching it on board.

Manual vocalisation detection

Acoustic data were analysed manually using Raven Pro 1.5 (Bioacoustics Research Program, Cornell University, www.birds.cornell.edu). All SRW vocalisations in each of the DSG recordings were highlighted and counted. Each vocalisation was assigned subjectively to one of nine types (*upcall*, *downcall*, *gunshot*, *high*, *pulsive*, *tonal low*, *very high*, *hybrid* or *blow*) based on a classification system determined previously (Chapter 2).

Automated vocalisation detection

All of the acoustic recordings were also examined using an automated detector (Urazghildiiev and Clark 2006) in the eXtensible BioAcoustic Tool (XBAT; Figueroa 2012) written in MATLAB (The Mathworks Inc., MA, USA). The automated call detection algorithm is specifically designed to detect *upcall* vocalisations produced by NARWs (Urazghildiiev and Clark 2006). The XBAT detector was set at a correlation threshold of 0.4, a value typically used for detections of NARW calls. Acoustic similarity between a call template and possible *upcall* events were assessed using a generalised likelihood ratio test (GLRT) based detection scheme, and all events exceeding this threshold were logged.

Verification of detector results

Manual and automated detections were compared in order to test the effectiveness and sensitivity of the algorithm for detecting SRW *upcalls*. I randomly selected 10% (n = 1443 calls) of the total recordings for analysis. Each recording was reviewed in XBAT using the *event palette* to display all of the detection events logged by the detector. The detection events were then annotated as either true or false *upcall* detections.

Following Charif and Pitzrick (2008), two measures of detector performance were applied (Figure 3.2). The first (Positive Predictive Value; PPV) represents the proportion of the *upcalls* logged by the detector that were judged by the human analyst to have been correctly assigned and thus accounted for false positives. The second measure enabled the detector's sensitivity (True Positive Rate, TPR) to be quantified; and is the number of correctly assigned *upcalls* logged by the detector and accounted for false negatives.

	SRW upcalls (confirmed by analyst)		**Performance metrics**
SRW upcalls (automatically detected)	True Positive (TP)	False Positive (FP)	Positive Predictive Value (PPV) = TP/(TP+FP)
	False Negative (FN)	True Negative (TN)	Negative Predictive Value (NPV) = TN/(FN+TN)
Performance metrics	True Positive Rate (TPR) = TP/(TP+FN)	False Positive Rate (FPR) = TN/(FP+TN)	

Figure 3.2. The possible outcomes relating to the detection of right whale *upcalls* and the metrics for quantifying the automated detector's performance. Shaded cells show outcomes and performance metrics that were able to be calculated. Adapted from Fawcett (2006).

The deviation of the automated detections from the number of manually detected *upcalls* was examined using a regression. In this context, the slope of the fitted line indicated the bias (1:1 = zero bias), while the fit of the line indicated consistency of assignment.

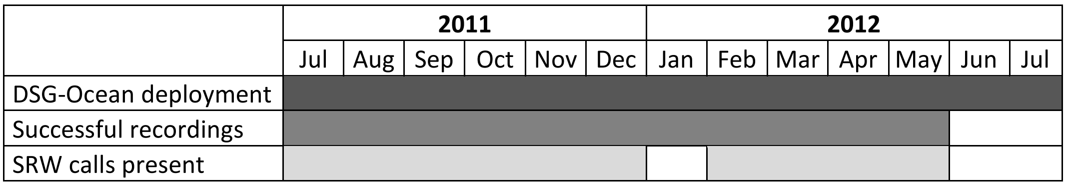
Statistical analyses

Acoustic recordings were examined for any seasonal or diel patterns in vocalisations. Data on the timing of sunrise, sunset, transit time and nautical dusk/dawn at Port Ross were obtained from Land Information New Zealand (LINZ, www.linz.govt.nz). Transit was defined as the maximum altitude of the sun relative to the horizon. Nautical twilight was defined as the period between nautical dawn (or dusk), when the sun is 12° below the horizon, and sunrise (or sunset). Each acoustic recording was assigned to one of five diel periods: dawn (nautical dawn to sunrise), morning (sunrise to transit), afternoon (transit to nautical dusk), dusk (sunset to nautical dusk) and night (nautical dusk to dawn). The duration of each diel period varied between season, with longer daylight hours in summer (mid-summer: dawn ≈2 h, day ≈14 h, dusk ≈ 2 h, night ≈ 6 h) than winter (mid-winter: dawn ≈1.5 h, day ≈8 h, dusk ≈ 1.5 h, night ≈ 13 h). Recordings were also classified by season; December to February was defined as Summer, March to May as Spring, June to August as Winter and September to November as Autumn.

All statistical analyses were carried out in Program R version 3.0.2 (R Development Core Team 2004, www.R-project.org). The hourly calling rates (all calls) and hourly *upcall* rates were calculated from the manual call appraisal to look at seasonal and diel variation. Diel patterns were examined by comparing rates during hour-long time bins based on local time (e.g. 00:00-01:00, 01:00-02:00) and diel periods (dawn, morning, afternoon, dusk, night). Call rates were adjusted to correct for the variation observed during the year, in terms of the total number of calls detected each day, i.e. to remove any influence of the high call rates in July and August. The corrections were calculated by subtracting the overall call rate (calls h^{-1}) for that 24-h day from the hourly call rate within a particular period (Oleson et al. 2007; Munger et al. 2008; Mussoline et al. 2012). This correction resulted in a mean adjusted call rate. A Zero Inflated Model (ZIM) with a negative binomial distribution was used to evaluate whether particular seasons and/or diel periods were important for explaining any differences in right whale call presence and call rate. A ZIM is a two component mixture model (Lambert 1992; Zeilis et al. 2008) which was used in preference to a Generalised Linear Model (GLM) because it accounted for the high number of recordings with no calls present. A log-likelihood ratio test (Zar 1999) was used to determine whether a poisson or negative binomial distribution best fitted the data; here the negative binomial model was significantly better.

3.3 Results

The acoustic recorder was deployed at the Auckland Islands for 347 days from 22 July 2011 during which there were a total of 302 recording days (80.5% of deployment days, Figure 3.3). No recordings were made after 24 May 2012 when the batteries ran out[1]. No data were collected from 3-5 August 2011 inclusive.



	2011						2012						
	Jul	Aug	Sep	Oct	Nov	Dec	Jan	Feb	Mar	Apr	May	Jun	Jul
DSG-Ocean deployment	■	■	■	■	■	■	■	■	■	■	■	■	■
Successful recordings	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨		
SRW calls present	░	░	░	░	░	░		░	░	░	░		

Figure 3.3 Timetable of recorder deployment in Laurie Harbour, Port Ross. Dark grey represents deployment duration, mid grey is recording duration and light grey is detections of right whale calls.

A total of 892 hours of acoustic data were recorded and there was only one month, June, in which there were no acoustic recordings (Figure 3.3). A total of 35,487 right whale calls were manually detected. Of these, 11,623 (33%) were identified as *upcalls* (Figure 3.4).

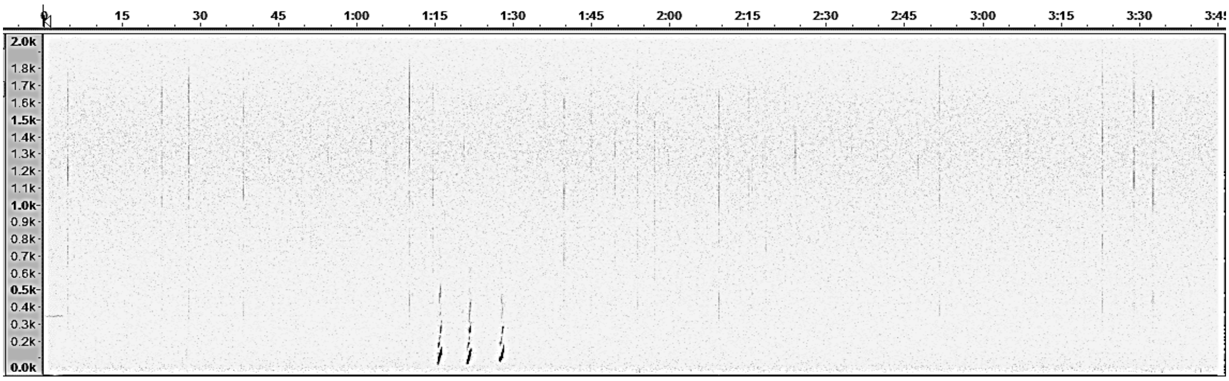


Figure 3.4. Spectrogram from the output of the DSG-Ocean recorder showing three typical right whale *upcalls* during a 3 min 45 s recording from the Auckland Islands, FFT: 2048 points, Hamming window.

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[1] There were two minor gaps in the data due to software bugs. Recordings were skipped between 01:30 and 03:00 on 25 September 2011 due to daylight saving, and the entire day on 1 March 2012 due to a leap year.

Seasonal variation

Vocalisations of SRWs were evident in all months with recordings except for January (Figure 3.5). Vocalisation rates varied dramatically during the deployment period (Figure 3.6) and were at extremely low levels during the summer months. Mean vocalisation rate (all calls combined) showed a strong seasonal trend with higher rates in winter than any other season (Figure 3.7). A similar seasonal pattern was evident when *upcalls* were examined separately (Figure 3.6).

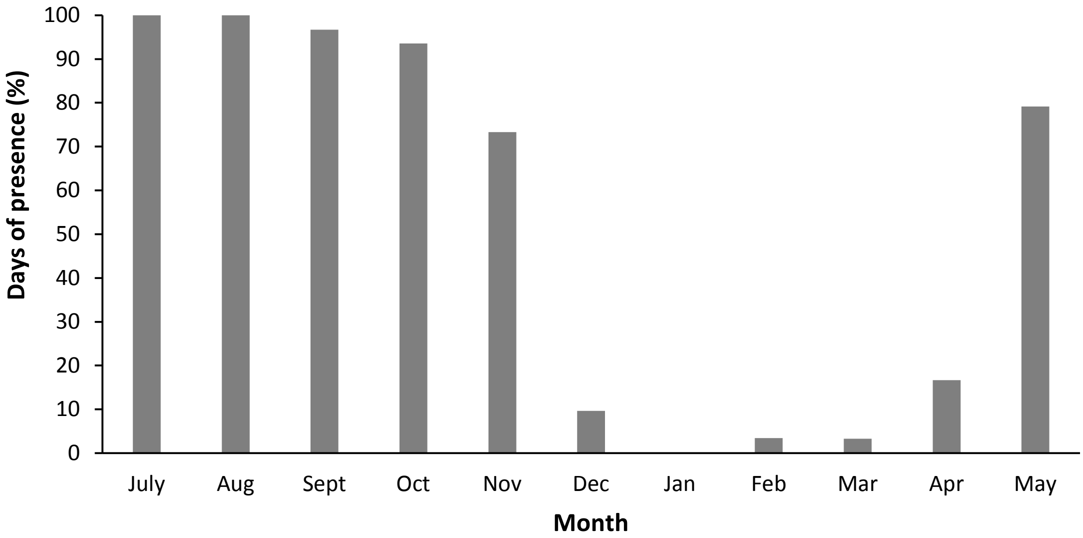


Figure 3.5 Percentage of days in each month (July 2011 to May 2012) that right whale calls were detected in Port Ross, Auckland Islands. N.B. data in July is from a ten day period during the trial deployment of the DSG-Ocean recorder.

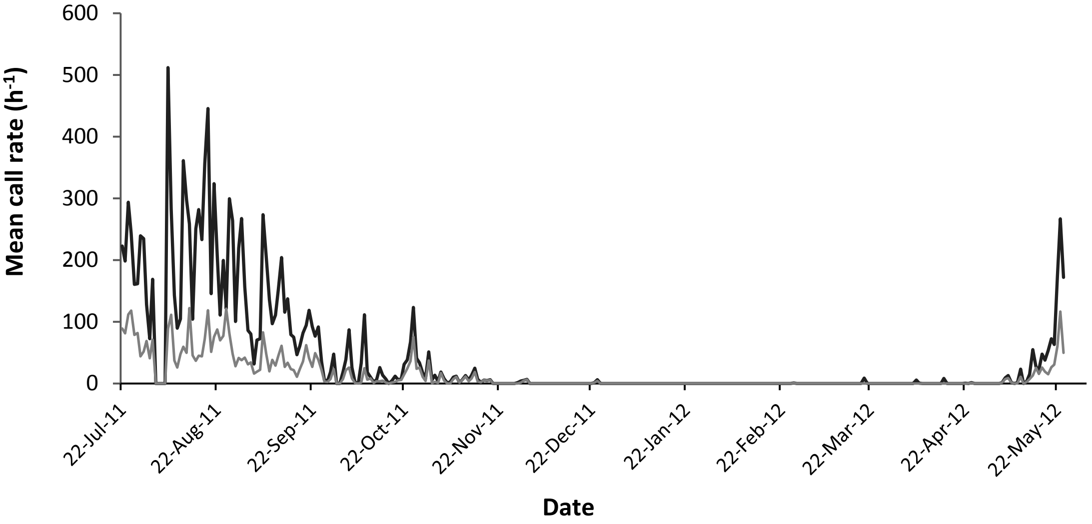


Figure 3.6 Mean number of all calls (black) and *upcalls* (grey) per day for right whales at the Auckland Islands. N.B. no data were collected from 2-5 August 2011 (inclusive).

The mean number of calls per hour was highest in August (288 ± 5.9 [SE]) and July (194 ± 8.3) (Figure 3.8). Mean vocalisation rates remained relatively high in September (91 ± 3.6 calls h^{-1}) before declining through October and November. No calls were observed in January and although calls were detected in December, February, March and April, the mean rate was very low (<1 calls h^{-1}). The vocalisation rate increased again in May (41 ± 2.9 calls h^{-1}) (Figure 3.8).

Upcalls were evident in all months that vocalisations were observed and *upcall* rate followed a similar trend to all vocalisations, although the proportion of all calls that were *upcalls* differed (Figure 3.6). *Upcalls* were the most prevalent of the vocalisation types (on average 30% to 100% of calls in each month). These vocalisations typically accounted for a smaller proportion of calls, 30 to 40%, between July and October when the overall call rate was high. This proportion rose to 93% in April and 100% in February when vocalisation rates were low. Mean *upcall* vocalisation rates were highest in July (76 ± 4.1 calls h^{-1}) and August (60 ± 2.2 calls h^{-1}).

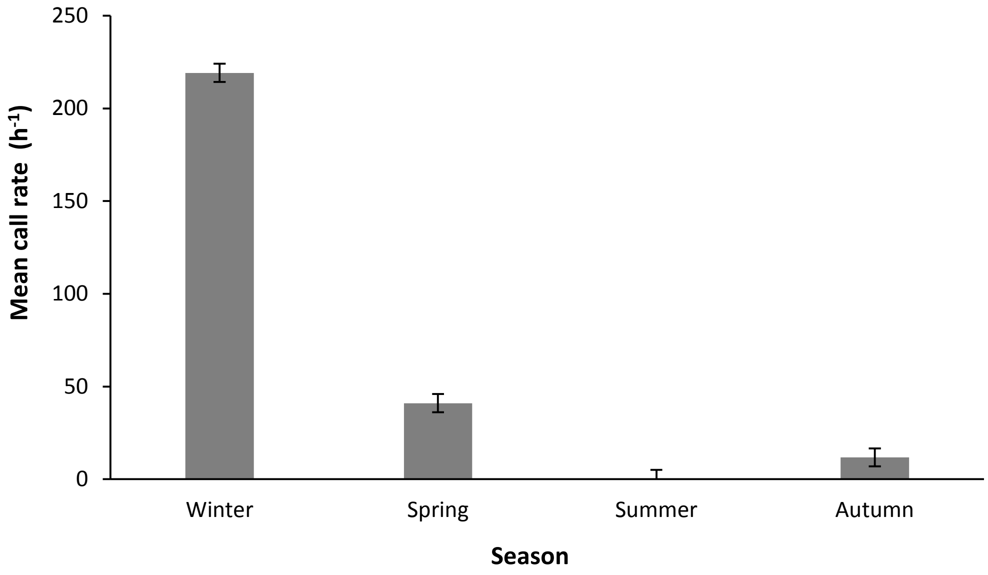


Figure 3.7 Mean vocalisation rate (calls h^{-1} ± SE) by season for southern right whales recorded at the Auckland Islands between July 2011 and May 2012.

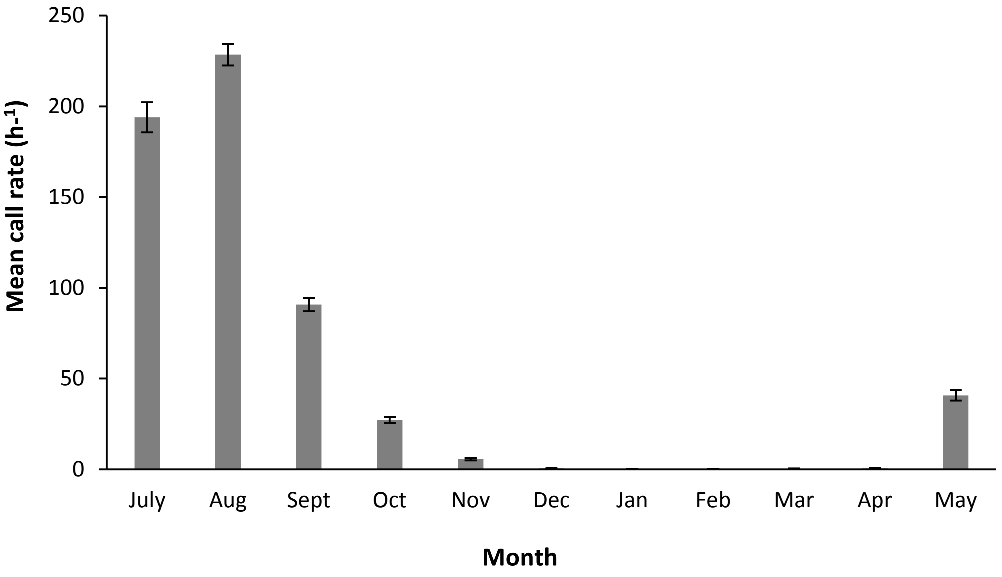


Figure 3.8 Mean vocalisation rate (calls h^{-1} ± SE) by month for southern right whales recorded at the Auckland Islands between July 2011 and May 2012.

Other vocalisation types (*downcall*, *gunshot*, *high*, *hybrid*, *very high* and *blow*) were observed much less frequently than *upcalls,* and in some months were not observed at all (Figure 3.9). Collectively, however, these vocalisation types accounted for 67 % of the total calls observed. *Hybrid*, *high* and *gunshot* vocalisations exhibited similar patterns of seasonal presence (Figure 3.9). *Very high* calls were only detected during a four month period between July and October and at very low levels (< 1 call h^{-1}). Seasonal patterns in vocal behaviour of right whales for the five most abundant call types (*upcall*, *tonal low*, *pulsive*, *downcall* and *gunshot*) showed that call rate for each call type was highest during winter months and lowest during summer months (Figure 3.10). The proportion of the five most abundant call types, however, varied little over the year; *upcall* rates were highest, then *tonal* and *pulsive* calls, and *gunshots* and *downcalls* were always the lowest (Figure 3.10).

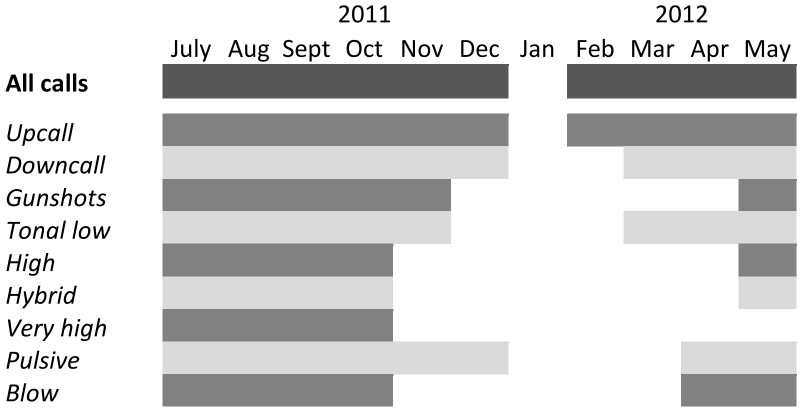


Figure 3.9 Diagram showing monthly presence/absence of different calls types for southern right whales recorded at the Auckland Islands between July 2011 and May 2012. Shaded bars indicate presence.

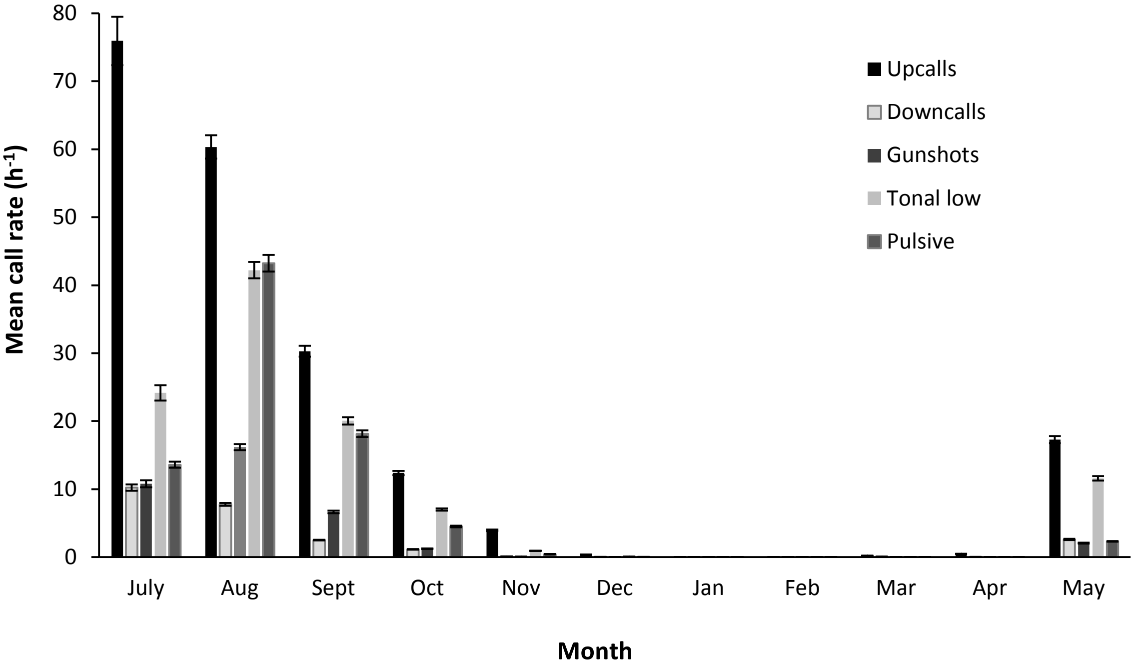


Figure 3.10 Mean call rate (calls h^{-1} ±SE) for the five most common call types (*upcall, downcall*, *gunshot*, *tonal low* and *pulsive*) in each month for southern right whales recorded at the Auckland Islands between July 2011 and May 2012.

Diel variation

While vocalisations were recorded during all hours of the day and night, call rate showed a strong diurnal pattern (Figures 3.11 to 3.14). Mean vocalisation rate increased during the evening and remained high throughout the night (Figures 3.13 and 3.14). When the recordings were categorised by diel period, higher vocal rates were evident at dusk and night and lower rates during the day (Figures 3.13 and 3.14). Mean adjusted call rates exhibited a similar diel pattern to mean call rates and accounted for the fact that call rates were higher during winter months (Figure 3.12 and 3.14). The same diel pattern was evident with higher call rates at dusk and night when *upcall* rate was examined separately.

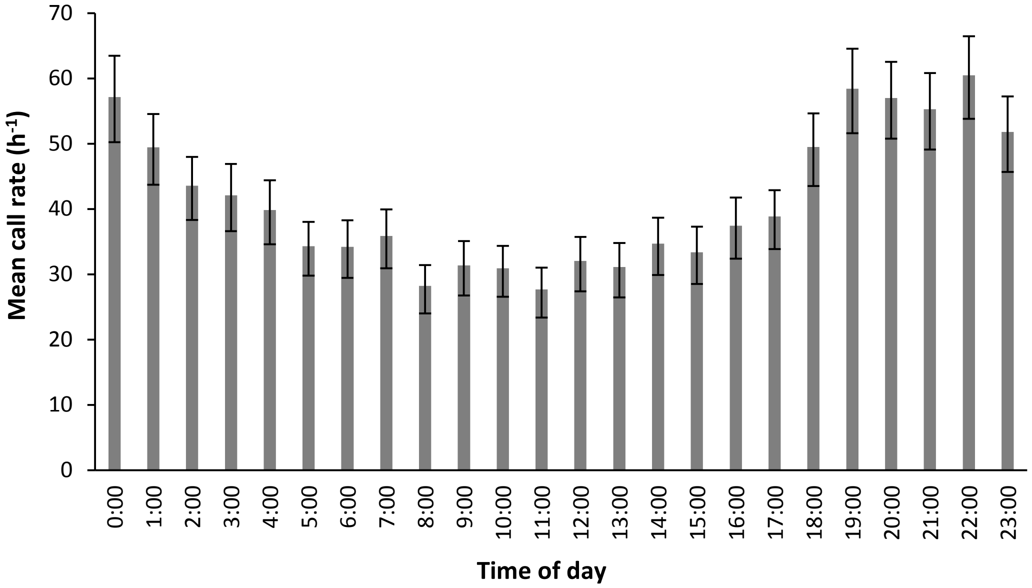


Figure 3.11 Mean hourly vocalisation rate (calls h^{-1} ±SE) for southern right whales recorded at the Auckland Islands between July 2011 and May 2012. The call rate is for the hour after each x axis label.

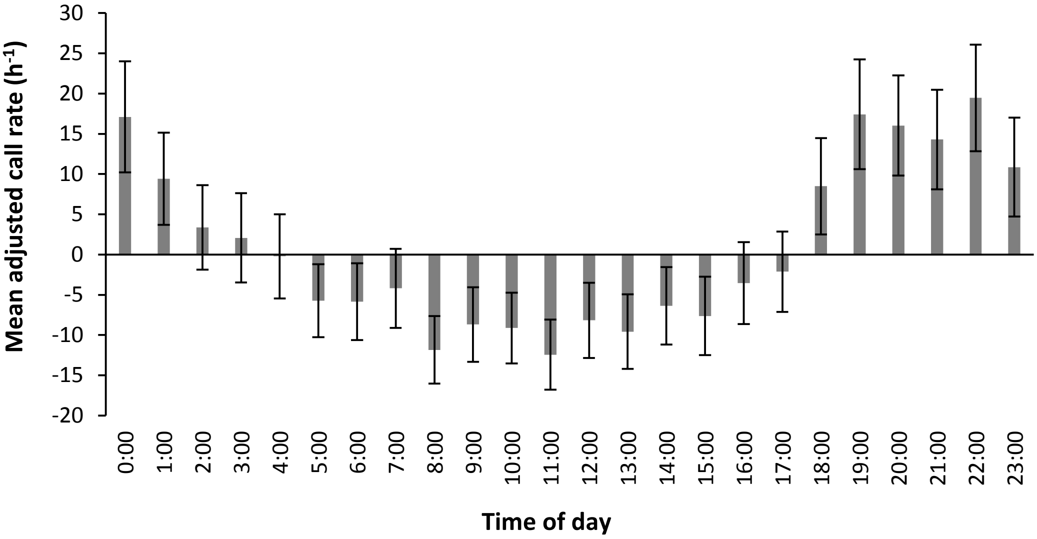


Figure 3.12 Mean adjusted hourly vocalisation rate (calls h^{-1} ±SE) for southern right whales recorded at the Auckland Islands between July 2011 and May 2012. Rates are adjusted to compensate for variation in call rate throughout the year. The call rate is for the hour after each x axis label.

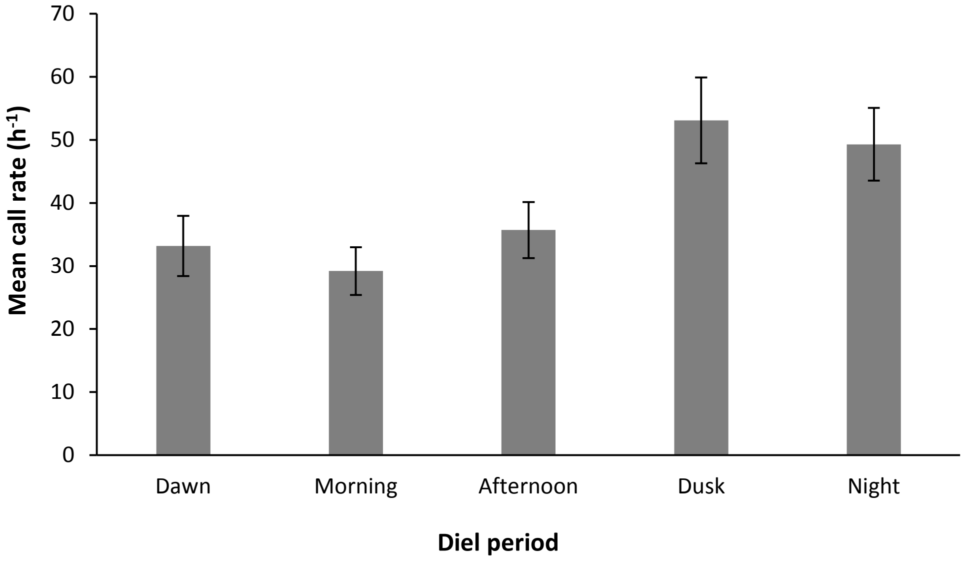


Figure 3.13 Mean call rate (calls h^{-1} ± SE) per diel period for southern right whales recorded at the Auckland Islands between July 2011 and May 2012.

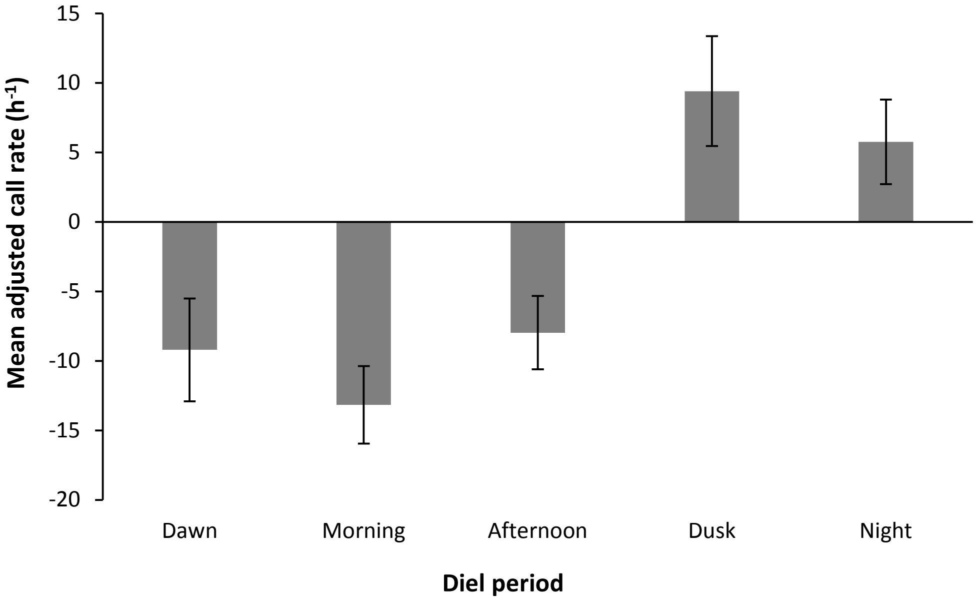


Figure 3.14 Mean adjusted call rate (calls h^{-1} ± SE) per diel period for southern right whales recorded at the Auckland Islands between July 2011 and May 2012. Rates are adjusted to compensate for variation in call rate throughout the year.

Diel patterns in call rate for the five most abundant call types (*upcall*, *tonal low*, *pulsive downcall* and *gunshot*) varied throughout the day with highest rates at dusk and during the night (Figure 3.15). There was no time of day when particular call types predominated; calls were used in similar proportions within each diel period (Figure 3.15).

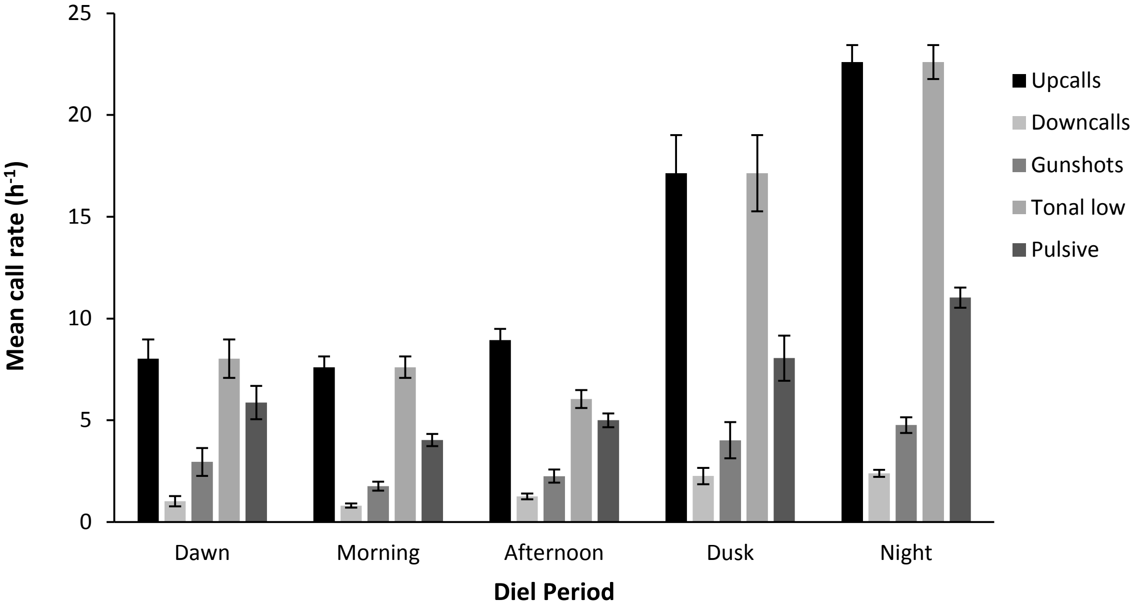


Figure 3.15 Mean call rate (calls h^{-1} ±SE) for the five most common call types (*upcall*, *tonal low, pulsive downcall* and *gunshot*) in each diel period for southern right whales recorded at the Auckland Islands between July 2011 and May 2012.

Statistical tests

The zero-inflated model results showed that season was more important than diel period for explaining the differences in call rate (Table 3.1). Winter in particular had significantly higher call rates than autumn (the reference season). The model showed that dusk and night had significantly higher call rates than the afternoon, but that afternoon rates were similar to those for dawn and morning (Table 3.1). Similar significant results were revealed when the effect of season and diel period on *upcall* vocalisation rate was tested (Table 3.2).

Count model coefficients **Variable**	**Estimate**	**SE**	**z value**	**Pr(>|z|)**
Season Spring	0.05	0.05	0.92	0.36
Season Summer	-0.54	0.28	-1.91	0.06
Season Winter	0.64	0.05	12.69	$<2.00 \times 10^{-16}$
Diel Period Dawn	0.02	0.08	0.32	0.75
Diel Period Dusk	0.28	0.07	3.99	6.52×10^{-5}
Diel Period Morning	-0.13	0.05	-2.62	0.01
Diel Period Night	0.25	0.04	6.27	3.66×10^{-10}
Zero-inflation model coefficients				
Season Spring	-1.61	0.06	-24.85	$<2.00 \times 10^{-16}$
Season Summer	3.65	0.32	11.35	$<2.00 \times 10^{-16}$
Season Winter	-4.80	0.11	-44.68	$<2.00 \times 10^{-16}$
Diel Period Dawn	0.00	0.13	-0.02	0.99
Diel Period Dusk	-0.47	0.12	-3.79	1.49×10^{-4}
Diel Period Morning	0.13	0.08	1.63	0.10
Diel Period Night	-0.66	0.07	-9.50	$<2.00 \times 10^{-16}$

Table 3.1 Results of the zero-inflated model examining seasonal and diel differences in call presence and rate for right whales recorded at the Auckland Islands. The reference level for diel period is afternoon and the reference level for season is Autumn. Significant results are highlighted in grey.

Count model coefficients

Variable	Estimate	SE	z value	Pr(>|z|)
Season Spring	0.08	0.06	1.43	0.15
Season Summer	-0.19	0.27	-0.69	0.49
Season Winter	0.26	0.06	4.76	1.92 x 10^{-6}
Diel Period Dawn	-0.14	0.09	-1.61	0.11
Diel Period Dusk	0.30	0.08	3.79	1.48 x 10^{-4}
Diel Period Morning	-0.01	0.06	-0.26	0.79
Diel Period Night	0.24	0.04	5.34	9.33 x 10^{-8}
Zero-inflation model coefficients				
Season Spring	-1.32	0.07	-18.19	<2.00 x 10^{-16}
Season Summer	3.35	0.32	10.39	<2.00 x 10^{-16}
Season Winter	-3.49	0.08	-42.20	<2.00 x 10^{-16}
Diel Period Dawn	-0.01	0.14	-0.06	0.95
Diel Period Dusk	-0.49	0.13	-3.93	8.62 x 10^{-5}
Diel Period Morning	0.15	0.08	1.83	0.07
Diel Period Night	-0.68	0.07	-9.56	<2.00 x 10^{-16}

Table 3.2 Results of the zero-inflated model examining seasonal and diel differences in *upcall* presence and rate for right whales recorded at the Auckland Islands. The reference level for diel period is afternoon and the reference level for season is Autumn. Significant results are highlighted in grey.

Effectiveness of automated detector

The automated detector designed to identify NARW *upcalls* (Urazghildiiev and Clark 2006) worked well for detecting SRW *upcalls* at the Auckland Islands. There was a positive relationship between the manually observed and automatically detected *upcalls*, although the automated detector picked out slightly more calls than the human analyst (Figure 3.16). The TPR (sensitivity) of the detector was high; 80.4% (SE ± 1.7) of manually categorised *upcalls* were identified by the detector. Thus the rate of missed calls was ~20%. The mean PPV of the detector was, however, relatively low with only 40.4% (SE ± 1.9) of detected *upcalls* correctly identified. Mean PPV was higher (47-67%) when monthly vocalisation rates were high, but dropped between October and April to a mean of 16% when vocal activity was minimal. Therefore, many false detections were made by the automated system, particularly when call rate was low. Some of the false detections however, were other right whale call types (e.g. part of a *hybrid* call). These were classified as false detections here because they were not *upcalls*.

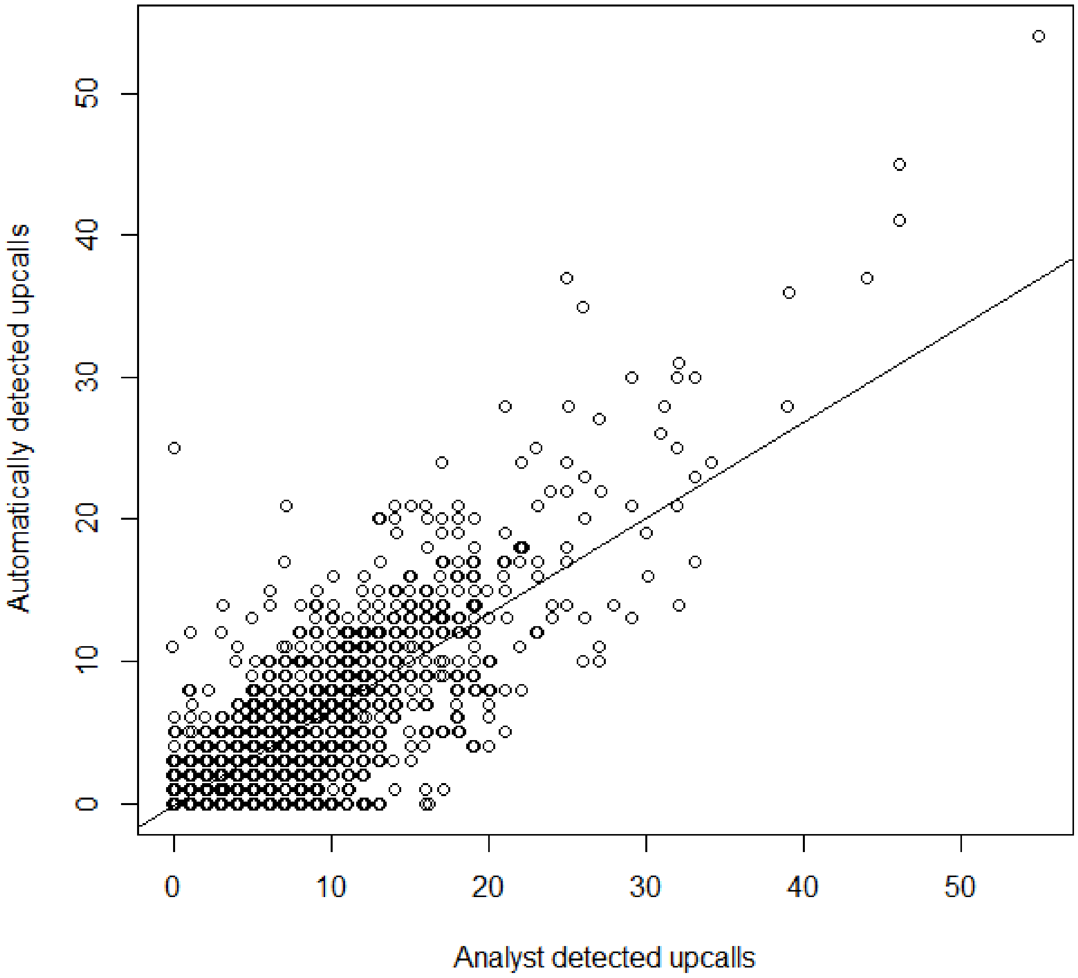


Figure 3.16 A comparison carried out using 10% of all of the recordings to examine the deviation of the number of automatically detected *upcalls* from the number of *upcalls* detected by the analyst. Right whale vocalisations were recorded at the Auckland Islands between July 2011 and May 2012. Best fit linear regression is shown ($y = 0.6743x - 0.1261$, $r^2 = 0.759$). Points have been jittered by 0.6 to offset and reveal overlapping points.

3.4 Discussion

This study has proven the effectiveness of using an autonomous passive acoustic recorder to provide detailed data on SRW vocal behaviour in a remote area seldom visited by vessels. Previously, information on habitat use in this area was limited to visual observations during relatively short visits in the austral winter (Patenaude 2000; Rayment et al. 2012, Appendix A). Acoustic studies have compelling additional benefits: they are viable 24 hours a day, are less restricted by bad weather and are much more affordable than deploying a visual survey team in a remote location for long periods. Additionally, as demonstrated in this study, acoustic data are much more amenable to automated analysis. The principal limiting factor for these particular recorders was battery capacity rather than data storage. Further technological development will likely minimise this constraint.

Seasonal variation

This study found that SRWs are present more often and for longer periods than previously observed at the Auckland Islands (Patenaude 2000). Call rates indicate that right whales are vocally active (and therefore routinely present) between May and November. Except for January, vocalisations were detected in every month during the rest of the year, indicating at least occasional presence in these months. Previously, SRWs were thought to be present at the Auckland Islands from early May to the end of September (Patenaude 2000). Long-term acoustic studies regularly find that marine mammals are present far more frequently than observed visually (Mellinger et al. 2007b; Morano et al. 2012). Peak vocalisation rates (July-August) occurred in the same months as previous visual observations of peak abundance (Patenaude 2000). If SRWs are only passing through or using the outer part of the harbour it is possible that they would not be detected due to the location of the recorder in the inner part of Port Ross. Vocal measures of presence should, therefore, be considered a conservative estimate of SRW presence at the Auckland Islands. It should also be noted that the long periods of silence, in January for example, are presumed to indicate that whales are not present at the Auckland Islands, rather than a change of behaviour that has resulted in the cessation of vocalisations.

The vocalisation rate in winter was four times greater than during any other season and consequently the ZIM results showed that seasonal variation was the biggest contributing factor to call presence. Strong seasonal trends in call occurrence have been observed in other populations of right whales (e.g. Mellinger et al. 2007a; Munger et al. 2008). Seasonal variability in call production is not surprising given that right whales are known to migrate between different feeding and calving grounds (Kenney 2009). Taken together, however, the acoustic studies show that right whales are present in particular habitats more often than expected given what was previously understood of their movements.

Variation in *upcall* rate at the Auckland Islands was similar to that of overall call rate throughout the year. *Upcalls* were the most abundant call type observed (33%) and remained so throughout the year. Recent research (Urazghildiiev and Parks 2014) on NARW vocalisations also found *upcalls* to be the most abundant call type, although they constituted a slightly higher proportion (49%) of all calls than in this study. This variation in proportion could be the result of comparing two different populations of different (although highly related) species. Given that *upcalls* appear to function as contact calls (Clark and Clark 1980; Clark 1982; Parks and Clark 2007) it makes sense that they are the most commonly produced call type. In the previous chapter, the *upcall* was one of the three most abundant call types alongside *tonal low* and *pulsive* calls, although not the highest. This is largely consistent with what we found here and any minor differences in the exact proportion of calls can be explained by the fact that not every call was counted in the previous chapter.

Previous studies have shown that right whales use different calls in different behavioural contexts (Clark 1983; Parks et al. 2005; Parks and Tyack 2005) and that the relative proportion of call types varies both seasonally and geographically (Van Parijs et al. 2009). In this study *very high*, *hybrid*, *high* and *gunshot* calls were only observed over a period of between four to six months of the year. This may indicate a seasonal change in behaviour, or it could simply reflect the low call rates outside the main winter period. *Gunshots*, *hybrid* and *high* calls are thought to be related to mating activities (Parks et al. 2005; Parks and Tyack 2005) and the relative proportion of these calls has been shown to increase during the breeding season (Van Parijs et al. 2009; Matthews et al. 2014). In contrast, calls were used in similar proportions in all seasons at the Auckland Islands - implying that changes in behaviour are relatively subtle compared to the changes observed elsewhere (Van Parijs et al. 2009). The Auckland Islands are the major calving grounds for SRWs in New Zealand waters (Patenaude 2000; Rayment et al. 2012, Appendix A), but it is currently unclear where most mating occurs. Despite extensive photo-identification work (Rayment, unpub. data), no female right whale has been seen at the Auckland Islands first without a calf, then in the subsequent year with a calf. If the gestation period spans approximately a year like that of SRWs in South Africa (Best 1994), the implication is that the Auckland Islands are not the principal mating site for SRWs in New Zealand. Further acoustic monitoring and exploration of other areas such as Campbell Island may help locate the main mating habitat for this population.

Diel variation

Call rates showed a clear diel pattern, with more vocalisations at dusk and during the night and reduced rates during the day (dawn, morning and afternoon). A similar pattern was evident when *upcalls* were examined separately and when vocalisation rates were calculated for each hour of the day. Mean adjusted vocalisation rates, which compensated for the high winter call rates, also exhibited the same diel pattern.

The rate at which right whales call varies with call type, activity of the whales, group composition and group size (Clark 1983; Matthews et al. 2001; Van Parijs et al. 2009). Right whale vocalisations are often more frequent during twilight periods and night in winter calving areas (e.g. Office of Naval Research 1997) and feeding grounds (e.g. Munger et al. 2008; Mussoline et al. 2012; Matthews et al. 2014). The primary prey of NARWs are copepods, whose diel vertical migration influences the whales' behaviour (Baumgartner et al. 2011). For example, Matthews et al. (2014) suggests an inverse relationship between foraging and call production. Daily activity cycles dictated by prey availability have also been observed for other mysticetes and are often linked to the vertical migration of prey (Stafford et al. 2005; Oleson et al. 2007). Sei whales (*Balaenoptera borealis*) called more frequently during the day when prey was unavailable and hence the whales were not feeding (Baumgartner and Fratononi 2008). Mussoline et al. (2012) considered that the high rate of NARW *upcalls* during twilight periods was a reflection of prey distribution, i.e. when prey are more dispersed and foraging intensity is lower, call rate increases. There is little evidence of right whales feeding at the Auckland Islands (Patenaude et al. 1998) and baleen whales rarely feed whilst on calving grounds (Corkeron and Connor 1999). It is therefore unlikely that vocalisation rates at the Auckland Islands are much affected by prey availability. Diel patterns in vocalisation rate could also indicate a change in social behaviour or a general increase in activity or communication (e.g. Clark 1983). In NARWs *gunshot* calls, which are potentially indicative of mating activity, are most frequent in the late afternoon and evening (Parks et al. 2012b). Chorusing by humpback whales on the wintering grounds in Hawaii increases at night, both in terms of amplitude and the number of whales involved (Au et al. 2000). At the Auckland Islands there was little change in the rate of different call types throughout the day which suggests that a diel change in behaviour is unlikely. SRWs do however vocalise more at dusk and night for all call types. This may simply be because reduced visual contact in the dark increases the need for acoustic communication, particularly between mother-calf pairs.

Detection of vocalisations

Throughout the year u*pcalls* were more prevalent than any other vocalisation type and were made at all times of the day. This makes them the most appropriate call type for automated detection, particularly given that they are produced by both males and females (Clark 1983; Parks and Tyack 2005). There is ongoing development of algorithms to detect other right whale call types (Baumgartner and Mussoline 2011; Urazghildiiev and Parks 2014), although traditionally only *upcalls* have been used for detection (e.g. Gillespie 2004; Mellinger 2004; Urazghildiiev and Clark 2006). Excluding *upcalls*, other vocalisation types (e.g. *gunshots* and tonal calls) comprised two thirds of the calls in this study. Although no call positive days were missed by using only an *upcall* detector, the addition of other call types would increase detection probability, particularly when call rates are low. Information on the use of different vocalisation types by right whales is essential for developing and improving passive acoustic monitoring capabilities.

There was a positive relationship between the manually observed and automatically detected *upcalls* in this study, although the automated detector picked out slightly more calls than the human analyst. A high percentage of manually identified *upcalls* was also identified by the automated detector and this was consistent throughout the year. Importantly, however, the false positive detection rate was high, particularly during periods of low vocal activity. The detection threshold of the algorithm could be increased to reduce the number of false positives, but this would also increase the rate of missed calls. In reality however, a proportion of these false detections were actually right whale vocalisations, though not strictly *upcalls*. In other geographical regions, by including these calls as right whale detections there is the potential for misclassifying other cetacean (e.g. humpback whales) calls as right whales. An additional problem with estimating the efficiency of a detection system is that it can never be known precisely how many calls are produced as efficiency can only ever be measured relative to a human analyst (Gillespie 2004).

The detection of calls and associated differences in vocalisation rate could potentially be influenced by ambient noise levels or acoustic propagation conditions. Variability in background noise is likely to change detection probability, as higher noise levels reduce the distances over which whales may be heard (e.g. Richardson and Würsig 1996). Ambient noise levels change with weather conditions (particularly wind and rain; Wenz 1962), activity cycles of biological sound sources such as fish and crustaceans (Radford et al. 2008), and have been shown to vary seasonally by as much as 10 dB peak-to-peak (Curtis et al. 1999).

Conclusions

Recordings from an autonomous acoustic system have provided valuable new insight into the occurrence and vocal behaviour of SRWs at the Auckland Islands, where long-term visual surveys are prohibitively expensive. Similar recordings would also be extremely valuable in areas around the New Zealand mainland where SRWs were historically abundant, but are now seen occasionally, in low numbers. Systematic visual surveys in these areas have a very high cost per sighting, because sightings are so infrequent. The automated detection system developed for NARWs (Urazghildiiev and Clark 2006) is effective for detecting SRW *upcalls* and vastly increases the speed of analysis for large acoustic datasets, particularly where call rate is low. Detailed acoustic data, as collected in this study, are invaluable for understanding the behaviour of cetaceans, and managing impacts on them (Van Parijs et al. 2009).

CHAPTER 4

A COMPARATIVE STUDY OF AMBIENT NOISE CONDITIONS ON RIGHT WHALE CALVING GROUNDS

4.1 Introduction

Ambient noise in the marine environment originates from a range of natural and anthropogenic sources (Wenz 1962; Richardson et al. 1995) and is the result of several cumulative contributing sound sources rather than one localised source (Hildebrand 2009). Natural sources contributing to ambient noise include physical phenomena such as seismic activity (Webb 1998), volcanic eruptions (Dietz and Sheehy 1954), lightning strikes (Dubrovskiy and Kosterin 1993), wind and rainfall (Ma et al. 2005). Biological sound sources include signals produced for communicating and sensing the environment made by marine mammals (Cummings and Thompson 1971; Watkins and Schevill 1977), fish (Brawn 1961; Bass and McKibben 2003) and invertebrates (Moulton 1957; Versluis et al. 2000; Popper et al. 2001). Anthropogenic noise dominates the lower frequencies. It is produced either intentionally, for example by sonar and seismic exploration (Greene and Richardson 1988); or as a by-product of other activities, for example cavitation and engine noise from shipping (Arveson and Vendittis 2000; Ross 2005), and turbine noise from wind-farms (Madsen et al. 2006).

Shipping noise is not uniformly distributed throughout the ocean (Halpern et al. 2008). The northern hemisphere is far busier in terms of shipping traffic than the southern hemisphere (Halpern et al. 2008; Kaluza et al. 2010) and is therefore noisier (Carey and Evans 2011). Newly built vessels are typically larger, more powerful, faster and noisier than their predecessors (Ross 2005). In combination with an overall increase in vessel numbers, these factors have led to a pronounced increase in ocean noise in recent times. Over the past few decades shipping noise has increased by up to 12 dB in areas such as the north-east Pacific (Andrew et al. 2002; McDonald et al. 2006). There has been as much as a 3 dB increase in ambient noise at low frequencies (30-50 Hz) per decade (McDonald et al. 2006), although this rate of increase appears to be slowing (Chapman and Price 2011). Propeller cavitation and machinery noise associated with shipping is the dominant source of underwater noise at low frequencies (i.e. <200 Hz) (Ross 1976; Carey and Wagstaff 1986).

Ambient noise is an important habitat characteristic for marine mammals, fish and other organisms, particularly animals that are dependent on sound for their daily activities. Prior to the addition of noise from anthropogenic sources, many species evolved to use sounds in a frequency range where ambient noise and propagation loss were minimal (Marten and Marler 1977; Wiley and Richards 1978). The impacts of anthropogenic noise can be physiological, vocal or behavioural (Richardson et al. 1995; Richardson and Würsig 1997; Nowacek et al. 2007; Tyack 2008; Ellison et al. 2012). Responses to noise vary in their severity and may include physiological damage (e.g. to the hearing mechanism, Popper et al. 2003; Smith et al. 2004) as well as effects for which the biological significance is less easy to determine (e.g. displacement from an area, Richardson and Würsig 1997; or an increase in call duration, Miller et al. 2000). Noise can also negatively affect the ability of an animal to detect sounds, thus masking the communication signals required to attract mates, find food, avoid predators or navigate (Clark et al. 2009). Impacts are likely to be most serious when an animals' vocal and hearing range overlaps with that of anthropogenic noise. For example, the low frequency sounds used for communication by right whales (Cummings et al. 1972; Watkins and Schevill 1972) overlap considerably with shipping noise. Acoustic pollution therefore has the potential to mask communication sounds and disrupt their behaviour. The busy shipping lanes off the eastern seaboard of the USA are of particular concern, as they overlap with the habitat of the endangered North Atlantic right whale (NARW; *Eubalaena glacialis*; Knowlton and Kraus 2001; Ward-Geiger et al. 2005). Right whales have responded acoustically to increased ambient noise levels by increasing the frequency (Parks et al. 2007) and amplitude (Parks et al. 2011) of their calls. In addition, increased noise levels have been correlated with elevated levels of stress hormones (Rolland et al. 2012).

Increased ambient noise levels are clearly an issue for right whales given that they have exhibited vocal and stress responses. A right whale's ability to communicate is limited by the level and dominant frequency of ambient noise and the propagation conditions of the underwater environment (Richardson et al. 1995). Low frequency noise has the potential to reduce the distance over which a right whale can be detected by a conspecific thus reducing the *active space* available for communication (Clark et al. 2009). The calving grounds of NARWs are in close proximity to shipping lanes and major ports in acoustically polluted waters. In contrast, southern right whales (SRWs; *Eubalaena australis*) around New Zealand inhabit waters with minimal shipping and other anthropogenic activity. Acoustically, the primary calving grounds at the sub-Antarctic Auckland Islands are near-pristine compared to the waters in the North Atlantic. In this chapter I aim to quantify ambient noise levels in these important right whale habitat areas at the Auckland Islands and off the south-east coast of the USA. A comparative analysis of these acoustically different environments and the major contributors to background noise will enable me to examine the potential for overlap with vocalisations and determine how ambient noise may affect the communication of right whales.

4.2 Methods

Data collection

Ambient noise recordings were made on right whale calving grounds in the North Atlantic Ocean and the Southern Ocean (Figure 4.1). The Auckland Islands, in sub-Antarctic New Zealand, are the main calving area for SRWs in New Zealand waters (Patenaude et al. 2000) and high concentrations of whales are found here in the austral winter (Rayment et al. 2012, Appendix A). The south-east coast of the USA is the primary calving area for NARWs during the boreal winter (Kraus et al. 1986b; Winn et al. 1986), and is defined as a *critical habitat* under the Endangered Species Act (NOAA 1994).

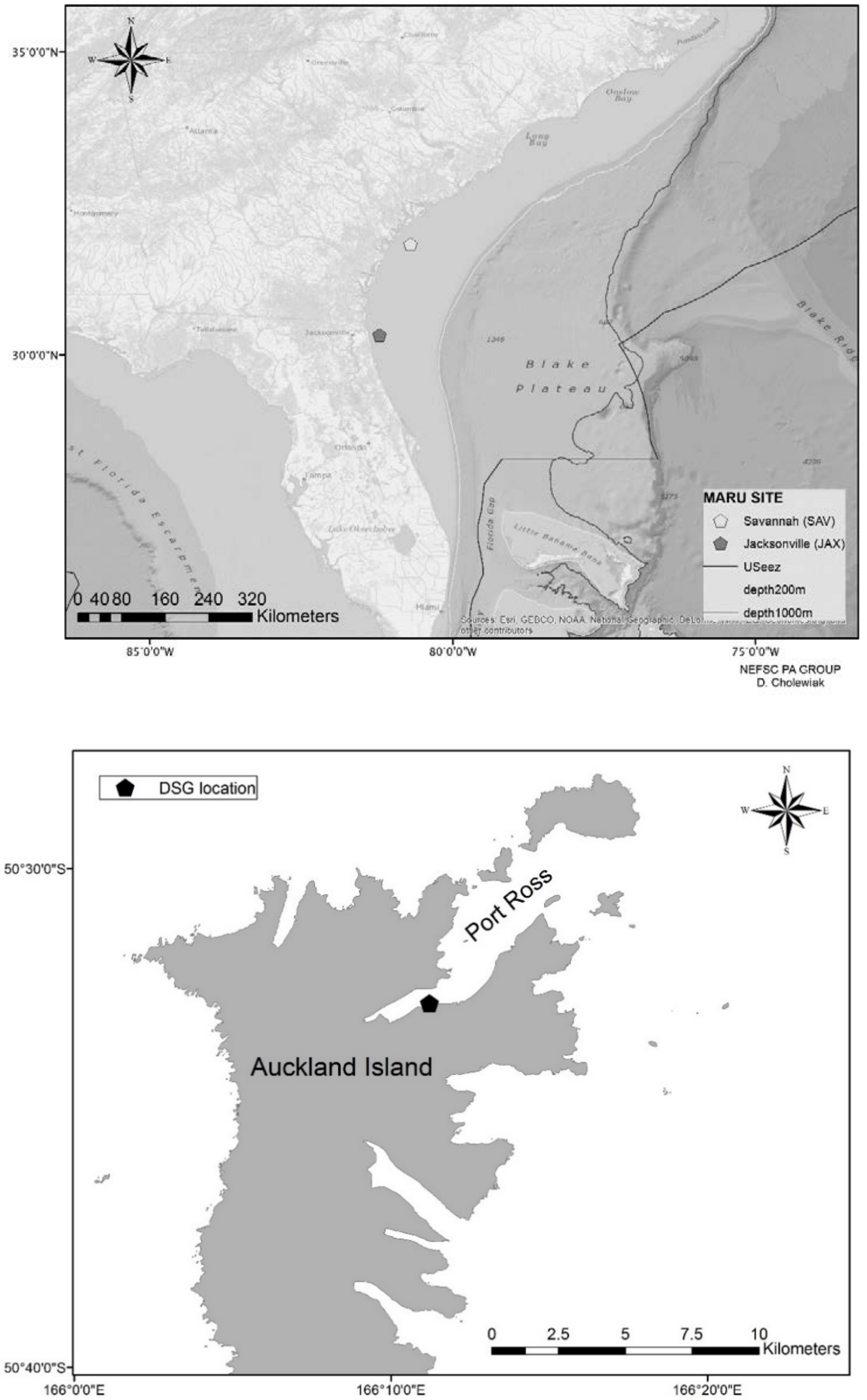


Figure 4.1 Locations of the autonomous acoustic recorders in right whale calving habitat off the south-east coast of the USA in the Atlantic Ocean (top) and in Port Ross, Auckland Islands, sub-Antarctic New Zealand in the Southern Ocean (bottom).

Ambient noise was quantified at two locations on NARW calving grounds; one off Jacksonville, Florida (30°20.2'N, 81°12.7'W) and another off Savannah, Georgia (31°49.7'N, 80°41.8'W) (Figure 4.1). The level of anthropogenic activity is high off this part of the coast with large ports in Georgia (Savannah and Brunswick) and Florida (Jacksonville) situated on major shipping lanes extending from the Gulf of Mexico to Boston and New York further north along the Atlantic coast. Savannah is the busiest port in the south-east region and is the second largest container port on the Atlantic coast (U.S. Army Corps of Engineers 2012). Comparative ambient noise recordings were gathered from Laurie Harbour in Port Ross at the northern end of the remote Auckland Islands (50°33.4'S, 166°12.3'E). Port Ross is a large, sheltered harbour with very low levels of anthropogenic activity. This region is not on any major shipping routes and the nearest commercial port is Bluff, 465 km away, on mainland New Zealand. The islands are uninhabited and there are only occasional visits from sub-Antarctic cruise ships, researchers and fishing vessels seeking shelter.

Two Marine Autonomous Recording Units (MARUs, Cornell Bioacoustics Research Program, USA) were used in the North Atlantic. Each MARU comprised a HTI-94-SSQ hydrophone with a sensitivity of -162 dB re 1V/µPa (frequency response: 10 Hz - 32 kHz ± 3dB). Both MARUs were deployed at a depth of 64 m and continuously recorded at a sampling rate of 2 kHz. Ambient noise recordings were made over a seven month period between 18 November 2009 and 4 June 2010 in Jacksonville and between 18 November 2009 and 16 March 2010 in Savannah, including peak calving time (December to March, Kraus et al. 1986b). A DSG-Ocean autonomous recorder (Loggerhead Instruments, USA, www.loggerhead.com) was deployed at a depth of 16 m in Port Ross. The DSG-Ocean recorder consisted of a single HTI-96-MIN hydrophone with a sensitivity of –185.6 dB re 1V/µPa (frequency response 20 Hz - 50 kHz ± 3dB). Ambient noise was recorded during a five month period between 7 August 2011 and 31 January 2012. This includes the peak calving period at the Auckland Islands in August (Patenaude et al. 2000). The DSG-Ocean recorded at a sampling rate of 4 kHz for a duty cycle of 3.75 min every 30 min.

Quantifying ambient noise

Ambient noise levels were measured using the Long-term Spectrogram (LT-Spec) tool (Cortopassi 2007) which runs in MATLAB v7.10 (The MathWorks Inc., MA, USA). LT-Spec computes long-term spectral averages, which are an effective way of analysing large quantities of ambient noise data (e.g. Soldevilla et al. 2014). Calibration values for the two different recorders were entered into LT-Spec software. The calibration values represent the sound pressure at the hydrophone per recorded bit in the sound file, and are calculated from the known hydrophone sensitivity, pre-amp gain and A/D conversion rate.

Fast Fourier Transform (FFT) resolution was chosen to ensure that data from the DSG-Ocean and MARU were being analysed at the same frequency and time resolution. Time resolution (ΔT) and frequency resolution (ΔF) were calculated using the formulae:

$$\Delta T = FFT/f_s{}^{*} \text{ and } \Delta F = f_s/FFT$$

Where: *FFT* is a fast fourier transform, f_s is sampling rate (*assuming no overlap).

Spectra were calculated to obtain resolutions as close to 1 Hz and 1 s as possible; for the DSG-Ocean recorder (f_s = 4 kHz) a 4096 pt FFT was used and for the MARU recorder (f_s =2 kHz) a 2048 pt FFT was used. Without overlap, this gave a frequency resolution of 0.98 Hz and a time resolution of 1.02 s. I also averaged over 225 s each hour (the DSG file sample length) to obtain a single measurement for each frequency band per hour (i.e. 24 measurements per day). A combined received level was calculated in LT-Spec via summing and averaging over two frequency bands (50-250 Hz and 50-1000 Hz) and at 40 Hz. The two frequency bands cover the fundamental frequency of most right whale calls (50-250 Hz) and the frequency range of most right whale calls including harmonics (50-1000 Hz). The 40 Hz frequency spectrum avoids right whale calls but contains ship noise (e.g. McKenna 2011).

Percentiles (95th, 75th, 50th, 25th and 5th) were calculated in LT-Spec for each of the frequency bins (Cortopassi 2007) and an empirical cumulative distribution function (ECDF) was calculated for ambient noise in each of the locations (e.g. Parks et al. 2009). The ECDF is a measure of the percentage of time that the ambient noise is above a particular sound level threshold and was calculated in Program R version 3.0.2 (R Development Core Team 2004, www.R-project.org) using the *ECDF* function in the *Stats* package. The ECDF was calculated for the 40 Hz spectrum level and the 50 to 250 Hz frequency band using the following formula.

$$Fn(t) = \frac{1}{n}\sum_{i=1}^{n} I(x_i \leq t)$$

Where: *Fn* is the ECDF, *t* is a given spectrum sound level measurement, *n* is the number of measurements in the period, *I* is an indicator function where x_i are all the measurements less than *t* (van der Vaart 1998).

4.3 Results

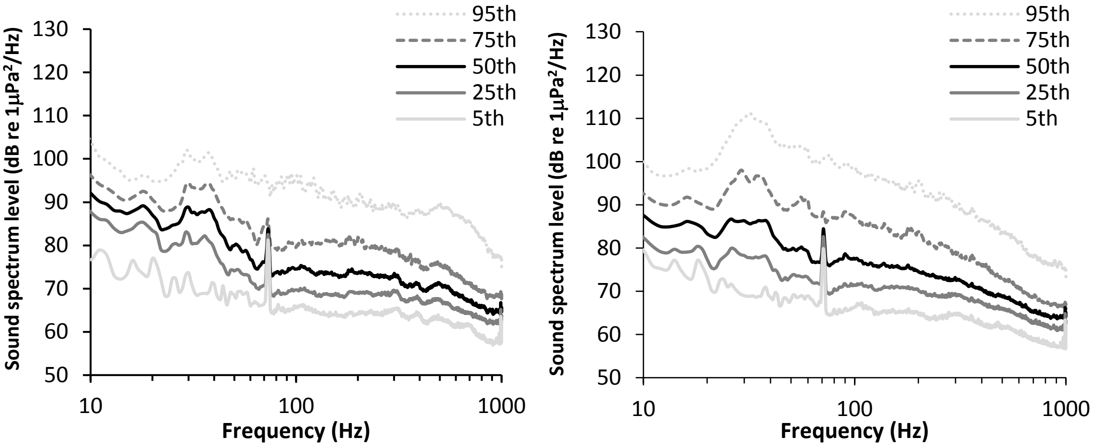
Quantifying ambient noise

A long-term statistical analysis of ambient noise was carried out at three sites; two on NARW calving grounds in the Atlantic Ocean and one on a SRW calving ground in the Southern Ocean (Table 4.1). The MARU at the Savannah site suffered from intermittent recording failures between mid-December and mid-January. Days were excluded from the analysis if there were less than five recording hours available for that particular day (12 December 2009 to 2 January 2011, 8 to 10 January 2011 and 13 to 14 January 2011). The DSG-Ocean recorder at the Auckland Islands also experienced gaps in the data due to software bugs. Recordings were skipped between 01:30 and 03:00 on 25 September 2011 due to daylight saving, and the entire day on 1 March 2012 due to a leap year. Again these data were excluded from analyses. There were distinct differences in the ambient noise levels at the three sites particularly between calving grounds for NARW and SRW. Ambient noise levels on the calving grounds in the Atlantic Ocean (Figures 4.2 to 4.4) were much higher than levels at the Auckland Islands (Figure 4.5).

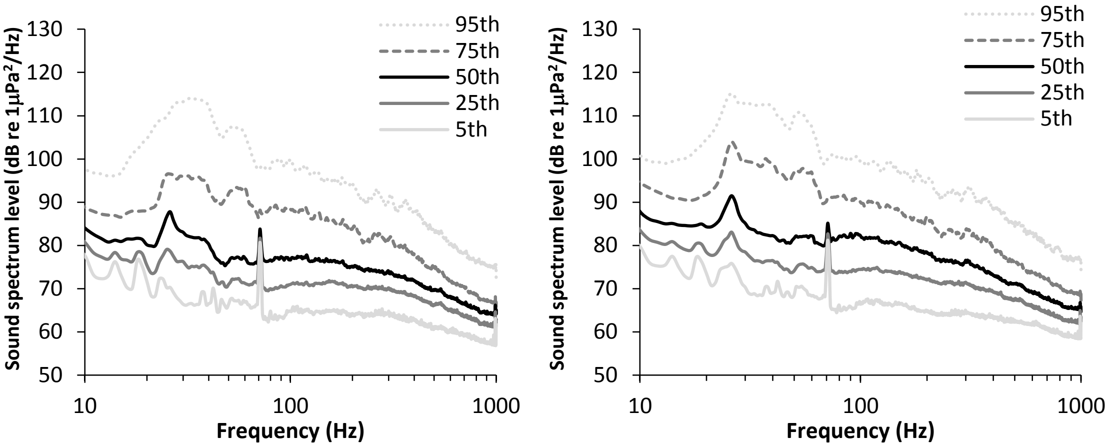
The Jacksonville and Savannah sites exhibited a similar pattern throughout the year with higher noise levels at lower frequencies (<200 Hz) and slightly lower noise levels above this frequency (Figures 4.2 to 4.4). The Auckland Islands site had a completely different pattern with consistently low levels of ambient noise across all frequency bands (10-1000 Hz) through the majority of the recording period (Figure 4.5). At the Auckland Islands, 95% of the time ambient noise levels were below 80 dB re 1μPa^2/Hz. The corresponding levels in the North Atlantic were far higher: below 110 and 120 dB re 1μPa^2/Hz for 95% of the time at Jacksonville and Savannah respectively.

Site	Number of days sampling	% of time sampling
Jacksonville, Florida	197	100[1]
Savannah, Georgia	98	100[1]
Auckland Islands, New Zealand	186	12.5

Table 4.1 Summary of acoustic recordings made at three sites on right whale calving grounds. ([1]Data were subsampled during analysis to match data from the Auckland Islands).

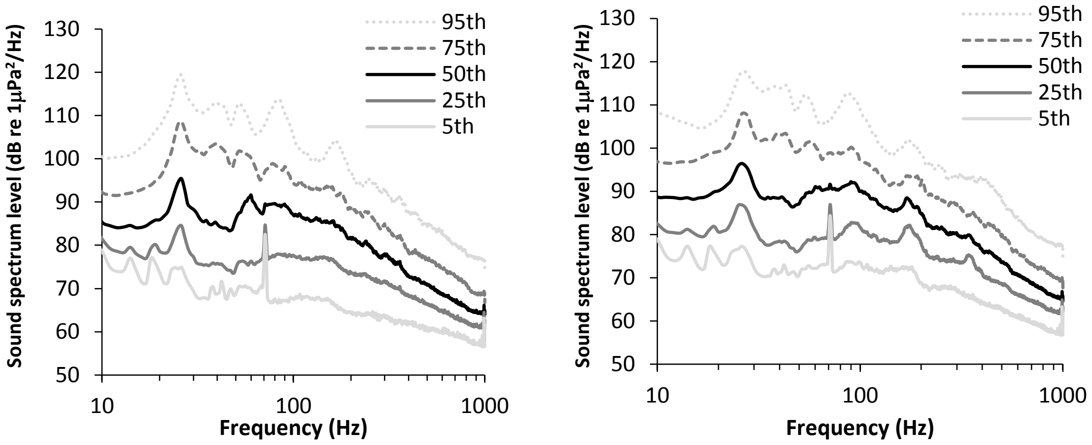


November **December**

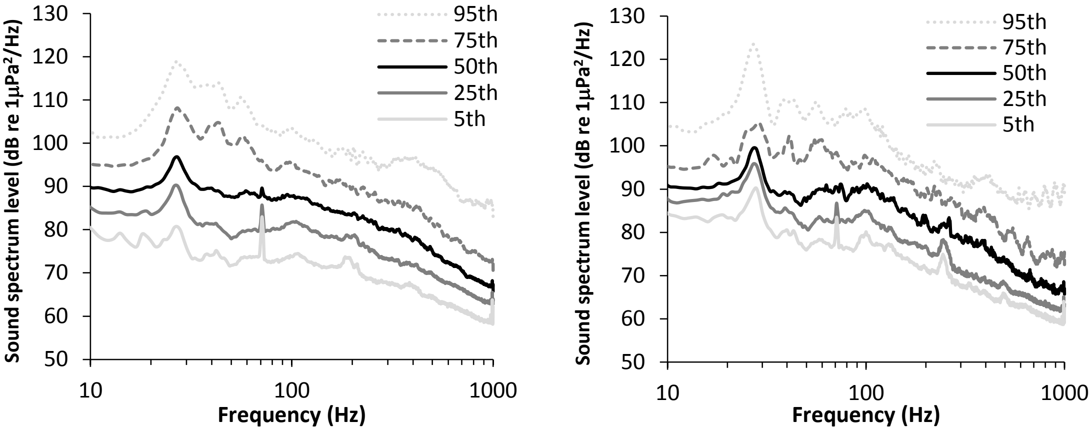


January **February**

Figure 4.2 Low frequency sound spectrum levels per month at Jacksonville from 18 November 2009 to 28 February 2010. Plots show the percentiles, or the sound levels below which a certain percentage of ambient noise measurements fall.

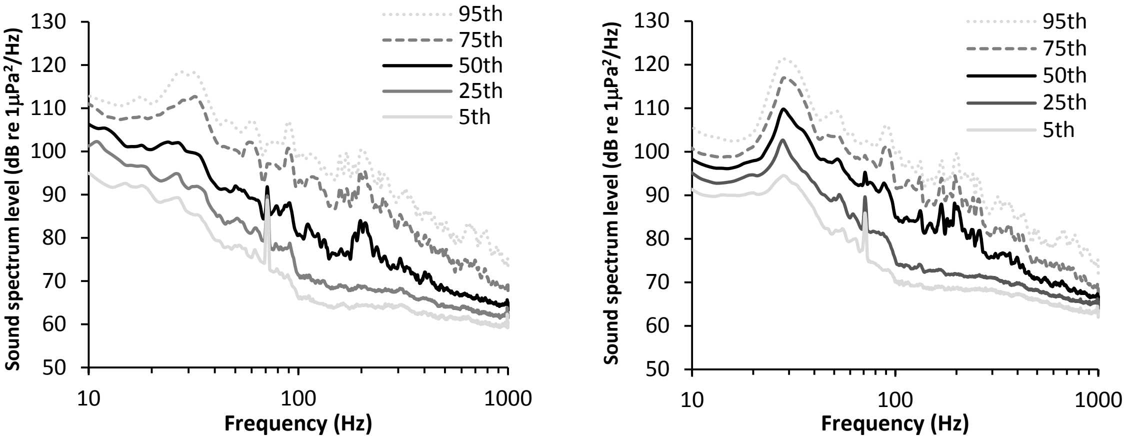


March **April**

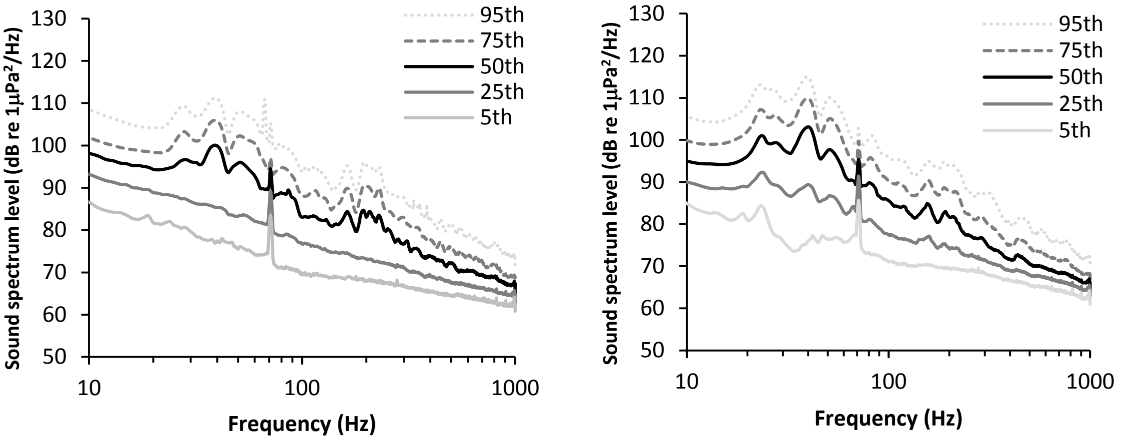


May **June**

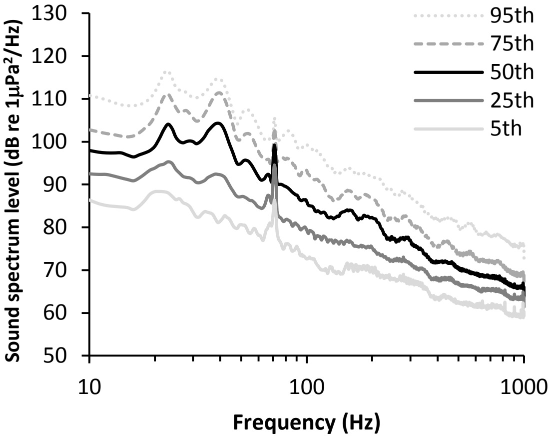
Figure 4.3 Low frequency sound spectrum levels per month at Jacksonville from 1 March 2010 to 4 June 2010. Plots show the percentiles, or the sound levels below which a certain percentage of ambient noise measurements fall.



November **December**

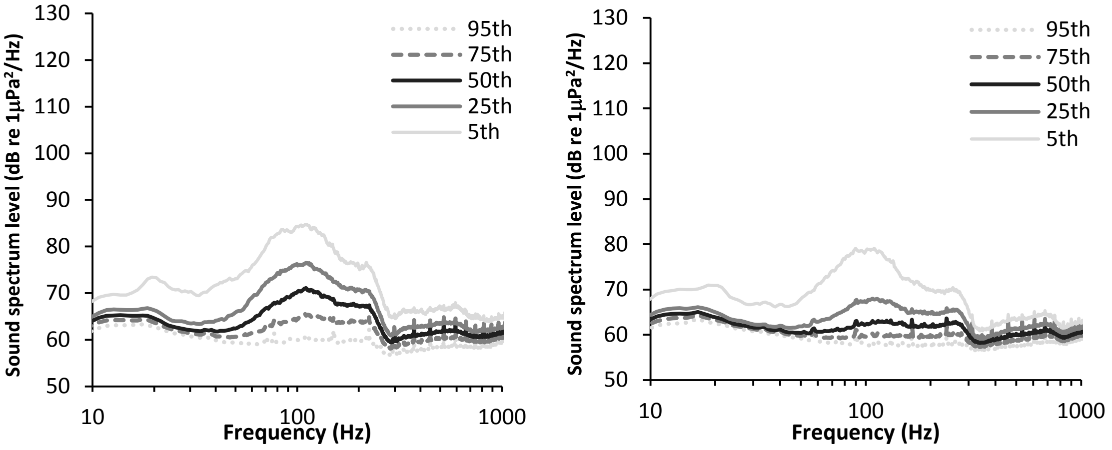


January **February**

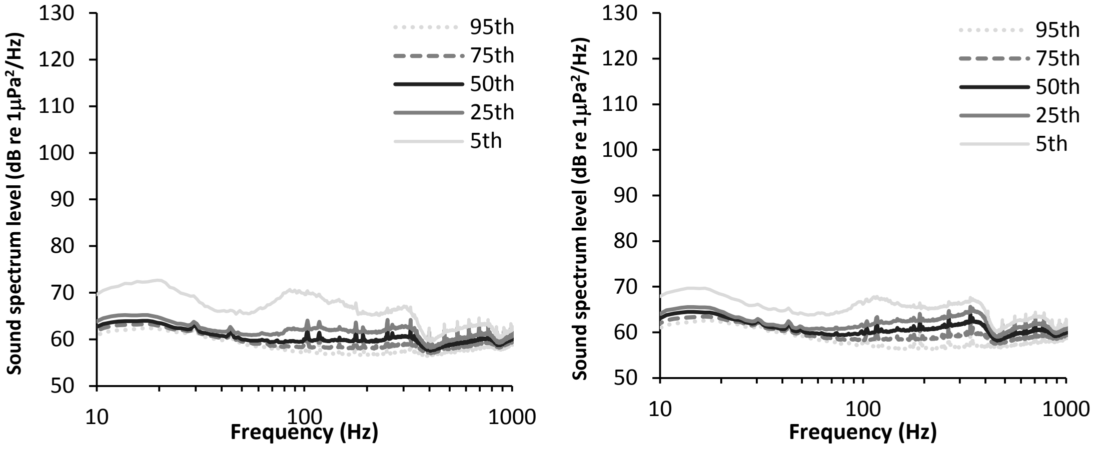


March

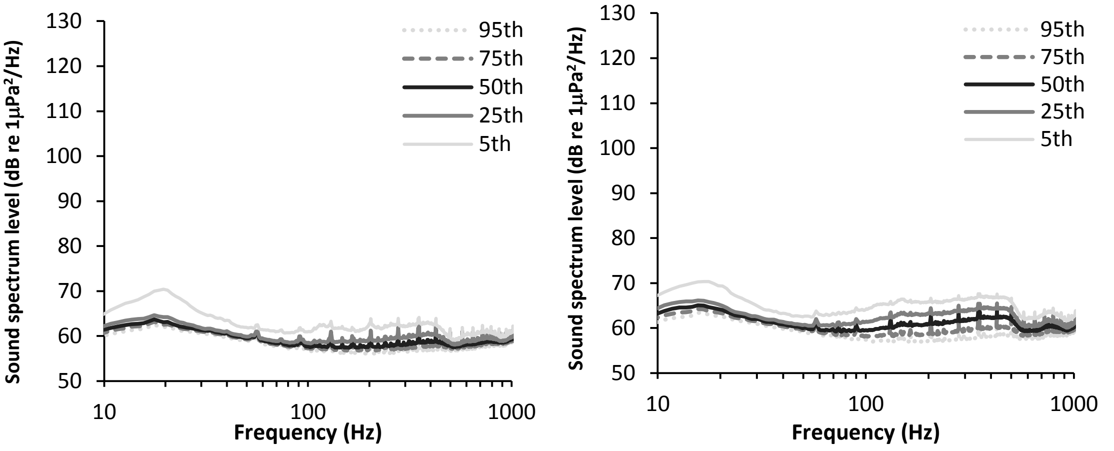
Figure 4.4 Low frequency sound spectrum levels per month at Savannah from 18 November 2009 to 16 March 2010. Plots show the percentiles or the sound levels below which a certain percentage of ambient noise measurements fall.



August **September**



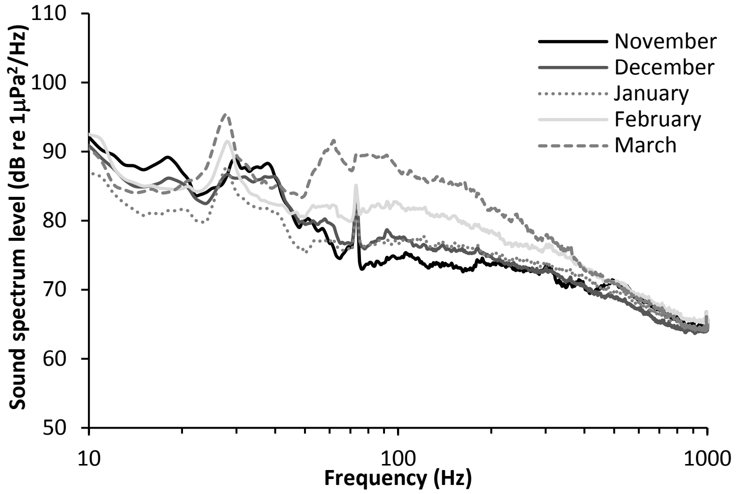
October **November**



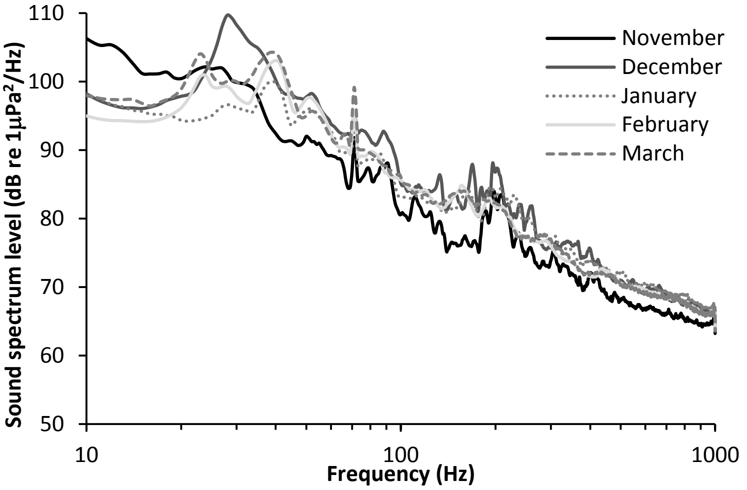
December **January**

Figure 4.5 Low frequency sound spectrum levels per month at the Auckland Islands from 7 August 2011 to 31 January 2012. Plots show the percentiles or the sound levels below which a certain percentage of ambient noise measurements fall.

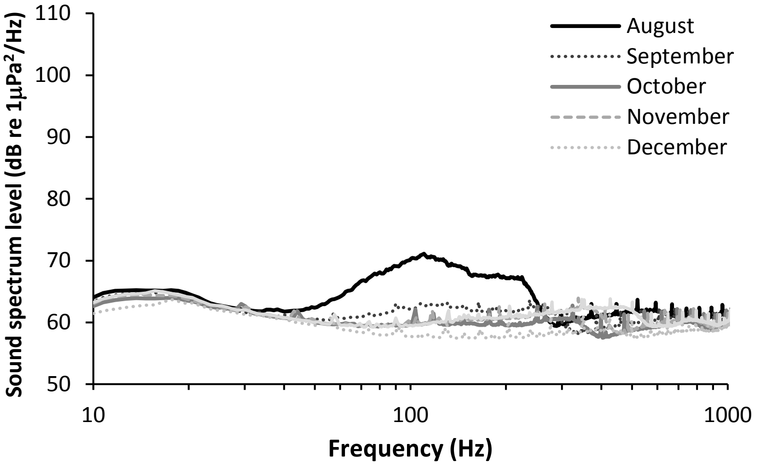
All sites displayed temporal variation in mean sound spectrum levels over the recording periods (Figure 4.6). Jacksonville exhibited higher noise levels during the boreal spring and early summer (March to June). No recordings were available during this time period in Savannah so it is unclear whether the same pattern would have been evident there. At the Jacksonville and Savannah sites there was a peak in ambient noise levels at ~30 Hz before a steady decrease at higher frequencies (up to 1000 Hz). Mean sound levels were consistently low for all months excluding August at the Auckland Islands. During August, however, there was a peak between 60 Hz and 250 Hz.



Jacksonville



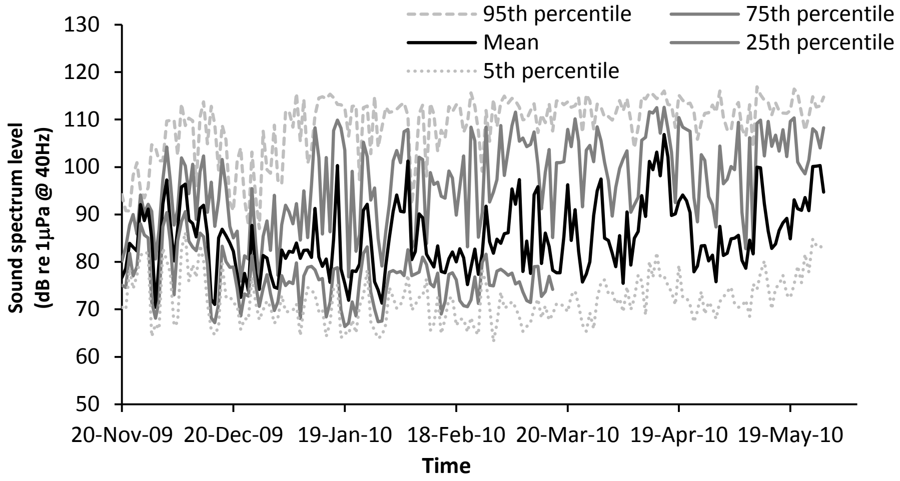
Savannah



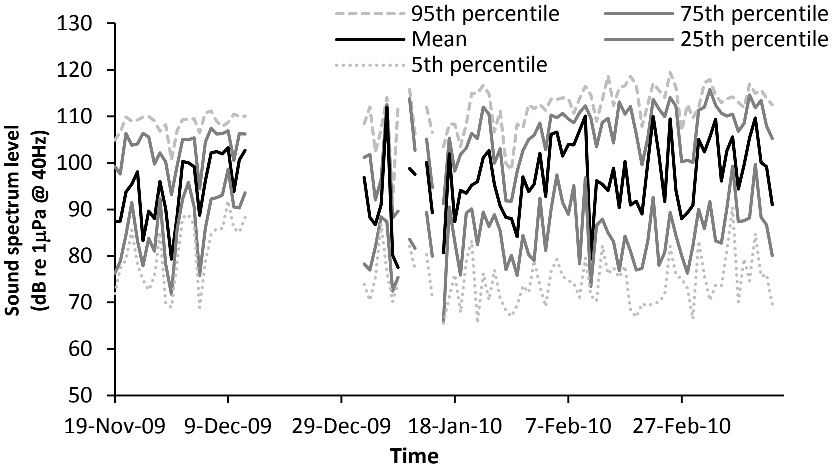
Auckland Islands

Figure 4.6 Summary of mean sound spectrum levels throughout the recording periods at the Jacksonville, Savannah and Auckland Islands sites.

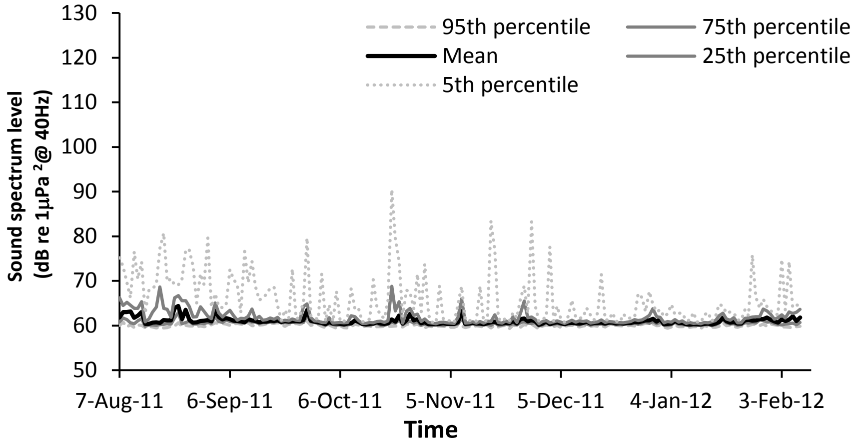
Ambient noise levels at the 40 Hz spectrum level (Figure 4.7) were examined to give an indication of low frequency noise including shipping but excluding right whale calls. It is acknowledged however that the 40Hz spectrum level may include other natural sources of sound e.g. wave noise. Savannah exhibited higher noise levels (mean: 96 ± 0.79 [SE] dB re 1μPa^2/Hz) than Jacksonville (mean: 85 ± 0.54 dB re 1μPa^2/Hz), and both sites had higher low frequency noise levels than the Auckland Islands (mean: 61 ± 0.05 dB re 1μPa^2/Hz). The noise levels at 40 Hz at the Auckland Islands were consistently low throughout the recording period, apart from sporadic peaks in the 5th percentile noise level which correspond with specific broadband noise events. The low frequency noise levels in the Atlantic were highly variable over time with differences of almost 30 dB re 1μPa^2/Hz over a matter of days during some parts of the recording period.



Jacksonville



Savannah



Auckland Islands

Figure 4.7 Sound spectrum levels at 40 Hz throughout the recording periods for Jacksonville, Savannah and the Auckland Islands (N.B. gaps in the Savannah data are due to intermittent hard-drive failure).

Mean ambient noise levels in the 50-250 Hz and 50-1000 Hz frequency bands were higher in the North Atlantic than in the Southern Ocean (Table 4.2), although the variability within these bands was smaller than the variability within the 40 Hz spectrum level. Noise levels were 21-24 dB re 1μPa^2/Hz higher in the 250-1000 Hz band at the two North Atlantic sites than the Auckland Islands. Levels of ambient noise were also higher in the 50-1000 Hz band at both sites in the Atlantic (by 16-22 dB re 1μPa^2/Hz). These are the primary frequency bands used by right whales, hence they include biological noise as well as anthropogenic and other natural sources.

Frequency band	Location	Mean	SE	Min	Max
50-250 Hz band	Jacksonville	108.2	0.2	85.7	142.1
	Savannah	106.5	0.2	59.6	126.6
	Auckland Islands	86.0	0.1	80.2	129.5
50-1000 Hz band	Jacksonville	109.7	0.1	88.9	143.0
	Savannah	107.4	0.7	88.6	126.9
	Auckland Islands	91.6	0.1	80.3	130.1

Table 4.2 Mean, standard error, minimum and maximum ambient noise levels (dB re 1μPa^2/Hz) at 50-250 Hz and 50-1000 Hz band at three recording locations.

The empirical cumulative distribution function (ECDF) metric was used to quantify variability for the 40 Hz spectrum level (Figure 4.8) and the 50-250 Hz band (Figure 4.9) across the three sites. The noise levels at the sites in the Atlantic were more variable than the Auckland Islands site for the 40 Hz spectrum level (Figure 4.8). The two Atlantic sites also had higher noise levels overall at the 40 Hz spectrum level. The noise levels at all three areas varied considerably for the 50-250 Hz band, but levels in the Auckland Islands were lower than the Atlantic (Figure 4.9). An abrupt step in the ECDF for the Auckland Islands is indicative of a sudden jump in noise levels within this 50-250 Hz band, likely coincident with the sudden increase in calling activity during the main calving season.

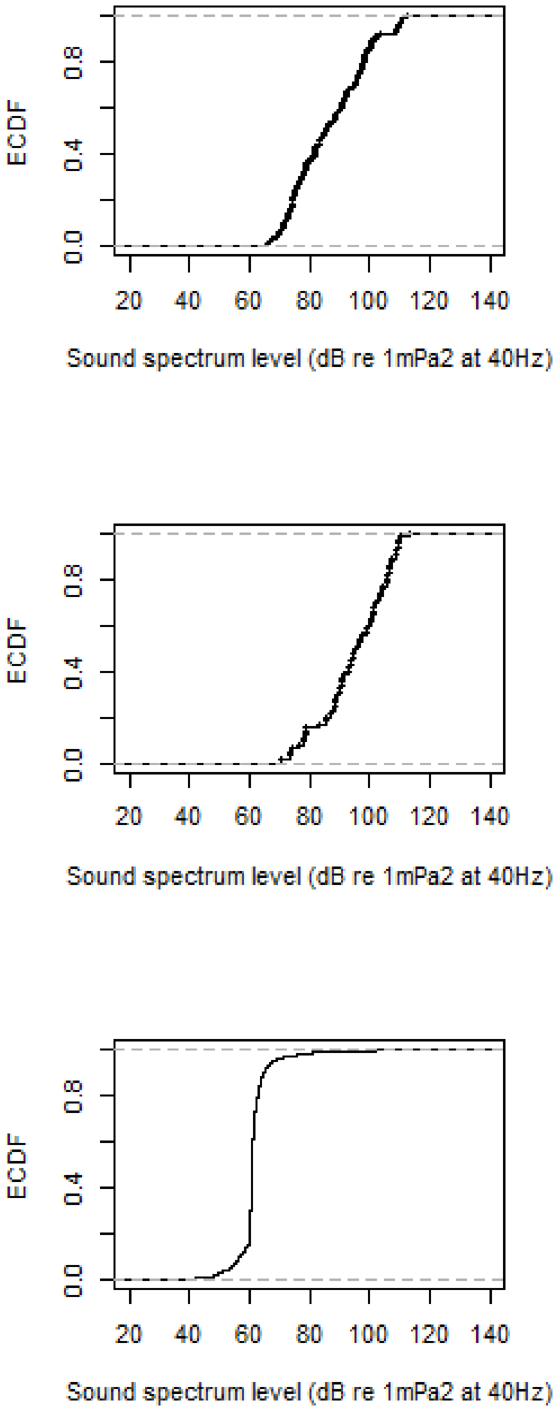


Figure 4.8 Empirical cumulative distribution functions for the 40 Hz spectrum level throughout the recording periods for Jacksonville (top), Savannah (middle) and the Auckland Islands (bottom).

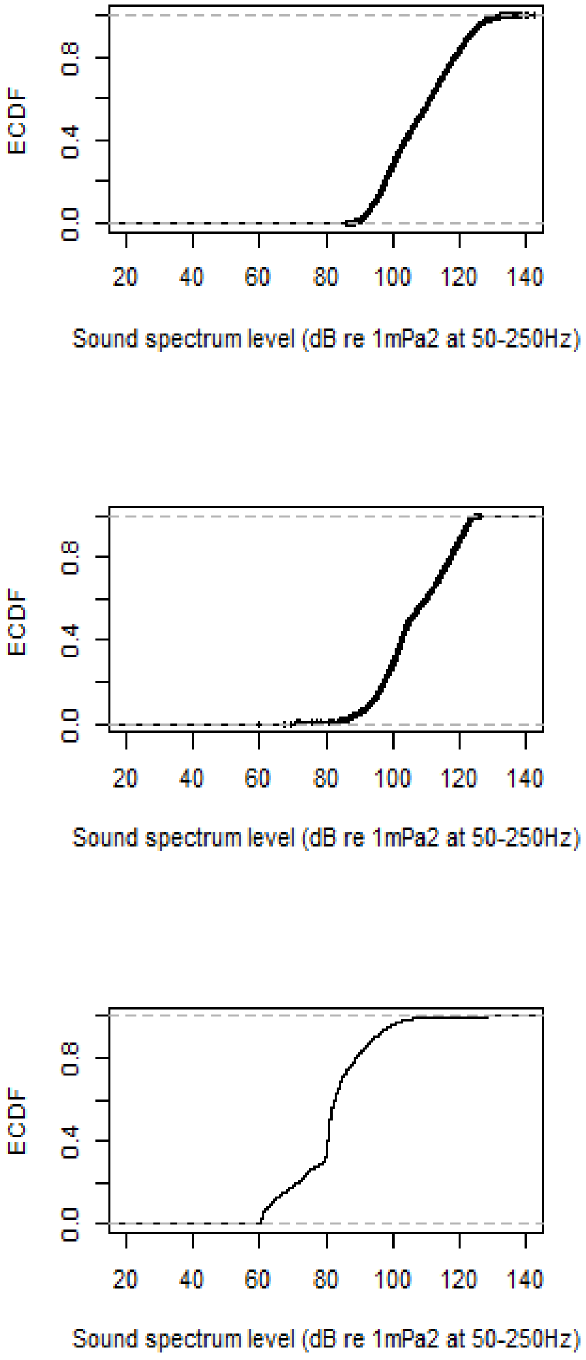


Figure 4.9 Empirical cumulative distribution functions for the 50 Hz to 250 Hz spectrum level throughout the recording periods for Jacksonville (top), Savannah (middle) and the Auckland Islands (bottom).

Several noise sources can be identified that contribute to ambient levels at the three sites. At the Auckland Islands there is a seasonal contribution from right whale calls, with the highest call rates in August and September (Figure 4.10). The fundamental frequency of most SRW calls is in the 50 to 250 Hz band. Broadband sounds at the Auckland Islands (Figure 4.11) were evident in the 5th percentile noise peaks (Figure 4.7) and their major frequency content was below 500 Hz. These peaks occurred less regularly when right whale calls were absent (January) and potentially these sounds are indicative of right whales (or sea lions) rubbing up against the hydrophone.

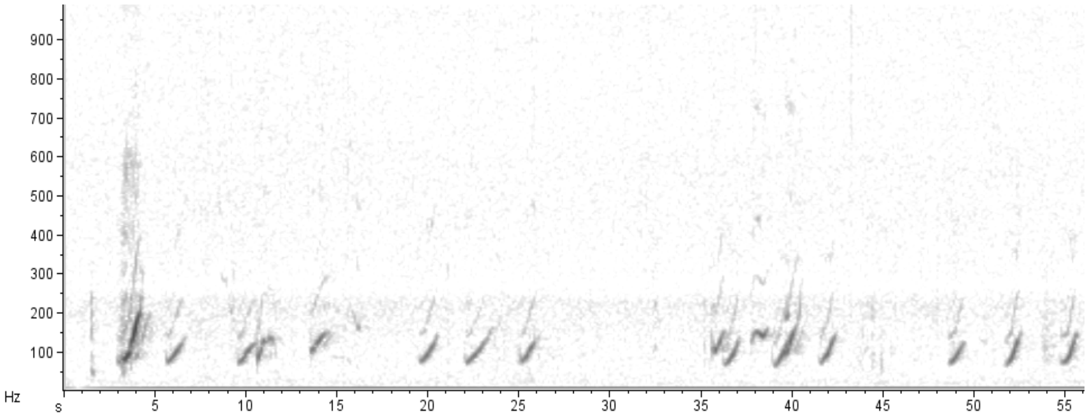


Figure 4.10 Example spectrogram of southern right whale calls recorded at the Auckland Islands.

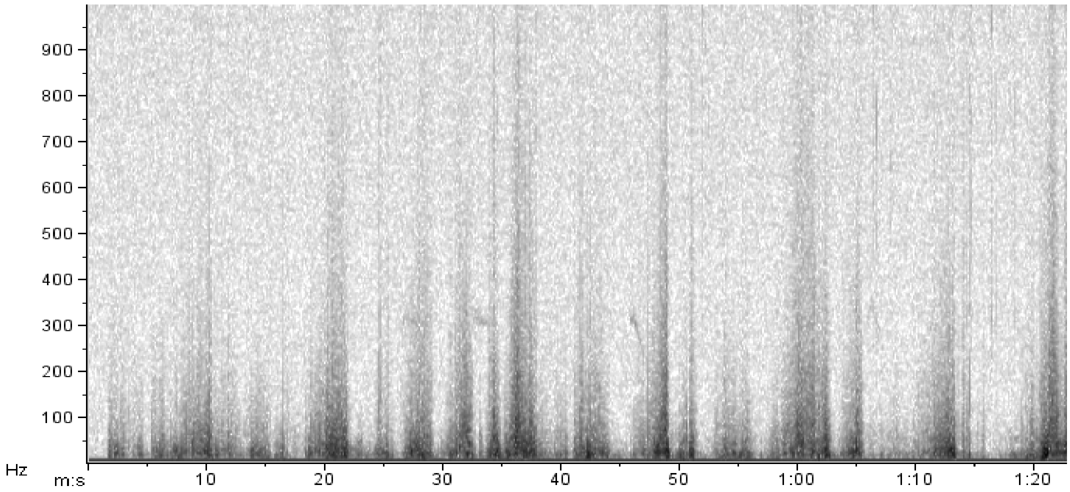


Figure 4.11 Example spectrogram of broadband rubbing sounds at the Auckland Islands.

In the North Atlantic several specific sound sources contribute to the ambient noise. Intermittent broadband banging sounds occurred at both the Jacksonville and Savannah sites (Figure 4.12). The predominant frequencies associated with these sounds were 30 Hz (fundamental), and 60 Hz and 90 Hz (harmonics); the bangs are thought to be correlated with tidal flow which causes the instrumentation to bump (Soldevilla et al. 2014). Low frequency shipping noise (Figure 4.13) was present throughout the day and night at both sites but was significantly more frequent in Jacksonville. Tonal sounds, thought to be aeroplane flyovers, were evident at both sites intermittently at frequencies of between 80 Hz and 200 Hz (Figure 4.14). Seasonal sounds from right whales were present from November to the end of February (Figure 4.15). Other biological sounds were recorded seasonally in March and April and were likely to be from fish, in particular black drum (*Pogonias cromis*) (Soldevilla et al. 2014). The choruses were most prolific during the night at a fundamental frequency of approximately 80 Hz (Figure 4.16).

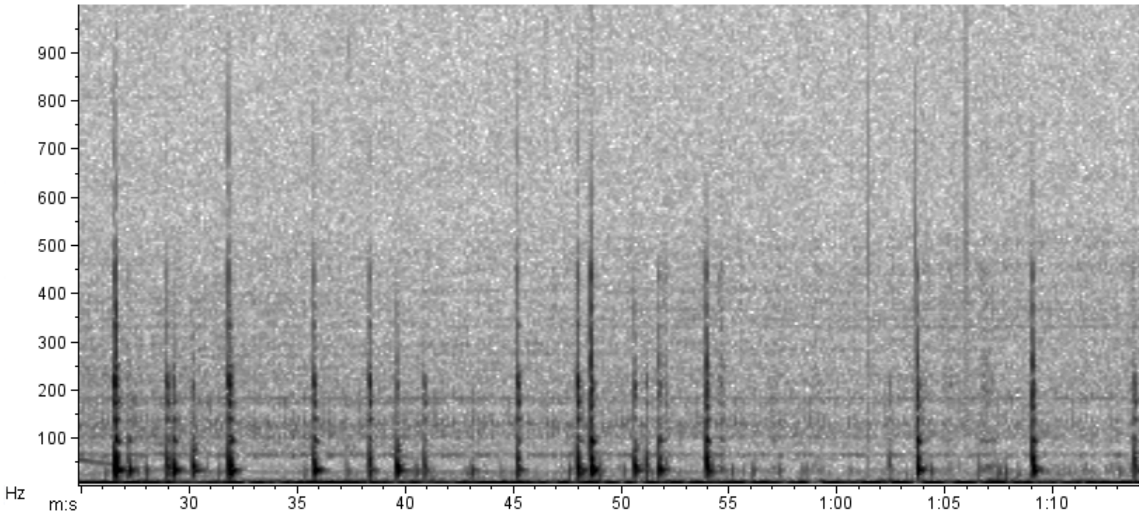


Figure 4.12 Example spectrogram of broadband tidal banging sounds in the Atlantic Ocean.

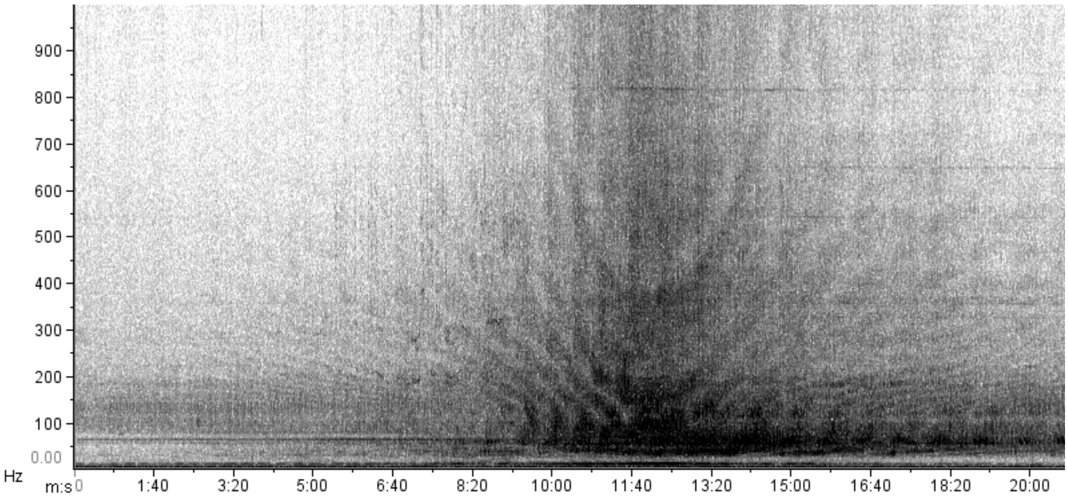


Figure 4.13 Example spectrogram of shipping noise in the Atlantic Ocean.

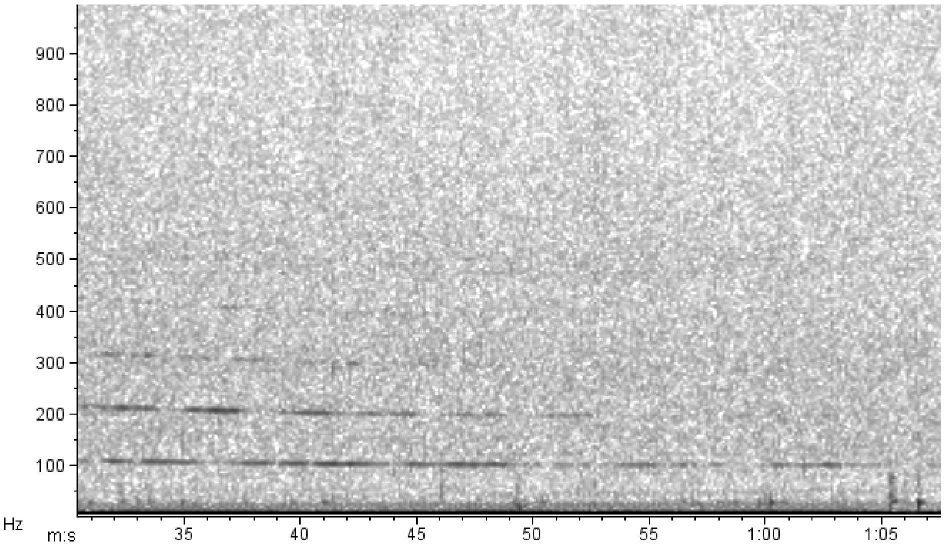


Figure 4.14 Example spectrogram of noise, likely from an aeroplane flyover in the Atlantic Ocean.

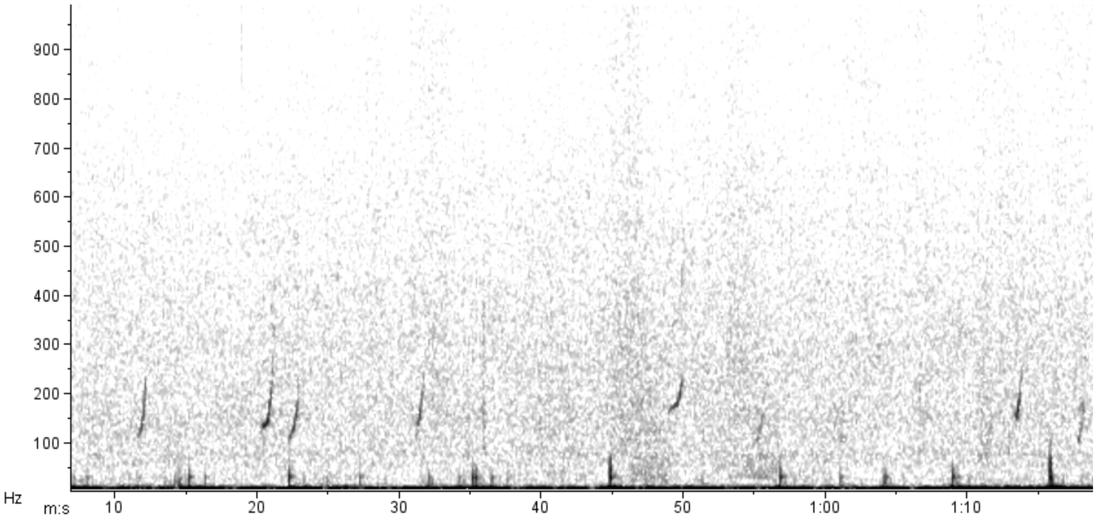


Figure 4.15 Example spectrogram of North Atlantic right whale calls.

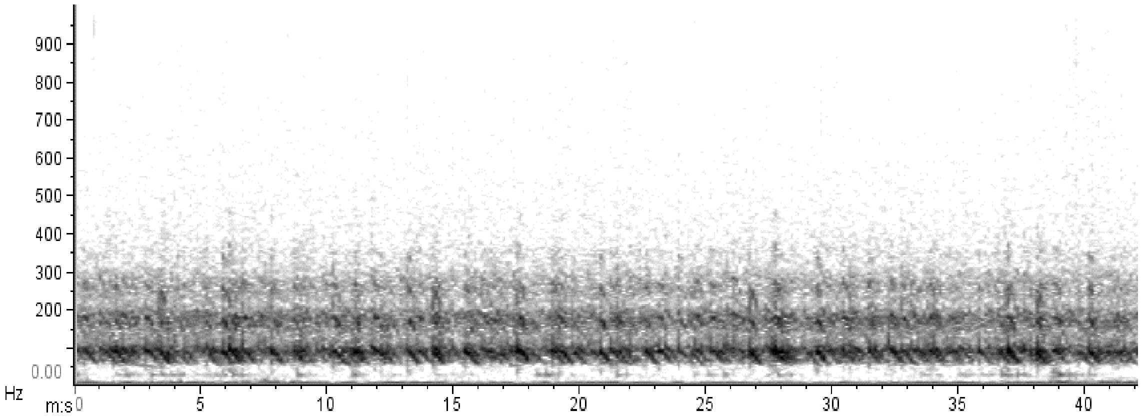


Figure 4.16 Example spectrogram of a black drum chorusing in the Atlantic Ocean.

4.4 Discussion

Ambient noise levels on right whale calving grounds were much lower in the Auckland Islands than in the North Atlantic, particularly at low frequencies (<200 Hz). Mean ambient noise levels at 40 Hz were up to 35 dB re 1μPa^2/Hz lower than in NARW habitat.

The differences in ambient noise levels are largely driven by anthropogenic noise pollution, particularly from shipping, which dominates at low frequencies. Ambient noise from shipping has increased dramatically over the last 50 years, particularly in the northern hemisphere (Andrew et al. 2002; Ross 2005; McDonald et al. 2006). The high ambient noise levels measured at Savannah and Jacksonville reflect the level of shipping in the vicinity of major ports on the south-east coast of the USA. Ambient noise levels measured off Savannah and Jacksonville are comparable with measurements from the Pacific Ocean off California (Point Sur, 90 dB re 1μPa^2 at 40 Hz, Andrew et al. 2002; San Nicolas, 85 dB re 1μPa^2 at 40 Hz, McDonald et al. 2006). In stark contrast, the low levels of low frequency ambient noise at the Auckland Islands are reflective of a shallow habitat sheltered from wind and swell (Rayment et al. 2014, Appendix B) with minimal anthropogenic activity. Measurements at the Auckland Islands were more consistent with levels of ambient noise in the Arafura and Timor Sea north of Australia (60 dB re 1μPa^2 at 40 Hz, Cato 1976) and off San Clemente, California (65 dB re 1μPa^2 at 40 Hz, McDonald et al. 2008). The low levels of ambient noise at San Clemente and Arafura are attributed to poor conditions for acoustic propagation, low wind speeds and shallow waters (Cato 1976; McDonald et al. 2008). The Arafura measurements (Cato 1976) however, were made in the 1970s when shipping activity was much lower than current levels (Ross 2005).

Ambient noise levels varied over time at all sites. These differences are likely due to variability in shipping and other anthropogenic activities, and also other biological and physical contributors, many of which have a seasonal component (Radford et al. 2008). Some of the temporal variation observed in this study has an immediately obvious cause. For example, the peak in the ambient noise at the Auckland Islands in August and September between 60 and 250 Hz coincides with the seasonal peak in right whale use of this area (Patenaude 2000). The spectral level at 100 Hz during the height of right whale activity in winter increased by 20 dB relative to summer levels. Current ambient noise levels at peak abundance are likely to be lower than historical levels at the Auckland Islands, as SRWs are still recovering from whaling, which severely reduced their numbers

(Carroll et al. 2014). Some of the temporal variation in ambient noise in the North Atlantic is from fish; for example, the black drum is vocally active during its breeding season (March-April), slightly after the right whale calving season in the boreal winter off the south-east coast of the USA (Soldevilla et al. 2014). Diel variation in aeroplane noise was evident in a study at the same Atlantic Ocean locations which suggested that there were more flights during the daytime (Soldevilla et al. 2014). Differences in ambient noise levels are also reflective of the physical location of the recorders. The Savannah and Jacksonville sites are in open-ocean on the continental shelf and are subject to noise from wind and waves, whereas the Auckland Islands recorder is in a sheltered bay. Temporal variability is also evident in some of the broadband sounds that occur at all three sites. At the Auckland Islands, sounds thought to be an animal rubbing on the hydrophone only cause sporadic peaks in ambient noise levels. Broadband sounds in Savannah and Jacksonville are more problematic and are likely due to tidal flow causing recorder movement and banging (Soldevilla et al. 2014). These broadband noises occur far more frequently than those at the Auckland Islands and have a considerable impact on the ambient noise levels in Jacksonville and in particular Savannah. Further work is required to exclude specific noise components (in particular tidal bangs) which are caused by interference with the instrument itself and may artificially inflate noise levels.

Similar to underwater noise, urban noise is louder at low frequencies. In noisy locations birds have been observed to sing louder and at a higher pitch (Nemeth and Brumm 2009; Luther and Baptista 2010). Even in vocal insects there is evidence that in a noisy environment they adjust their calls to avoid acoustic interference problems (Greenfields 1988). Common marmosets have also responded to increased noise levels by increasing the source level of their vocalisations (Brumm et al. 2004). Anthropogenic noise has been shown to be detrimental to a range of terrestrial animals (especially birds) through impairment of mate attraction, territory defence, masking of predators or associated alarm calls, as well as causing stress (e.g. Slabbekoorn and Ripmeester 2008). If noise has such an impact on terrestrial animals, the impact on marine mammals, which rely heavily on sound as their primary sense, is likely to be far greater.

Observed changes in vocal behaviour of NARWs due to acoustic pollution (Parks et al. 2007; 2010; 2011) show that noise is of consequence to right whales and has caused elevated levels of stress (Rolland et al. 2012). Acoustic pollution therefore may become an increasingly important habitat feature for right whales. If SRWs continue to make a comeback and increasingly recover to the New Zealand mainland (Carroll et al. 2014), noise may become an important factor to consider when choosing which areas to re-colonise. Anthropogenic noise, particularly shipping and other low frequency sounds (< 200 Hz), have the potential to overlap considerably with right whale calls. It is possible that habitats used historically by right whales around the New Zealand mainland may no longer be appealing if whale calls suffer from masking due to increases in noise.

For animals that depend on acoustic signals, ambient noise is an important aspect of the marine environment and will be increasingly so as noise levels rise (e.g. Ross 2005). Time-series data from different habitats are needed to document changes in noise levels and provide baselines for the future, as well as to examine habitat suitability for right whales. Information on ambient noise will enable us to evaluate the impacts of anthropogenic activities (e.g. shipping, seismic surveys and seabed mining) on the whales' ability to communicate. Marine mammals have already been observed to lengthen their calls in response to sonar (Miller et al. 2000), and to noise (Miksis-Olds and Tyack 2009), and reduce the number of callers in response to seismic survey activity (Cerchio et al. 2014). These modifications do not come without cost (Patricelli and Blickley 2006) and it is likely that the effects of anthropogenic noise reach more widely than is currently realised.

Conclusion

Large differences were evident between the ambient noise levels at right whale calving grounds in the North Atlantic and Southern Ocean. Low frequency noise was significantly higher at both sites in the North Atlantic, potentially due in part to shipping noise which has implications for the effective communication ranges of right whales.

CHAPTER 5

A COMPARATIVE STUDY OF RIGHT WHALE CONTACT CALLS ON CALVING GROUNDS

5.1 Introduction

Marine mammals use sound to communicate, navigate and locate prey (Schevill and Watkins 1965; Payne and McVay 1971; Evans 1973). Increased anthropogenic noise in the marine environment (Andrew et al. 2002; Ross 2005; McDonald et al. 2006) and its impact on marine mammals is well documented (Richardson et al. 1995; Richardson and Würsig 1997; Nowacek et al. 2007; Weilgart 2007; Tyack 2008; Ellison et al. 2012) although it is unclear how these effects become evident at the population scale. Sounds produced either intentionally or inadvertently by human activities can cause a diverse range of impacts on marine life, including effects on behaviour (Engås et al. 1996; Frankel and Clark 2000; Engås and Løkkeborg 2002; Morton and Symonds 2002), acoustic behaviour (Van Parijs and Corkeron 2001; Fristrup et al. 2003; Castellote et al. 2012), physical injury and/or physiological responses (McCauley et al. 2003; Jepson et al. 2003; André et al. 2011; Rolland et al. 2012). This chapter focusses only on acoustic responses to noise.

Acoustic interference can reduce the distance over which animals are able to communicate (Clark et al. 2009). Some animals are able to use a variety of mechanisms to modify their communication strategies to compensate for an increase in ambient noise (Tyack 2008; Bradbury and Vehrencamp 2011). Common modifications include increasing the amplitude of a call (the Lombard effect), changing the frequency or temporal structure of a signal or changing the timing of the call delivery. All of these mechanisms increase the probability that vocalisations will be detected, in a noisy environment, by conspecifics. For example, during the breeding season male humpback whales (*Megaptera novaeangliae*) were observed to increase the length of their calls significantly when exposed to low frequency sonar (Miller et al. 2000). Foote et al. (2004) showed that killer whales (*Orcinus orca*) significantly increased their call duration in the presence of boat noise. In the event of continuous or intense urban noise several bird species increase the minimum frequency of their vocalisations (Slabbekoorn and Peet 2003; Slabbekoorn and Ripmeester 2008; Hu and Cardoso 2010) or shift the energy of the call into higher frequencies (Wood and Yezerinac 2006). These kinds of responses are not restricted to mammals and birds. Several species of amphibian change their calling rate in the presence of aeroplane and motorcycle noise (Sun and Narins 2005). Southern brown tree frogs (*Litoria ewingii*) also vocalise at higher frequencies in the presence of urban noise, albeit a smaller difference than those observed for birds (Parris et al. 2009). If ambient noise patterns are predictable and consistent, then changes may occur over the long-term via song learning (e.g. Slabbekoorn and Peet 2003) or over longer timescales via natural selection (e.g. Parris et al. 2009), but given enough flexibility in a species' sound production mechanism, vocal changes over shorter timescales are possible (e.g. Miller et al. 2000). It is important to note, however, that these changes seldom come without cost. Calling more often, for example, increases energy expenditure and may make the caller more obvious to predators (Deecke et al. 2005).

The *upcall* is typically the most common call made by right whales (*Eubalaena* sp.; Clark 1982; McDonald and Moore 2002; Parks et al. 2011) and is thought to be the primary contact call used to communicate with conspecifics (Clark 1982). The current study on southern right whales (SRWs, *Eubalaena australis*) in New Zealand showed that *upcalls* were one of the three most common call types (*tonal low* 17.4%, *pulsive* 16.6%, *upcall* 16.1%) used in winter (Chapter 2), although not all calls were included in this analysis. Over the duration of the long-term study, however *upcalls* were the most prevalent vocalisation type (33% of all calls; Chapter 3). This low-frequency tonal upsweep vocalisation is species-specific (Clark 1982; Van Parijs et al. 2009) and is known to be produced by juveniles and adults of both sexes (Clark 1983; Parks and Tyack 2005). *Upcalls* are used in many different behavioural contexts in a wide range of habitats (Clark 1983; Vanderlaan et al. 2003; Parks and Tyack 2005; Van Parijs et al. 2009) including on calving grounds (Trygonis et al. 2013). Although little is known about communication between right whale mother-calf pairs, there is evidence that *upcall*s are used when the pair become separated (Parks and Clark 2007). Clark (1982) observed that the *upcall* coincides with a low noise band in the spectrum of natural ambient noise (~100-200 Hz) and this, coupled with the fact that low frequencies travel further than higher frequencies, means that *upcalls* are ideally suited to long-range communication.

Increasing noise pollution off the east coast of the USA, largely from shipping (Ross 2005; Hildebrand 2009), is affecting the vocal communication of the North Atlantic right whale (NARW, *Eubalaena glacialis*; Parks et al. 2007; 2009; 2011). Their short-term response has been to raise the average fundamental frequency of their *upcalls,* call louder, and call less often when ship noise is intense (Parks et al. 2007; 2011). A comparison between historical and contemporary right whale *upcalls* in the Atlantic and in the Golfo San Jose, Argentina, showed a significant increase in the start frequency of calls over a period of 44 years and 23 years, respectively; which suggests a long-term behavioural response to ambient noise (Parks et al. 2007). Differences between species were also evident with NARWs calling at higher frequencies than SRWs (Parks et al. 2007).

Right whale habitat around New Zealand’s sub-Antarctic Auckland Islands is far less influenced by anthropogenic noise (Chapter 4). The waters surrounding these uninhabited islands are designated as a marine reserve and shipping traffic and other activities are minimal. The aim of this chapter is to compare the characteristics of *upcall* vocalisations of right whales on their major calving grounds in the Atlantic Ocean and around New Zealand under very different noise conditions. The vocal repertoire of NARWs is comparatively well studied (e.g. Matthews et al. 2001; Vanderlaan et al. 2003; Parks and Tyack 2005; Trygonis et al. 2014) and it has already been demonstrated that call characteristics have changed coincident with changes in anthropogenic noise (Parks et al. 2007; 2011). Recent work on the vocal repertoire of right whales has been reported for New Zealand waters (Chapters 2 and 3). The occurrence of a congeneric population in a near-pristine acoustic habitat provides an opportunity for a spatial comparison. This study could provide additional evidence for the response of NARWs to noise as well as providing baseline data for SRWs.

5.2 Methods

Data collection

In order to compare the vocal characteristics of the right whale *upcall* in similar behavioural contexts acoustic recordings were made on calving grounds in the North Atlantic Ocean and in the Southern Ocean (Figure 5.1). To record SRW vocalisations a recorder was moored in Laurie Harbour in Port Ross at the northern end of the remote sub-Antarctic Auckland Islands (50°33.4'S, 166°12.3'E). Port Ross is a large, sheltered harbour and is the main calving area for SRWs in New Zealand waters (Patenaude et al. 2000). High concentrations of whales are found throughout Port Ross in the austral winter (Rayment et al. 2012, Appendix A). The Auckland Islands have minimal levels of anthropogenic activity. The region is not on any major shipping routes and the nearest commercial port is Bluff, 465 km away, on mainland New Zealand. The islands are uninhabited and receive only occasional visits from sub-Antarctic cruise ships, researchers and fishing vessels seeking shelter. To record NARW *upcalls*, autonomous recorders were deployed at two different locations on NARW calving grounds; one off Jacksonville, Florida (30°20.2'N, 81°12.7'W) and another off Savannah, Georgia (31°49.7'N, 80º41.8'W). The south-east coast of the USA is the primary calving area for NARWs during the boreal winter (Kraus et al. 1986b; Winn et al. 1986) and has been designated as *critical habitat* (NOAA 1994). The level of anthropogenic activity is high and the large ports off Georgia (Savannah and Brunswick) and Florida (Jacksonville) are situated on major shipping lanes which extend from the Gulf of Mexico north to Boston and New York. Savannah is the busiest port in the south-east region and is the second largest container port on the Atlantic coast (U.S. Army Corps of Engineers 2012).

In the North Atlantic, two marine autonomous recording units (MARUs, Cornell Bioacoustics Research Program, USA) were used. Each MARU included a HTI-94-SSQ hydrophone (sensitivity: -162 dB re 1V/µPa and frequency response: 10 Hz - 32 kHz ± 3dB). Acoustic recordings were made over a four month period when calving was at its peak (Kraus et al. 1986b) between 18 November 2009 and 16 March 2010 in Savannah and Jacksonville. Both MARUs recorded continuously at a sampling rate of 2 kHz. In New Zealand, a DSG-Ocean autonomous recorder (Loggerhead Instruments, USA, www.loggerhead.com) was deployed to record *upcalls*. DSG-Ocean recorders use similar hydrophone technology (High Tech Inc., www.hightechincusa.com), namely a single HTI hydrophone, HTI-96-MIN (sensitivity: –185.6 dB re 1V/μPa and frequency response: 20 Hz - 50 kHz ± 3dB). Recordings were made over a three month period from July to September in 2011 and 2012 when calving and abundance at the Auckland Islands are at their peak (Patenaude 2000). During a test phase (22 July 2011 to 1 August 2011) the DSG-Ocean recorded at a sampling rate of 50 kHz for a duty cycle of 2.5 min every 30 min. For the longer term deployment (between 6 August and 30 September 2011) the sampling rate was set at 4 kHz, recording for 3.75 min every 30 min. The same sampling rate and duty cycle was used the following year between 5 August and 30 September 2012.

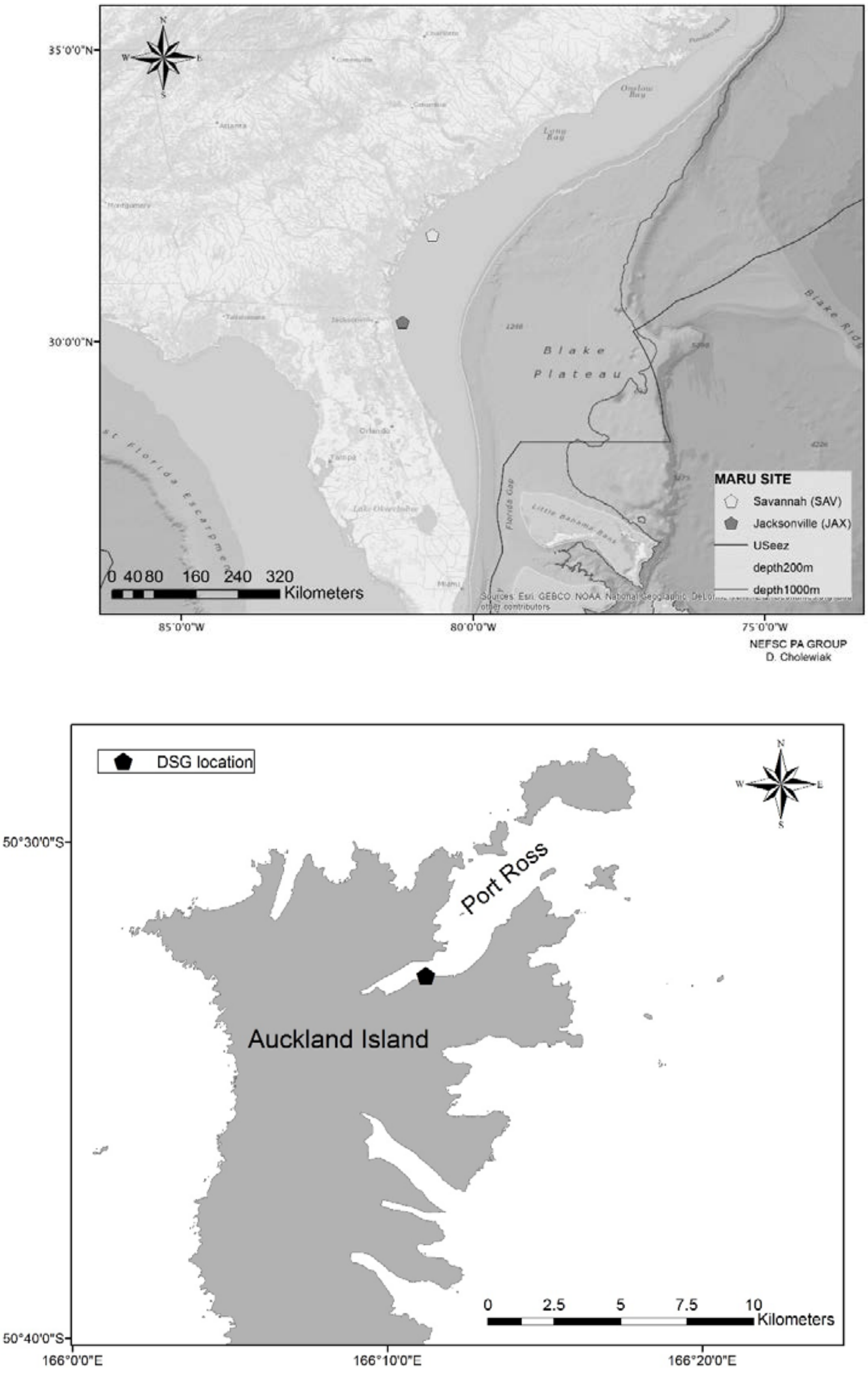


Figure 5.1 Locations of the autonomous acoustic recorders in right whale habitat off the SE coast of the USA in the Atlantic Ocean (top) and in Port Ross, Auckland Islands, sub-Antarctic New Zealand in the Southern Ocean (bottom).

Measurement of call parameters

Upcall vocalisations were examined using the sound analysis software Raven Pro v1.5 (Bioacoustics Research Program, Cornell University, www.birds.cornell.edu). Prior to analysis, the data recorded in New Zealand were down-sampled to 2 kHz in MATLAB v7.10 (The MathWorks Inc., MA, USA) to match the sampling rate for the North Atlantic recordings. All *upcall*s were analysed at a sampling rate of 2 kHz via a spectrogram with 3.91 Hz frequency resolution and 19.0 ms time resolution (FFT: 512 points, Hamming window, 85% overlap). No filters were applied to the acoustic data.

A software detector developed specifically for NARW *upcalls* (Urazghildiiev and Clark 2006) in the eXtensible BioAcoustic Tool (XBAT; Figueroa 2012) was used to highlight hours with *upcalls* present for the data from the North Atlantic. Data from New Zealand had already been explored for another research component (Chapter 3) so recordings with *upcalls* present had already been highlighted. Recordings (of SRWs and NARWs) were then browsed for *upcalls* visually and aurally in Raven by the same analyst. Calls were selected by drawing a user-defined selection border around the fundamental frequency of the call. Any vocalisations that were not clearly visible on the spectrogram or that overlapped with calls from other individuals were excluded from the analysis. Only calls with a signal to noise ratio (SNR) over 10 dB (e.g. Parks et al. 2011; Risch et al. 2013; Baumann-Pickering et al. 2013) were included in the analyses.

Parameter	Units	Description
Maximum frequency (f_{max})	Hz	The upper frequency limit of the annotation box.
Minimum frequency (f_{min})	Hz	The lower frequency limit of the annotation box.
Delta frequency (Δf)	Hz	Total bandwidth, calculated by high frequency (f_{max}) minus low frequency (f_{min}) as defined by the limits of the annotation box.
Delta time (Δt)	s	Total duration, calculated by end time (t_{max}) minus start time (t_{min}).
Peak frequency (f_{peak})	Hz	The frequency at which peak power occurs within the selection.
Centre frequency (f_c)	Hz	Frequency that divides the selection into two frequency intervals of equal energy.
1st quartile ($f_{25\%}$) and 3rd quartile frequencies ($f_{75\%}$)	Hz	The frequencies that divide the selection into two frequency intervals containing 25% and 75% of the energy in the selection, where the summed energy exceeds 25% and 75% of the total energy, respectively.
Inter-quartile bandwidth (B_{IQR})	Hz	The difference between $f_{25\%}$ and $f_{75\%}$.
Inter-quartile duration (t_{IQR})	s	The difference between the two points in time that divide the selection into two time intervals containing 75% (t_{75}) and 25% (t_{75}) of the energy in the selection, i.e. t_{75} minus t_{25}.
Frequency 5% ($f_{5\%}$), frequency 95% ($f_{95\%}$)	Hz	The frequency that divides the selection into two frequency intervals containing 5% and 95% of the energy in the selection, where the summed energy exceeds 5% and 95% of the total energy, respectively.
Bandwidth 90% ($B_{90\%}$)	Hz	The difference between $f_{5\%}$ and $f_{95\%}$.
Duration 90% (t_{90})	s	The difference between the two points in time that divide the selection into two time intervals containing 95% (t_{95}) and 5% (t_5) of the energy in the selection, i.e. t_{95} minus t_5.
PFC max frequency, PFC min frequency	Hz	Measurements are taken from the peak frequency contour (PFC) that traces the peak frequency against time throughout the selected call.
PFC max slope, PFC min slope, PFC average slope	Hz/ms	A measurement of slope taken directly from the PFC that traces the peak frequency throughout the selected call; where the slope is at its maximum, minimum and averaged throughout the call.
PFC inflection points	none	The number of inflection points from the PFC that traces the peak frequency against time throughout the selected call.

Table 5.1 The parameters used to measure and compare right whale *upcalls* from the North Atlantic and New Zealand.

The call characteristics measured were based on variables previously used to train an *upcall* detector (Gillespie 2004) and previous work on SRW repertoire at the Auckland Islands (Chapter 2). Twenty call feature parameters relating to frequency and time were measured for each vocalisation (Table 5.1). All of these variables were automatically extracted as standard output parameters within Raven (Charif et al. 2010).

Call analysis

All classification analyses were conducted in program R version 3.0.2 (R Development Core Team 2004, www.R-project.org). A Random Generalised Linear Model (RGLM) in the R package *randomGLM* (Song et al. 2013) was used to investigate the differences between NARW and SRW *upcall* parameters and to assess which variables were most important for distinguishing between the *upcalls* of the two species. RGLM is a multivariate predictive technique that combines Random Forest (RF) and Generalised Linear Models (GLM) by using bootstrap aggregation (bagging). RF analysis (Breiman 2001) has become popular in genetic research (e.g. Shi et al. 2005; Díaz-Uriarte & Alvarez De Andres 2006; Ward et al. 2006) and has more recently been employed for acoustic classification tasks (Briggs et al. 2012; Risch et al. 2013; Hannay et al. 2013). Random forest models have performed well in tests against other classifiers including discriminant function analysis, support vector machines and neural networks (Breiman 2001; Liaw and Wiener 2002; Armitage and Ober 2010). RGLM has the benefits of incorporating the predictive accuracy, variable importance and accuracy measures from RF, along with the advantage of interpretability from GLM, and has been shown to outperform alternative prediction methods (Song et al. 2013).

Data were partitioned prior to analysis with 70% of the data used for training and 30% used for testing the RGLM model. Species was used as the response variable and each of the 20 call parameters were included as predictor variables (Table 5.1). There are two main RGLM input parameters which are defined by the user. The first, *nBags,* is the number of bootstrapped datasets used in the model (default 100). The second, *nFeaturesInBag,* is the number of variables chosen randomly for each bag (or dataset) without replacement. *Out-of-bag* (*OOB*) *error* was used to refine choices about parameter values for *nBag* and *nFeaturesInBag*. *OOB error* is an estimate of the proportion of right whale calls unsuccessfully classified to species level (or prediction accuracy), and is based on the 30% of observations that were not used to train the model.

The first step of the RGLM model is to bootstrap the datasets based on random sampling from the original training dataset. Then, for each dataset, variables (*nFeaturesInBag)* are randomly selected without replacement. Next, for each dataset or bag, the variables are ranked according to their correlation with the outcome measure. The s*tepAIC()* function in the R package *MASS* (Venables and Ripley 2002) uses a forward selection procedure to choose a multivariate GLM model for each bag based on the minimum value of Akaike's information criterion (AIC). Finally, the predictions from each dataset are aggregated. The proportion of right whale calls unsuccessfully classified to species level was then used to evaluate the prediction accuracy of the model. The importance of the call parameters to the final result were ranked using the *varImp()* function in the R package *caret* (Kuhn 2008). Variable importance is defined as the number of times a parameter is selected by forward regression across all datasets. The parameters that are repetitively selected for the RGLM models are deemed the most important.

In order to investigate the effect of the most important predictors on the response variable, a single GLM was constructed. Only variables which featured in more than 50% of the best models from the RGLM procedure were included in the single GLM. Prediction accuracy of the single model was tested using *leave-one-out* cross validation (LOOCV). LOOCV is a form of multi-fold validation, where training models are built using all but one of the datapoints, and validated using the final datapoint. This process is repeated until each datapoint has been used once for validation. The average prediction error is then calculated and used to evaluate the predictive power of the model. In order to avoid using the same data for model building and validation, the single model was validated using only the *OOB data,* i.e. the 30% of the original dataset which was not used in the construction of the RGLM models. The predictive accuracy of the RGLM and the single GLM were then compared (e.g. Song and Horvath 2013).

5.3 Results

Data collection and measurement of call parameters

Upcalls were selected from the main calving periods during winter in both locations; a total of 1158 calls were selected for SRWs and 691 calls for NARWs (Table 5.2).

Location	Year	Number of days	Number of calls	Mean number of calls per day
Savannah, Georgia, USA (*NARW calving ground*)	2009/10	105	227	2.16
Jacksonville, Florida, USA (*NARW calving ground*)	2009/10	90	464	5.15
Auckland Islands, New Zealand (*SRW calving ground*)	2011	71	593	8.35
	2012	56	565	10.09

Table 5.2 Sample sizes of *upcall* data selected and measured for North Atlantic right whale and southern right whale.

Several differences were evident in call parameters between SRWs and NARWs. The frequency of NARW *upcalls* was higher than those from SRWs in terms of minimum, peak and maximum frequencies (Table 5.3, Figure 5.2). The greatest difference was in the maximum *upcall* frequency between the two species (Figure 5.2). The average maximum frequency was over 40% (67 Hz) higher for NARW than SRW *upcalls*, whereas mean minimum and peak frequencies were approximately 30% (19.7 Hz) and 9% (9.1 Hz) higher, respectively. Mean total duration differed between species with duration of NARW *upcalls* only 0.1 s longer than SRW *upcalls* (Table 5.3, Figure 5.3). A greater difference was however evident in the 90% duration variable (*i.e.* the difference between the two points in time that divide the call into two time intervals containing 95% and 5% of the energy), with duration for NARW approximately 0.25 s longer.

Call parameter	**SRW** (*n* = 1158)	**NARW** (*n* = 691)
Minimum frequency (Hz)	65.41 (± 0.42) 25.1 – 125.4	85.14 (± 0.63) 46.6 – 143.4
Maximum frequency (Hz)	167.11 (± 0.76) 103.9 – 258.1	234.20 (± 1. 31) 143.4 – 358.4
Peak frequency (Hz)	111.31 (± 0.66) 50.8 – 199.2	120.46 (± 1.47) 50.8 – 293.0
Bandwidth/ Δ frequency (Hz)	101.70 (± 0.62) 46.6 – 193.5	149.06 (± 1.29) 78.9 – 279.6
Duration /Δ time (s)	0.88 (± 0.01) 0.6 – 1.7	0.97 (± 0.01) 0.5 – 1.6
90% duration (s)	0.49 (± 0.01) 0.1 – 1.2	0.74 (± 0.01) 0.1 – 1.5

Table 5.3 A comparison of summary measurements for key variables comparing *upcalls* on calving grounds for southern right whale and North Atlantic right whale. The mean (± SE) and range are given for each variable.

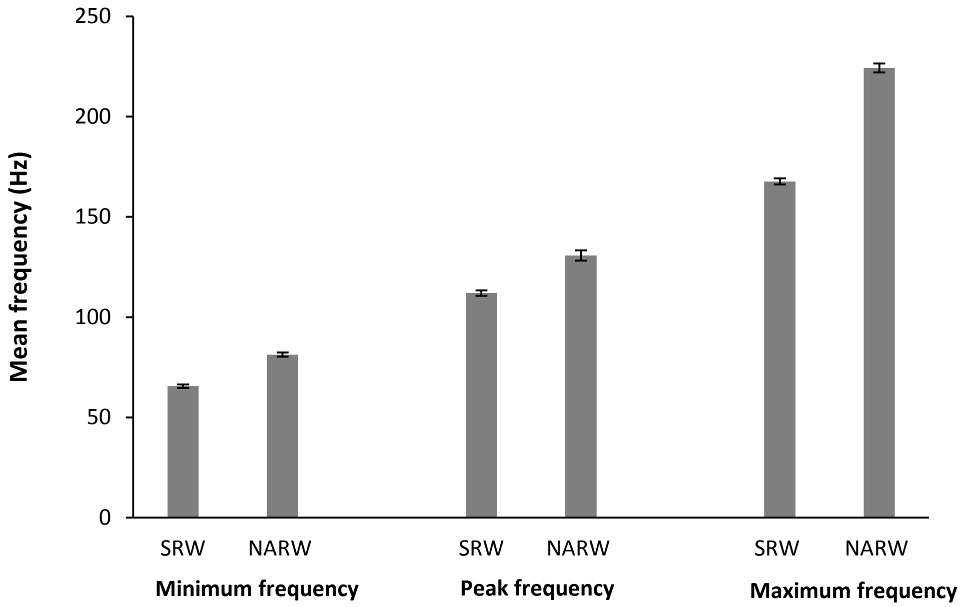


Figure 5.2 Comparisons of the mean minimum, peak and maximum frequencies (± 95% confidence intervals) of *upcalls* for southern right whale and North Atlantic right whale on their respective calving grounds.

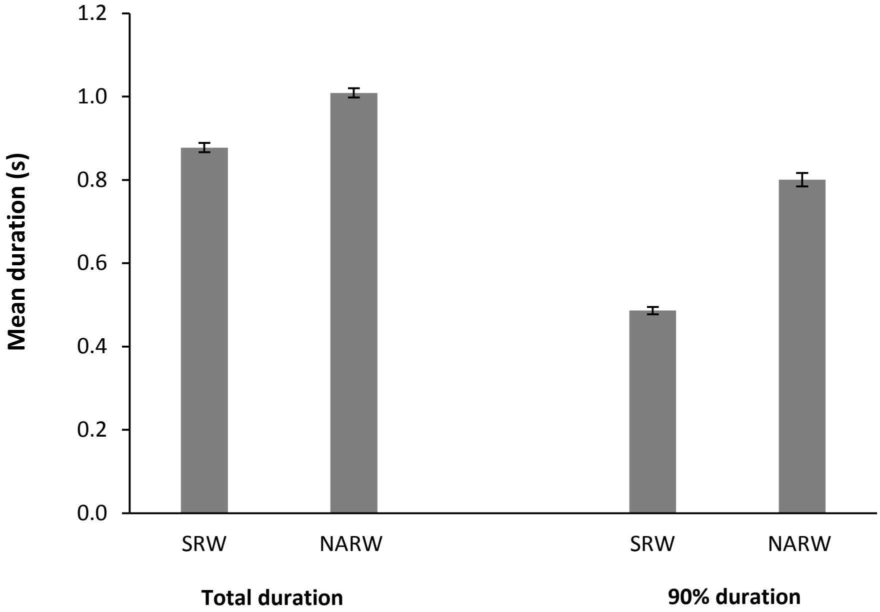


Figure 5.3 Comparison of the total duration and 90% duration of *upcalls* (±95% confidence intervals) for southern right whale and North Atlantic right whale on their respective calving grounds.

Call analysis

A RGLM was performed to examine whether *upcalls* of SRWs and NARWs could be discriminated using the measured data. The RGLM was also used to assess the variability across all of the *upcalls* and to identify the parameters that best described the differences.

The model highlighted several *upcall* parameters which were important in discriminating the species (Table 5.4). The top five variables for describing differences between the *upcalls* of both species were the number of inflection points in the peak frequency contour (PFC), maximum frequency, PFC average slope, interquartile (IQR) duration and PFC maximum frequency. The peak frequency of the call was considered to be one of the least important measured variables (Table 5.4).

Parameter	**Rank**	**Variable importance**
PFC inflection points	1	78
Maximum frequency (f_{max})	2	75
PFC average slope	3	72
Inter-quartile duration (t_{IQR})	4	71
PFC max frequency	5	65
Duration 90% (t_{90})	6	57
Minimum frequency (f_{min})	7	53
Delta time (Δt)	8	50
Centre frequency (f_c)	9	48
PFC min slope	10	46
Delta frequency (Δf)	11	44
Frequency 95% ($f_{95\%}$)	12	43
Frequency 5% ($f_{5\%}$)	13	40
Bandwidth 90% ($B_{90\%}$)	14	39
PFC max slope	15	32
3rd quartile frequency ($f_{75\%}$)	16	30
PFC min frequency	17	26
Inter-quartile bandwidth (B_{IQR})	18	23
Peak frequency (f_{peak})	19	22
1st quartile frequency ($f_{25\%}$)	20	17

Table 5.4 Rank and variable importance of the parameters used to discriminate between southern right whale and North Atlantic right whale *upcalls* using a Random Generalised Linear Model (RGLM). The variable importance value is the number of times a parameter was selected by forward regression across all datasets.

The RGLM was easily able to differentiate SRW *upcalls* from NARW *upcalls* with a high degree of accuracy. Using the training set of data the *OOB error rate* or misclassification rate between species was predicted to be only 0.06%.

A single GLM, built using the only the top eight variables (used in over 50% of the models) showed that maximum frequency was the most important factor for explaining the differences between SRW and NARW *upcalls* (Table 5.5). Five of the other eight top variables were also significant for explaining the differences, excluding minimum frequency and interquartile duration (Table 5.5).

Parameter	**Estimate**	**Std. Error**	**z value**	**Pr(>|z|)**
Minimum frequency	0.01	0.01	1.37	0.17
Maximum frequency	-0.14	0.01	-10.86	$<2.00 \times 10^{-16}$
Interquartile duration	-0.48	1.90	-0.25	0.80
Delta time	2.94	0.96	3.05	0.002
Duration 90%	-5.81	1.43	-4.07	4.64×10^{-5}
PFC average slope	7.30	2.00	3.65	0.0003
PFC maximum frequency	0.06	0.01	6.25	4.03×10^{-10}
PFC number of inflection points	-0.30	0.04	-6.82	8.85×10^{-12}

Table 5.5 Results of the single generalised linear model (GLM) examining differences between the top eight variables used in over 50% of the models to describe differences between southern right whale and North Atlantic right whale *upcalls*. Statistically significant results are highlighted.

The single GLM using the top eight variables works well for explaining the differences between SRW and NARW *upcalls*. When compared to the original RGLM, the single GLM makes similar predictions with 92.7% of *upcalls* assigned to the correct species (Figure 5.4).

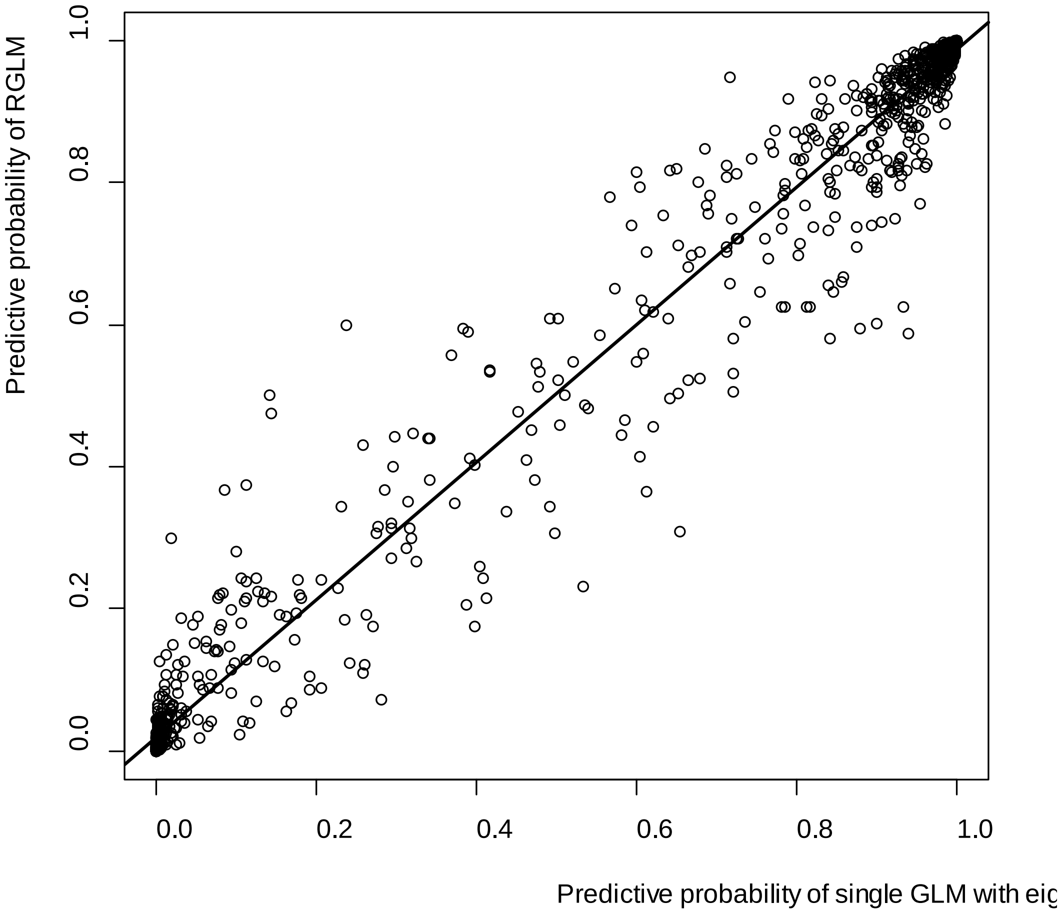


Figure 5.4 Plot comparing the predictive power of the Random generalised linear model and the single general linear model for assigning *upcalls* to either southern right whales or North Atlantic right whales.

5.4 Discussion

A random generalised linear model (RGLM) proved effective for distinguishing SRW and NARW *upcalls* from one another and the misclassification rate was low (<0.1%). To my knowledge this is the first time that RGLM has been used successfully for acoustic classification. RGLM has proved highly accurate for predictions with genomic data sets (e.g. Song et al. 2013) and this technique has potential for ecological classification research. This study highlights some significant differences between *upcall* characteristics for congeneric species of right whale on calving grounds in the North Atlantic and Southern Ocean. NARWs produce *upcalls* with significantly higher maximum, minimum and peak frequencies (40%, 30% and 9%, respectively) than SRWs in New Zealand. Call duration was also significantly longer for NARWs than SRWs. The RGLM showed that maximum frequency was the most important factor for explaining the differences between SRW and NARW *upcalls*.

One of the potential explanations for the differences in the frequency and duration of *upcalls* in this study is the influence of ambient noise. Shipping noise dominates the low frequency noise band below 200 Hz (Ross 2005; Tyack 2008; Hildebrand 2009) and densities of shipping traffic in the Atlantic Ocean are particularly high (Halpern et al. 2008). Ambient noise from shipping has increased rapidly over the last decade (Hildebrand 2009) due to a greater number of ships, an increase in their size and horsepower and a change in propulsion systems (Ross 2005). Ambient noise levels on the calving grounds of NARWs are much higher than the calving grounds in the acoustically quiet areas of the Auckland Islands (Chapter 4). The acoustic recording sites in the Atlantic Ocean are in close proximity to shipping lanes and major ports, whereas the site at the Auckland Islands has minimal traffic and has no close ports.

Signal to noise ratio plays an important role in an animal’s ability to detect and recognise a call (Lohr et al. 2003). Modifying a call in a noisy environment may reduce the effect of masking and increase the likelihood of a call being detected by conspecifics (Clark et al. 2009). One common compensation technique is to move the frequency of a call outside the noise band. An increase in frequency of calls in urban environments has been observed in birds (e.g. Slaabekoorn and Peet 2003; Nemeth and Brumm 2009; Francis et al. 2010) and amphibians (Parris et al. 2009). Frequency shifts have also been demonstrated in marine mammals in noisy underwater environments (Lesage et al. 1999). Right whales in the North Atlantic have made significant adjustments to their calls to compensate for low frequency noise particularly from shipping (Parks et al. 2007; 2010; 2011). NARWs and SRWs both made long-term changes to the frequency structure of vocalisations; specifically, start and end frequencies for NARW *upcalls* were 29% and

25% higher, respectively than SRW *upcalls* in Argentina (Parks et al. 2007). Contemporary *upcalls* were also higher in frequency than historical *upcalls* for both species (Parks et al. 2007). The percentage difference between the minimum frequency for SRWs and NARWs in Parks et al. (2007) was similar to this study; but there was a larger difference in the maximum frequency between species in this study. In Brazil, right whale *upcalls* measured at a low traffic location, Gamboa, had a lower minimum frequency (68.2±18.6 [SD] Hz) than those from a high traffic location, Ribanceira, (70.1±24.8 [SD] Hz) (Parks et al. 2014). Interestingly, the mean minimum frequency of *upcalls* recorded in the low noise environment off Brazil (Parks et al. 2014) is similar and only 3 Hz higher than the minimum frequency measured at the quiet Auckland Islands location in this study. The minimum frequency of right whale *upcalls* is at the lower end of the shipping noise band, so an increase in minimum frequency would move calls into the middle of that band. With maximum frequency however, an increase would move part of the *upcall* above background shipping noise.

Another way for species to improve the chance of detection is to increase call duration (Miller et al. 2000). Manatees have been shown to compensate for noise by increasing the duration of vocalisations (Miksis-Olds and Tyack 2009). Parks et al. (2007) found that the duration of NARW *upcalls* increased slightly through time, but did not find a significant difference between the duration of NARW and SRW calls. In this study, although NARW *upcalls* were significantly longer than SRW *upcalls,* the difference was subtle in comparison to the variation in frequency. However, it is possible that this difference is yet another way that NARWs can increase the probability of their calls being detected in a noisier environment.

Modifications to call characteristics do not come without potential costs (Patricelli and Blickley 2006; Barber et al. 2010). Higher frequency calls may be subject to higher attenuation given that higher frequencies do not travel as far (Brenowitz 1986). At the frequencies used by right whales, however, attenuation differences would be small. For example, if NARWs trebled the peak frequency of their *upcalls* from 120 Hz to 360 Hz (an inconceivably large change), attenuation would be increased by <0.01 dB/km (formula from Richardson et al. 1995). Call production can be both energetically expensive and inefficient (Hawkins and Amorim 2000), and altering natural call structure to a higher frequency or to a longer duration may involve increased energy expenditure. A frequency shift may enable detection by predators or prey that would otherwise be unable (or less able) to hear a signal to eavesdrop on vocalisations (Deecke et al. 2005), leading to increased predation risk. It is also possible that changing the frequency structure or length of the call may modify the call to such an extent that the caller, or the call's meaning, is no longer recognisable (Patricelli and Blickley 2006).

An alternative explanation for variation in the frequency composition of *upcalls* is body size. There is an inverse relationship between size and call frequency in many species, with larger animals generally producing lower-frequency calls (Ryan and Brenowitz 1985; Fitch 1997). Parks et al. (2007) showed that there were no clear frequency differences between calls produced by juvenile or adult NARWs and that age was a non-significant factor, suggesting that size is also unimportant. Visual health assessment has shown that NARWs often have poor body condition (Pettis et al. 2004) and the difference in body condition of SRW and NARW is immediately obvious in the field (pers. obs.). There is however no evidence in the literature of major size differences between NARWs and SRWs (Best and Ruther 1992; Tormosov et al. 1998; Moore et al. 2004; Fortune et al. 2012). The mean size attained by adult SRWs in historical whaling data (14.34 ± 1.03 m [SD], Tormosov et al. 1998) is similar to estimates from aerial photogrammetry (13.85 ± 0.7 m [SD], Best and Ruther 1992). Length measurements were obtained from a small number of stranded mature NARW individuals (13.5-14.5 m; Moore et al. 2004) and via aerial photogrammetry (males: 12.87 ± 0.48 m [SD], and females: 13.44 ± 0.61 m [SD], Fortune et al. 2012). Together these data suggest that differences in size is an unlikely explanation for the significant differences in *upcall* frequency.

NARW call patterns vary between different regions, likely due to variation in the behaviour of individuals (Van Parijs et al. 2009; Parks et al. 2009). For example, minimum *upcall* frequency was slightly higher in the Bay of Fundy (BOF) and Cape Cod Bay (CCB) than off the calving grounds in Georgia, and in BOF and Georgia calls were shorter than in CCB (Parks et al. 2009). Different behaviour has been observed to lead to differences in acoustic repertoire (Clark 1983; Van Parijs et al. 2009). Here I attempted to control for behavioural differences by comparing one calving habitat against another. Another possible explanation for differences in call frequency is the variation in the individuals that are producing calls (e.g. a difference in the proportion of younger animals). Again, however, Parks et al. (2007) showed no indication that juvenile and adult calls were different in terms of frequency.

We should also remember that right whale calls are not likely to be completely innate. The way in which humpback whale songs evolve, sometimes showing very rapid change across individuals within a breeding area (Noad et al. 2000) demonstrates that these songs have a strong learned component. This is likely to be true, at least to some extent, in all mysticetes and suggests that the learning process itself may introduce variation which shows as differences between areas, as it does in bird song dialects (e.g. Jenkins 1978).

Conclusion

There is convincing evidence that NARW and SRW *upcalls* are different and can easily be separated using predictive models. Evidence from this study and previous research (Parks et al. 2007; 2011; 2014) suggests that right whales have a certain amount of vocal flexibility and have the ability to make changes to the frequency and duration of *upcalls* to compensate for increased noise conditions. The available evidence suggests that right whale calls at the Auckland Islands have the characteristics of a population that is unimpacted by noise. This study also provides a good baseline against which to assess future change.

CHAPTER 6

GENERAL DISCUSSION

Right whales, like other cetaceans, are highly vocal and sound is critical to their everyday lives as their primary mode of communication. Right whales use short-range vocalisations to maintain close contact with other individuals, for example, the vocal contact between mother and calf is critical to the calf's survival (Clark et al. 2007). Longer range communication, over several kilometres (e.g. Clark and Clark 1980; McDonald and Moore 2002), enables an individual to find social groups for mating opportunities or locate feeding or migrating conspecifics. Using these communication sounds to monitor marine mammal populations is an increasingly popular non-invasive approach (e.g. Mellinger et al. 2007b; Van Parijs et al. 2009; Sousa-Lima et al. 2013). As sound has the ability to travel long distances and because cetaceans spend a large proportion of their lives underwater, acoustic monitoring typically has a higher probability of detecting whales than visual surveys (McDonald and Moore 2002; Širović et al. 2004; Barlow and Taylor 2005; Clark et al. 2010). Acoustic monitoring is particularly effective for rare species at low densities, in remote and inaccessible places, in poor weather or at night, when visual methods are impractical (Mellinger and Barlow 2003; Mellinger et al. 2004; Moore et al. 2006). As technology improves, so too does our ability to monitor marine mammals acoustically, enabling us to record for longer periods at higher resolution.

Much is known about the acoustic behaviour of the North Atlantic right whale (NARW, *Eubalaena glacialis*) over the extent of its range (e.g. Matthews et al. 2001; Laurinolli et al. 2003; Vanderlaan et al. 2003; Mellinger 2004; Parks and Tyack 2005; Parks et al. 2005; 2007; Mellinger et al. 2007a; Van Parijs et al. 2009; Parks et al. 2009; 2010; Clark et al. 2010; Trygonis et al. 2013; Matthews et al. 2014) and there is an increasing amount of work on the North Pacific right whale (NPRW, *E. japonica*) despite its critically low population level (e.g.

McDonald and Moore 2002; Mellinger et al. 2004; Munger et al. 2008; 2011). Southern right whale (SRW, *E. australis*) vocalisations have been studied in South America (Cummings et al. 1972; Clark and Clark 1980; Clark 1980; 1982; 1983; Parks et al. 2014) and limited work has been carried out in South Africa (Hofmeyer-Juritz 2010). This thesis describes the first research to focus on the acoustic behaviour of the SRW population in New Zealand waters.

6.1 Implications for passive acoustic monitoring

Passive acoustic monitoring (PAM) is increasingly being used to answer important ecological questions about occurrence and distribution (Frankel et al. 1995; Verfuss et al. 2007), movements (Risch et al. 2013), behaviour (Watkins 1981; Clark 1990) and abundance (Barlow and Taylor 2005) of marine mammals. PAM is also used to help understand and mitigate the impacts of anthropogenic noise including seismic activities, pile driving, shipping and sonar (Barlow and Gisiner 2006; Brandt et al. 2011). In order to use PAM efficiently and accurately for these purposes, first there is a need to collect basic information about the acoustic repertoire of the particular species of interest.

Reliably assigning vocalisations to a species is a crucial step prior to describing the acoustic characteristics of their sounds. The Auckland Islands provide a fantastic opportunity to unequivocally assign calls to right whales as no other cetacean species are known to regularly use the area (Baker 1977). Indeed, during five visits to the Auckland Islands (2008, 2010 to 2013) no other cetacean species were observed (pers. obs.). In 20 years of research prior to that there were only three sightings of other cetacean species; one humpback whale, one pod of unidentified dolphins and one pod of pilot whales offshore (Childerhouse pers. comm.). A previously undescribed call, a *long tonal low*, which was in some cases up to 25 s in duration was discovered as part of this study (Chapter 2). Most examples of this call were recorded when researchers were present in upper Port Ross whilst in visual contact with right whales, and simultaneously right whale *upcalls* were evident on recordings. In other regions with multiple baleen whale species it would not be possible to definitively assign this call to right whales, without the aid of localisation.

The variety of tonal and pulsive sounds produced by right whales at the Auckland Islands (Chapter 2) was broadly similar to the repertoire of NARWs (e.g. Parks and Tyack 2005; Trygonis et al. 2014) and other SRW populations (e.g. Clark 1982). The most prevalent vocalisations in the long-term dataset from the Auckland Islands were *upcalls* (Chapter 3). When calls were examined from the peak calving period (July to August) only, three call types were predominant (*upcalls*, *pulsive* and *tonal lows*) and the contribution of each was similar (between 16% and 17.5% of total calls, Chapter 2). It is important to remember however that only a sample of calls (n = 4355) were selected for the analyses in Chapter 2, whereas all calls were analysed in Chapter 3 and hence are most representative. The benefit of recording during the research trip to the Auckland Islands was that I could capture the high resolution detail of calls without any issues concerning battery life or storage capacity of recording equipment. This enabled me to capture the variation in measured acoustic characteristics between call types. The multivariate technique Random Forest (RF) analysis proved to be highly accurate for classifying calls, particularly for tonal calls and *gunshots* (Chapter 2). This method allowed call types to be correctly predicted based on measured variables in 82% of cases. RF is a robust method which could be replicated easily to facilitate comparative studies of calls from different habitats and geographical areas.

An understanding of how vocalisations vary both seasonally and daily (Chapter 3) is also important for effective passive acoustic monitoring. There was a seasonal trend in sound production at the Auckland Islands, with whales vocally active and routinely present between May and November. Except for January, vocalisations were detected in every month during the rest of the year. This is similar to what we know about seasonal presence from visual observations (Patenaude 2000), but PAM is much more effective than visual surveys for detecting low densities of cetaceans (e.g. Rayment et al. 2011). There was no major change in the proportion of different call types used throughout the year. This either suggests that there was no major change in behaviour or that a change was undetectable due to the low call rates outside the main winter period. There was a clear diel pattern in call rate, with more calls detected at dusk and during the night compared to the day. The simplest explanation is that reduced visual contact in the dark increases the need for acoustic communication, particularly between mother-calf pairs. Vocal measures of SRW presence at the Auckland Islands should be considered a conservative estimate of occurrence, as whales could be present but silent.

Detailed long-term acoustic data are invaluable for understanding the behaviour of cetaceans and managing the impacts on them (Van Parijs et al. 2009).

6.2 Implications for automated detection

Non-automated analysis of acoustic data is time consuming and laborious. To facilitate the rapid processing of vast quantities of data, automated call detection is a useful tool (e.g. Mellinger and Clark 2007). In order to build automated detectors, detailed data on a species' call characteristics and repertoire are required (Chapter 2). Significant resources have been channelled into designing and implementing algorithms to detect *critically endangered* NARWs. Traditionally, recognition algorithms to detect right whales have focused on *upcalls* (Gillespie 2004; Mellinger 2004; Urazghildiiev and Clark 2006; 2007; Urazghildiiev et al. 2009; Dugan 2010a; 2010b; Mohammad and McHugh 2011; Pourhomayoun et al. 2013) as they are species-specific and produced by adults and juveniles of both sexes (Clark 1983; Parks and Tyack 2005). *Upcalls* likely function as contact calls (Clark 1982; Parks and Tyack 2005) and whales have been observed calling back and forth over several kilometres (Clark and Clark 1980).

Understanding how, when and how frequently *upcalls* are used by right whales (Chapters 2 and 3) helps to work out the limitations of using just this one call type for detection. An automated detector built for NARWs (Urazghildiiev and Clark 2006) was tested and found to be effective for detecting SRWs in New Zealand, although the false detection rate was relatively high when call rate was low (Chapter 3). Knowledge of the false detection rate is particularly relevant for studying right whale populations in remote locations and populations with low densities of whales (McDonald and Moore 2002, Mellinger et al. 2004). The ultimate aim of detection algorithms is to maximise the number of true call detections, whilst minimising false detections and missed calls.

Upcall rate varies between habitats and seasons (Urazghildiiev and Parks 2014). For example, *upcalls* are not the most frequently recorded call in surface active groups of NARWs (Parks and Tyack 2005). They are, however, the most commonly produced sound in many other contexts (Clark 1982; McDonald and Moore 2002; Parks et al. 2011); this is also true for SRWs recorded at the Auckland Islands (Chapter 3). Despite *upcalls* being the most numerous call, almost two-thirds of SRW vocalisations were of other call types (Chapter 3). In my study, no call-positive days were missed by using a detector (Urazghildiiev and Clark 2006) focussing only on *upcalls* (Chapter 3), however, using other call types would increase detection rates, particularly when call rate is low. Reliable, repeatable measurements of call characteristics (Chapter 2) are therefore crucial for designing and optimising algorithms for automated detection. The RF method used for classifying SRW calls highlighted the important features for defining call types (e.g. maximum ceiling frequency and number of inflection points), again aiding the development of efficient detection systems. Future research into the development of pitch-tracking systems and other complex detection techniques should include non-*upcall* vocalisations (Baumgartner and Mussoline 2011; Urazghildiiev and Parks 2014). This may be of particular importance in critical habitat areas where detection has serious conservation implications. For example, where automated detection is used in near-real-time to inform mariners of NARW presence in busy shipping lanes (Spaulding et al. 2009). A missed vocalisation in such circumstances could have severe repercussions, leaving whales vulnerable to ship strike.

6.3 Significance of acoustic pollution

An increase in anthropogenic noise in the ocean can have serious implications for marine mammals (Richardson and Würsig 1997; Nowacek et al. 2007; Ellison et al. 2012). The effects of noise range in severity, and have been detected in many species of cetacean. They include: call lengthening (Miller 2000), increased whistle production (Rendell and Gordon 1999), longer dives (Frankel and Clark 1998) and displacement from a region (Ellison et al. 2012). Consistent or even intermittently high noise levels may cause masking (Clark et al. 2009), thus affecting the probability of a whale detecting a conspecific. Right whales in the Atlantic have already changed their vocal behaviour in response to noise (Parks et al. 2007; 2010; 2011).

Given the observed changes in the vocal behaviour of NARWs due to acoustic pollution, noise is potentially of concern for SRWs. Currently SRWs at the Auckland Islands are exposed to much lower noise levels than NARWs (Chapter 4), particularly at the low frequencies characteristic of shipping noise. The significant differences in the frequency content of calls produced by NARWs and SRWs at the Auckland Islands supports the theory that noise is of consequence to right whales and that they have modified their communication signals (Chapter 5) in response to higher ambient noise levels in the North Atlantic. The sub-Antarctic Islands of New Zealand have minimal influence from anthropogenic acoustic sources, and provide a useful yardstick against which to compare ambient noise in the much more modified habitats occupied by other most other right whale populations.

Compared to vocalisations produced by other cetaceans, right whale calls are not very loud. This makes them particularly vulnerable to the effects of masking from low frequency noise such as shipping (Clark et al. 2009). NARWs and NPRWs in particular, have low population densities (Wade et al. 2006; Marques et al. 2011) which adds to the challenge of detecting them. Low call rates (in certain behavioural contexts) coupled with low call intensity and a lack of song (or varied call patterns) lead to a greater risk of masking in right whales relative to other mysticetes (Hatch et al. 2012). Hatch et al. (2012) state that “even when right whales were at pre-whaling abundance and call density was greater, call density would not have added substantially to background noise”. This may be true for NARWs but was certainly not the case here for SRWs at the Auckland Islands (Chapter 4). Even though right whales in New Zealand are still at a fraction of their former pre-whaling abundance (Jackson et al. 2008), ambient noise increased significantly (by 20 dB re 1μPa^2 at 100 Hz) in August, the month with highest call densities (Chapter 4). This means that SRW calls are a significant feature of the soundscape.

If SRWs continue to make a comeback and recover to mainland New Zealand (Carroll et al. 2014), environmental noise could be an important factor governing the choice of areas that they re-colonise. The New Zealand coastline is increasingly becoming industrialised and the level of noise producing activity including ports and shipping (Statistics New Zealand 2014), aquaculture (Ministry of Economic Development 2007), dredging, construction, mining activities, seismic testing and recreation, continues to grow. Historically, when the right whale population in New Zealand was more abundant anthropogenic activity around the coast was at much lower levels. The cumulative impact of many activities in the coastal zone has likely led to an increase in noise in recent years. Historically, right whales regularly used sheltered inshore regions, such as Wellington Harbour, Otago Harbour and Akaroa Harbour (Richards

2002; Carroll et al. 2014). These places have since seen an increase in anthropogenic activities, for example, cruise ships are now a regular occurrence in Akaroa (Shone et al. 2014), and regular dredging is needed to maintain the port in Otago (Smith et al. 2010). It is possible that these historical right whale habitats may no longer be as appealing due to increase in noise and masking potential. Information on ambient noise (Chapter 4), combined with work undertaken on SRW habitat preferences (Rayment et al. 2014, Appendix B), could assist with predictions of re-colonisation around the mainland and management of acoustic impacts in the coastal zone.

6.4 Significance for management and conservation

Previous knowledge of when right whales were present at the Auckland Islands came from visual surveys over winter only (e.g. Patenaude 2000). The autonomous recorders used here allowed me to gather data over a continuous period of almost 11 months at this remote location (Chapter 3). SRWs use this habitat for much more of the year (10 of the 11 months monitored; only in January were no *upcalls* detected) than was previously thought which clearly indicates the effectiveness of PAM as a tool for detecting whales (e.g. McDonald and Moore 2002; Clark et al. 2010). How right whales use their habitat is important for managing the population. The Auckland Islands is an extremely important site for SRWs and nowhere else in New Zealand are whales found in such high numbers (Patenaude 2000; Rayment et al. 2012, Appendix A). SRWs are considered a priority species by the New Zealand Department of Conservation (DOC, Suisted and Neale 2004) and a critical part of their lifecycle (calving) is undertaken in these waters due to the sheltered conditions (Rayment et al. 2014; Appendix B). DOC considers acoustic disturbance a priority issue for SRWs and has identified three key actions: protecting the recovering sub-Antarctic population from tourism, promoting recovery of the mainland population and protecting significant habitats from coastal development and aquaculture (Suisted and Neale 2004). The research undertaken here means that we better understand how and when SRWs use Auckland Island habitat (Chapter 3) and that we have baseline data on ambient noise (Chapter 4).

The management of acoustic impacts will likely become more of an issue in future, as human populations and associated activities increase in the coastal zone, and society's awareness of the impact of noise on marine life increases. Considering its importance as a key habitat, continued protection from disturbance and development in Port Ross, would be wise, as well as determining strategic locations around the mainland and increasing protection. For example, keeping noise pollution to a minimum in “sensitive” areas by limiting oil and gas exploration, aquaculture activities and tourism interests. Speed limits for shipping could be considered in key areas, as lower speeds typically equate to lower sound levels (Ross 2005). Collisions with vessels result in considerable numbers of NARW mortalities (Kraus et al. 2005) and SRWs in New Zealand have not escaped such interactions (pers obs.). A reduction in shipping speed increases a whales’ chance of survival significantly (Vanderlaan and Taggart 2007). High levels of noise are known to cause stress in right whales (Rolland et al. 2012) and have resulted in them modifying their communication signals (Parks et al. 2007; 2010; 2011). Noise pollution at the Auckland Islands could be seriously detrimental to the SRW population, particularly as whales show strong habitat preferences for Port Ross, and occur at very high density in a relatively small area. Displacement from areas of high noise have been observed in other cetacean species (Richardson and Würsig 1997; Ellison et al. 2012). Were this to happen at the Auckland Islands, New Zealand’s SRWs would be denied their most important calving habitat. As this habitat is an isolated island in the middle of the Southern Ocean, there is no nearby alternative for them to find shelter during the calving period.

Traditionally, marine protected areas in New Zealand have only managed extractive activities such as fishing and mining. The marine reserve and marine mammal sanctuary at the sub-Antarctic Auckland Islands extends out to 12 n.mi offshore and within its boundaries no commercial fishing is permitted and there is a moratorium on commercial whale-watching in winter. This research (Chapters 4 and 5) emphasises that managing acoustic pollution is also a very important consideration. In the USA, permits are currently required for any anthropogenic activities that lead to the exposure of baleen whales to impulsive sounds >160 dB re 1µPa at 1 m, or continuous sounds >120 dB re 1µPa at 1 m (NOAA 2005). These regulations do not currently apply to shipping and Hatch et al. (2012) highlighted that the average area ensonified (> 120dB dB re 1µPa at 1 m) by a tanker transiting through the Stellwagen Sanctuary was approximately the same size as the sanctuary itself. Sound does not adhere to the boundaries established for a sanctuary or protected area and is able to cross these boundaries and cover large areas quickly. Regulations need to extend well beyond the core protected area to a buffer zone in order to provide sufficient protection from noise or other activities that have far reaching effects (e.g. Agardy et al. 2011)

6.5 Limitations of research

There are many challenges associated with passive acoustic monitoring. One of the issues is identifying whether an absence of calls means an absence of whales, or whether the whales are just silent. It is important to recognise that variability in vocalisation rate could be due to a change in the number of right whales using an area or a change in their vocal behaviour, or potentially due to temporal variation in ambient noise. This can only be resolved via expanding our limited knowledge of right whale acoustic behaviour (e.g. Clark 1983; Parks and Tyack 2005) and studying the specific behaviours of whales at the Auckland Islands.

Call categories (Chapter 2) were modelled on the acoustic classification system for SRWs in Argentina in which classes were based on observations of vocalising individuals that were localised in real-time (Clark 1982). At the Auckland Islands it proved impractical for localisation to be undertaken in real-time and thus assign behaviours to individuals. Without simultaneous behavioural observations there is a limit to what can be inferred from the different sounds produced, and the resulting call classification might not be biologically meaningful (e.g. Deecke et al. 1999).

Ambient noise measurements (Chapter 4) currently encompass a certain amount of noise generated by tidal banging (in the Atlantic Ocean) and rubbing on the hydrophone (at the Auckland Islands). Ideally these noises would be eliminated from the analysis, so that ambient noise levels are not artificially inflated.

6.6 Further research

The work undertaken here lays the foundation for future studies on southern right whale acoustic behaviour and ambient noise in New Zealand.

Remote acoustic monitoring using DSG-Ocean recorders has proved highly effective for long-term data collection (Chapter 3). This same methodology could prove valuable for monitoring the New Zealand mainland coast where right whale densities are currently too low for systematic visual surveys (e.g. Te Waewae Bay, Preservation Inlet, Otago Harbour) but where it is hoped that right whales will increasingly recover to (Carroll et al. 2014). Autonomous recorders would be a cheap and efficient way for gathering long-term datasets in other remote locations such as sub-Antarctic Campbell Island. Further acoustic monitoring and exploration of areas such as Campbell Island and offshore in the Southern Ocean may enable us to locate potential mating and feeding grounds for this population.

Monitoring ambient noise over time at different locations is important. This is how we learn about long-term trends in noise (e.g. Andrew et al. 2002; McDonald et al. 2006; Chapman and Price 2011) and temporal variation (Radford et al. 2008), and are able to examine potential impacts on life in the ocean. This is particularly important as noise is implicated in a wide range of adverse impacts on marine life. Related to this would be continued monitoring of right whale *upcalls* over time to investigate whether particular parameters (e.g. minimum or maximum frequency) increase as anthropogenic noise increases (e.g. Parks et al. 2011; 2014). As an aside, data on right whale body size gleaned via photogrammetric methods may be of use for ruling out size as a potential reason for lower frequency calls. These data would also allow us to determine the size-class makeup of individuals found at the Auckland Islands.

Gathering simultaneous behaviour data is key to furthering acoustic research on right whales at the Auckland Islands. This would enable us to examine what animals are doing when they produce particular calls and which calls are produced by which animals. For example, establishing whether gunshots are made only by males (e.g. Parks et al. 2005) and screams only by females (e.g. Parks and Tyack 2005). Further information on the sex and age of individuals could be gleaned using photo-identification and an underwater pole-cam (e.g. Webster et al. 2008). A system for recording simultaneous acoustic and visual data could incorporate for example, a theodolite on the hill overlooking Sandy Bay, at least three moored hydrophones and a video camera. This would allow acoustic behaviour and source levels to be investigated.

How vocalisation rates vary over time must be understood if we seek to estimate abundance via passive acoustic monitoring. One study has found that right whale moan rates are correlated with aggregation size (e.g. Matthews et al. 2001), however, Clark et al. (2010) found no strong relationship between the number of whales and the number of contact calls produced. Mysticete vocalisation rates often vary more with behaviour than with the number of individuals present (e.g. Payne and McVay 1971; Oleson et al. 2007). Typically, vocalisations are not produced uniformly over time and lengthy periods of silence have been observed in right whales, particularly associated with foraging (Matthews et al. 2014; Webster and Jaquet, unpublished data).

6.7 Concluding remarks

In light of the findings here (Chapters 2 to 5) and other recent research on habitat preferences and distribution of right whales at the Auckland Islands (Rayment et al. 2012; 2014, Appendices A and B), now would be a good time to update the Marine Mammal Action Plan for right whales (Suisted and Neale 2004). There is an opportunity to proactively manage the recovering population of SRWs in New Zealand waters. For example, by considering ways to limit noise increase in areas likely to be recolonized by whales. Right whales in the Atlantic Ocean currently suffer entanglement in fishing gear, ship-strike and noise pollution (Knowlton and Kraus 2001; Parks et al. 2007). Right whales do respond to mitigation efforts; for example, a reduction in shipping noise led to an immediate reduction in stress hormone levels (Rolland et al. 2012). Hypothetically, if the shipping lanes in the Bay of Fundy had been moved earlier (in 1970) to avoid overlap with NARW habitat then 67% of all NARWs collisions would have been avoided (Kraus and Rolland 2007). SRWs in New Zealand are not immune to these issues, for example, there are known cases of ship strike even though shipping is at far lower densities in the southern hemisphere. Here we have a chance to learn from the problems facing NARWs and manage these impacts effectively so that the SRW population can continue to recover.

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APPENDIX A

Distribution of southern right whales on the Auckland Islands calving grounds

William Rayment, Anthony Davidson, Steve Dawson,
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2012

New Zealand Journal of Marine and Freshwater Research
Vol. 46, No. 3, September 2012, 431–436

SHORT COMMUNICATION

Distribution of southern right whales on the Auckland Islands calving grounds

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(*Received 17 February 2012; final version received 24 April 2012*)

Southern right whales (*Eubalaena australis*) were virtually extirpated from New Zealand by commercial whaling, but are now recovering. Previous research at the Auckland Islands has suggested that Port Ross, a sheltered embayment at the northern end of the islands, is the primary calving ground for right whales in New Zealand. However, an abundance of potentially suitable calving areas exist outside Port Ross, raising the question of whether the growing population might be expanding its distribution to occupy new or former habitats. To address this we conducted the first systematic line-transect survey of potential right whale calving habitat at the Auckland Islands in winter 2011. High densities of southern right whales were sighted inside Port Ross, including all but one of the 21 mother-calf pairs recorded. The survey confirmed that Port Ross is the principal calving area for southern right whales in the Auckland Islands. This conclusion has implications for the estimation of demographic parameters of right whales in New Zealand, which have thus far relied on data gathered largely in Port Ross, and highlights the importance of protecting this habitat.

Keywords: southern right whale; *Eubalaena australis*; line-transect survey; Auckland Islands; New Zealand; distribution; calving habitat

Introduction

Prior to commercial exploitation, southern right whales (*Eubalaena australis*) congregated in coastal waters around New Zealand during austral winter, when females give birth and nurse their young (Richards 2002). They were virtually extirpated from New Zealand by whaling in the 19th and 20th centuries leaving only a small remnant population, thought to have been centred on remote Campbell Island (Richards 2002, 2009; Jackson et al. 2008). Since protection in 1935, the New Zealand population has recovered slowly, and was estimated to number 908 individuals (CV = 0.10) in 1998 (Carroll et al. 2011a). Currently, the sub-Antarctic Auckland Islands are believed to be the primary calving ground for New Zealand southern right whales (Patenaude et al. 1998; Patenaude & Baker 2001), with smaller numbers wintering at Campbell Island (Stewart & Todd 2001) and around the New Zealand mainland (Patenaude 2003; Carroll et al. 2011b).

The first dedicated research on right whales in the Auckland Islands was a series of expeditions to investigate distribution and abundance in the winters of 1995–1998 (Patenaude et al. 1998; Patenaude & Baker 2001). Land-based visual observations and surveys from small boats were conducted in and around Port Ross, a sheltered embayment at the northern end of the archipelago. Whales were present in high concentrations in Port Ross and the nearby waters around Enderby Island, and a few sightings were made in the adjacent bays (Patenaude & Baker 2001). During July 1996, a

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ISSN 0028-8330 print/ISSN 1175-8805 online

http://dx.doi.org/10.1080/00288330.2012.697072
http://www.tandfonline.com

film crew working with the expedition chartered a helicopter and searched the length of the Auckland Islands. The observers confirmed that the main aggregation of right whales was limited to Port Ross, despite what appeared to be suitable habitat along the eastern coast of Auckland Island (Patenaude & Baker 2001).

Parturient southern right whales seek shallow, sheltered habitats in winter, presumably to reduce energy expenditure by their calves (Elwen & Best 2004). Barrett (2000) concluded that calving females in the Auckland Islands preferred areas within 200 m from shore in water depths less than 20 m. As noted by Patenaude & Baker (2001), areas of Port Ross clearly satisfy these habitat requirements, but an abundance of apparently suitable habitat also exists elsewhere. For example, the east coast of Auckland Island has a series of bays of varying sizes, all sheltered from the prevailing westerly swells, and Carnley Harbour, at the southern end, also offers a large protected habitat. Since the last abundance estimate in 1998, the New Zealand population of right whales is thought to have continued recovering (Carroll 2011). This raises the question of whether competition for space will result in right whales expanding their distribution and colonising new, or possibly former, habitats outside Port Ross. To address this we conducted the first systematic line-transect survey to quantify distribution of southern right whales in the Auckland Islands.

Methods

On the 2 and 3 August 2011 we carried out a visual line-transect survey of Port Ross, the east coast of Auckland Island and Carnley Harbour (Fig. 1). The purpose was to compare the high density area in Port Ross with areas which had not been formally surveyed and hence we did not include the north coasts of Enderby and Auckland Islands. The survey was timed to coincide with peak abundance of southern right whales at the Auckland Islands (Patenaude 2002). The survey platform was the 21 m *RV Polaris II*. Survey speed was 8 knots. The survey team consisted of five observers, three of which were on survey effort at any one time standing on the roof of *Polaris II*'s wheelhouse. Eye heights were measured for each observer (mean = 5.22 m above sea level). Observers used Fujinon 7 × 50 marine binoculars with inbuilt compasses and reticles. One observer scanned from straight ahead to abeam (90° to the vessel's track) on the starboard side of the vessel and one scanned from straight ahead to abeam on the port side. Observers alternated scans between using binoculars and naked eyes. The third observer acted as recorder, entering details of sightings and survey effort into a palmtop computer running custom-written software and interfaced with a GPS. To avoid fatigue, observers worked sequentially for 20 minutes at each station, and then had a 40 minute break.

For each sighting of a southern right whale, the following details were recorded: compass bearing to sighting; number of reticles below the horizon or land/sea interface; observer identity and position; ship's heading (measured by the recorder); group size and composition; Beaufort sea state and swell height. Whales were considered part of the same group if they were within one and a half body lengths of each other, and a calf was defined as a whale less than half the length of an accompanying adult (Patenaude 2002; Carroll et al. 2011a). The survey track was recorded via the computer storing a GPS fix every 30 s. All survey effort was carried out in good visibility (>10 km) at sea states of Beaufort 5 or less, with 89% being completed in Beaufort 3 or less.

Radial distances to each sighting were calculated as in Lerczak and Hobbs (1998a,b). The radial distance, the vessel's GPS position at the time of the sighting and the angle to the sighting relative to the vessel's heading were then used to calculate the position of each whale group. The vessel's track and whale sightings were plotted using ArcMap v.10. In order to highlight hotspots of whale density, a kernel density surface was calculated using ArcMap's 'Kernel Density' tool. Output cell size was 50 m, with a search

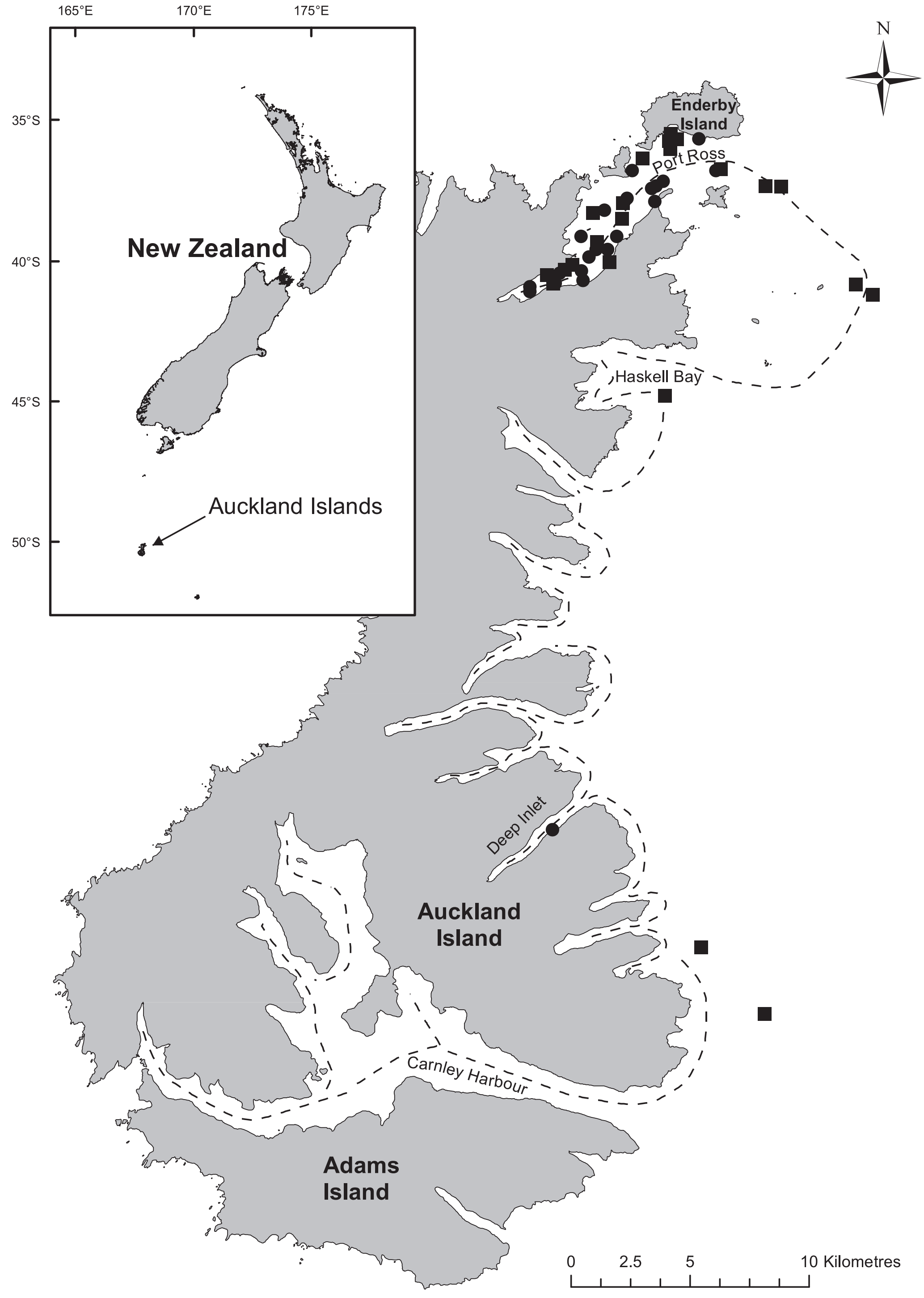

Figure 1 Survey effort and southern right whale sightings on line-transect survey of the Auckland Islands in August 2011. Dashed line shows track of survey vessel. Closed circles show sightings of mother-calf pairs. Closed squares show sightings of all other whales. Inset shows location of Auckland Islands.

radius of 1000 m chosen in order to confine the density estimate to Port Ross. Note that the density surface is not intended to be a measure of absolute density, as no estimates of availability or perception bias (Dawson et al. 2008) were obtained.

Results

In surveying Port Ross, the east coast of Auckland Island and Carnley Harbour we completed 85 n.mi. of line-transect survey effort (Fig. 1). We made 43 sightings of southern right whale groups (mean group size = 1.7, range = 1–3) of which 49% contained mother-calf pairs. Only eight sightings were made outside Port Ross; four sightings of single adults in the approaches to Port Ross, one outside Haskell Bay, two on the south-eastern coast of Auckland Island and one mother-calf pair in Deep Inlet (Fig. 1). No sightings were made in Carnley Harbour despite comprehensive survey effort in excellent sighting conditions (no swell, sea state <4).

The kernel density analysis confirmed that Port Ross had by far the highest concentration of whale sightings (Fig. 2). The highest densities of whales occurred in the southwestern upper reaches of the harbour, the middle of Port Ross and along the southern shore of Enderby Island. Note that densities displayed in Figure 2 are minimum values as availability and perception biases have not been incorporated.

Discussion

The survey confirmed that Port Ross harbours a high concentration of southern right whales during winter and is the primary calving ground for right whales in the Auckland Islands. By inference, Port Ross is also the primary calving ground for all New Zealand right whales, although it should be noted that no surveys have been conducted at Campbell Island since 1997 (Stewart & Todd 2001). Given that the population of whales in the Auckland Islands is thought to be increasing (Carroll 2011), and an abundance of apparently suitable calving habitat exists, it is surprising that only one mother-calf pair was sighted outside Port Ross. There are several plausible explanations for this highly localised distribution. Firstly, the growth of the population may have not yet reached the level where demand for space in Port Ross has resulted in range expansion. However, it has been hypothesised that right whales from the sub-Antarctic are now recolonising the historical calving ground around mainland New Zealand (Carroll et al. 2011b). Secondly, the precise habitat requirements of calving females are not well understood and hence our assessment of potential calving habitat may be misguided. Thirdly, as noted by Pirzl (2008), social factors probably influence the distribution of right whales such that proximity to conspecifics might be more important than the physical habitat. Lastly, our survey was conducted over only two days; whilst we are confident our results are an accurate representation of right whale distribution at that time, further surveys over the course of a winter and in multiple years would be required to strengthen our conclusions. Furthermore, note that our data only represent the proportion of the population sighted during the survey and we have not attempted to correct for variations in sighting probability. However, any such variations have been minimised through adherence to strict sighting protocols.

Our results have implications for the estimation of demographic parameters of southern right whales in New Zealand. To date, the estimates of right whale abundance and population growth have utilised genetic and photo-ID mark-recapture data gathered in Port Ross (Patenaude 2002; Carroll 2011; Carroll et al. 2011a). Confirmation that Port Ross is the primary wintering ground for right whales, and that no significant other calving habitats exist in the Auckland Islands, mean that the current demographic estimates are likely to be representative of the entire New Zealand population. Similarly, there are implications for conservation and management. The present study highlights the importance of Port Ross

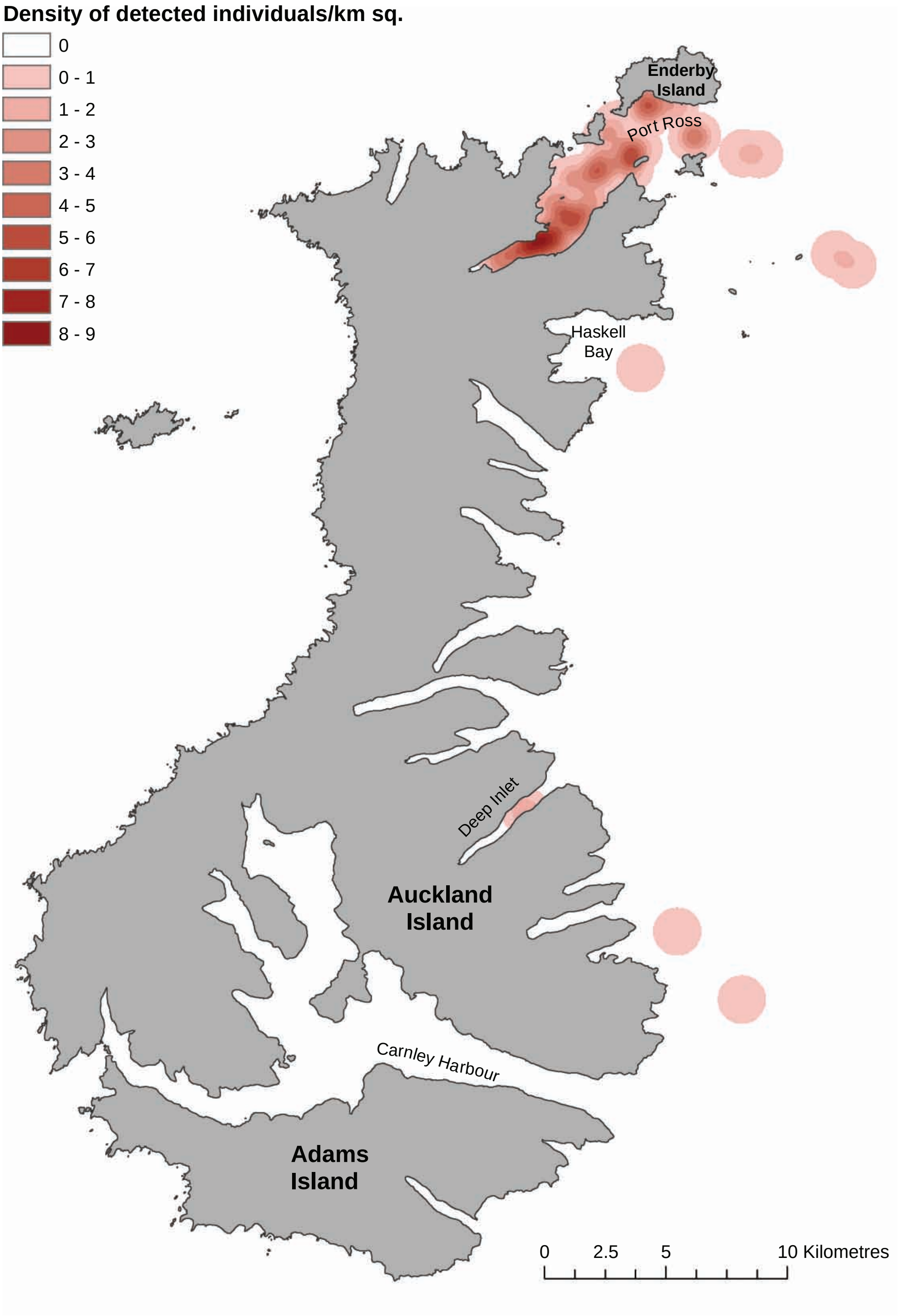

Figure 2 Kernel analysis of southern right whale density in the Auckland Islands.

as a habitat for southern right whales, and supports the requirement for protection from disturbance and development. We recommend that additional surveys of the Auckland Islands and Campbell Island be conducted to further investigate the status and habitat preferences of this recovering population.

Acknowledgements

The research was funded by the Foundation for Research, Science and Technology (FRST), the New Zealand Whale and Dolphin Trust and the University of Otago Marine Science Department. We thank the crew of *Polaris II*; Bill Dickson, Phil Heseltine, Steve Little and Tim Lever, for getting us safely to and from the Auckland Islands, and the staff at the Marine Science Department for logistical support, including Daryl Coup who wrote the palmtop software. We thank Department of Conservation staff; Pete McLelland, Laura Boren, Doug Veint, Jo Hiscock, Gilly Adam and Kath Blakemore, for assistance with permitting and quarantine. Rhys Richards provided valuable information about historical whale sightings and Simon Childerhouse gave assistance when planning the research. The research was conducted under Marine Mammal Permit Per/NO/2010/05. W Rayment was supported by a FRST post-doctoral fellowship and T Webster by a University of Otago PhD scholarship.

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APPENDIX B

Breeding status affects fine-scale habitat selection of southern right whales on their wintering grounds

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2014

Journal of Biogeography (J. Biogeogr.) (2014)

ORIGINAL ARTICLE

Breeding status affects fine-scale habitat selection of southern right whales on their wintering grounds

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ABSTRACT

Aim To develop and validate a model for fine-scale distribution of southern right whales (*Eubalaena australis*) on their calving grounds, accounting for breeding status.

Location Port Ross, a harbour at the northern end of the sub-Antarctic Auckland Islands, approximately 450 km south of mainland New Zealand.

Methods Species–habitat surveys were conducted during annual winter expeditions to the Auckland Islands from 2010 to 2012. Presence locations for groups including calves (calf groups; $n = 462$) and not including calves (non-calf groups; $n = 313$) were recorded during small-boat surveys of Port Ross, and an equal number of pseudo-absence locations were generated in a GIS analysis. Explanatory variables tested were water depth, seabed slope, distance to coast, distance to shelter from prevailing wind and average wave exposure (estimated from a custom-built wave model). The occurrence of calf groups and non-calf groups was separately related to explanatory variables using binomial generalized additive models, with best models chosen via the minimum Akaike information criterion score. Multi-fold validation was conducted to assess model performance and temporal variation in distribution.

Results The best models for calf groups were consistent, always including wave exposure, distance to shelter, depth and distance to the coastline. In contrast, the best non-calf group models were more variable and explained only a small proportion of the variation in the data. Validation metrics indicated that the calf group models were useful predictors of distribution in Port Ross during winter, and that the calf group models performed better than the non-calf models using the same suite of environmental variables.

Main conclusions Breeding female southern right whales seek sheltered, nearshore waters during the early life-stages of their calves and are more selective of these habitats than non-calving whales. The results highlight the importance of sheltered habitat for taxa with vulnerable life-history stages, and the need to account for reproductive status to refine species–habitat models.

Keywords

Auckland Islands, calving habitat, *Eubalaena australis*, New Zealand, shelter, southern right whale, species–habitat model, wave model.

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INTRODUCTION

Studies of habitat preferences are useful for explaining species' distributions and predicting suitable habitat in a changing environment (Marsden & Fielding, 1999; Guisan & Zimmermann, 2000; Torres *et al.*, 2013; Herrera *et al.*, 2014). Habitat preferences vary at a range of temporal scales. Migratory species have predictable seasonal shifts in habitat requirements, often associated with reproductive status (Festa-Bianchet, 1988; Blouin-Demers & Weatherhead,

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2001). Many species of baleen whale, for example, undergo extensive annual migrations between summer foraging habitat and winter calving habitat (Stern, 2009). What constitutes good quality foraging habitat for baleen whales is relatively well understood: productive regions with oceanographic or bathymetric features that concentrate their zooplankton prey (Baumgartner *et al.*, 2003; Friedlaender *et al.*, 2006; Santora & Reiss, 2011). In contrast, what constitutes good calving habitat is less clearly defined. It is often suggested that parturient females select sheltered habitat, either to reduce the energetic demands on calves in their early life or to reduce the risk of separation of mother and calf (Corkeron & Connor, 1999; Ersts & Rosenbaum, 2003; Elwen & Best, 2004a; Cartwight *et al.*, 2012). We addressed the idea that parturient females select sheltered environments by examining the fine-scale distribution of the New Zealand stock of southern right whales (SRWs), *Eubalaena australis* (Desmoulins, 1822), which spend winter in the high energy environment of the Southern Ocean (Dawbin, 1986; Patenaude *et al.*, 1998).

SRWs were reduced to a small fraction of their former abundance in New Zealand by commercial whaling in the 19th century (Dawbin, 1986; Jackson *et al.*, 2008). Similarly, the extent of the area in which calving takes place was reduced from the former range throughout New Zealand coastal waters to remnants in the sub-Antarctic islands (Dawbin, 1986). Currently, the primary calving location in New Zealand is Port Ross, a relatively sheltered inlet in the remote, sub-Antarctic Auckland Islands (Fig. 1; Patenaude *et al.*, 1998; Rayment *et al.*, 2012), where approximately 70 calves are born each winter (W. Rayment, unpublished data). Non-calving whales, including adult males and immatures of both sexes, also visit the Auckland Islands in winter, presumably to gain either mating opportunities or social experience (Patenaude *et al.*, 1998; Rayment *et al.*, 2012; Carroll *et al.*, 2013). Given that these non-calving whales should not have the specific habitat requirements of nursing mothers, we expect that groups containing calves will be more selective of sheltered habitats than groups without calves. We compared

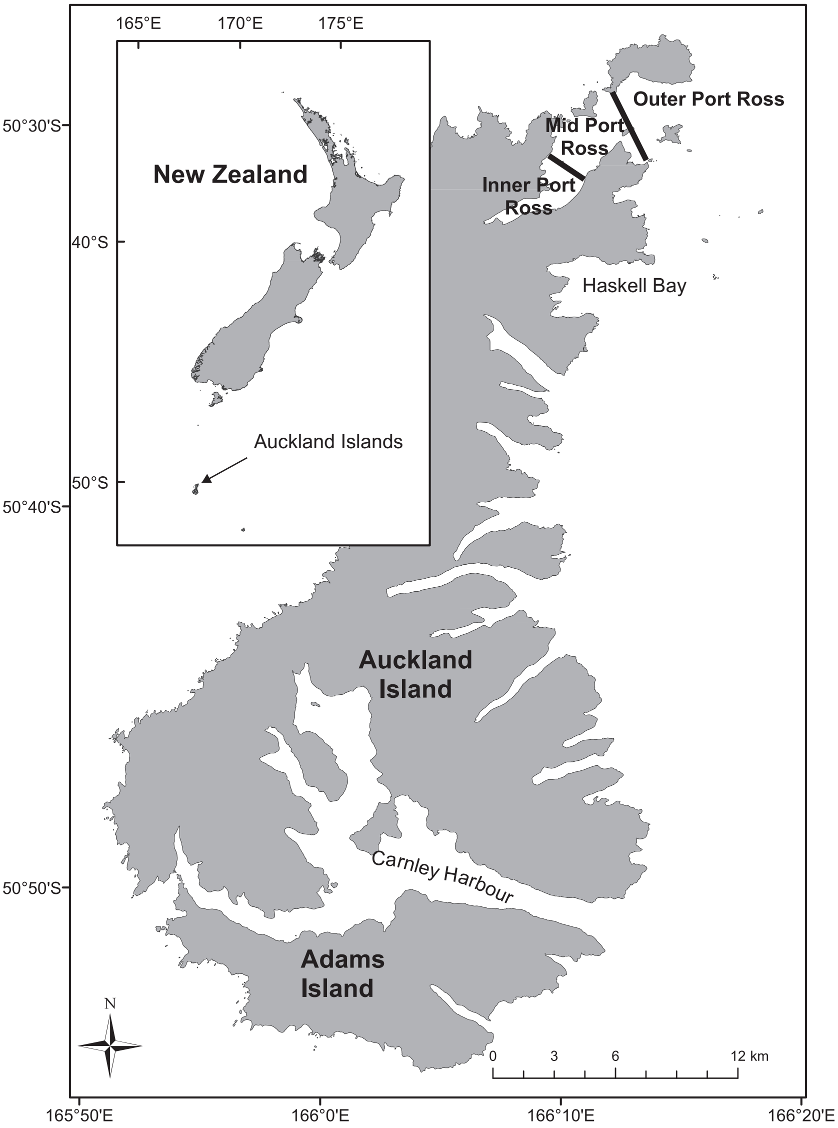

Figure 1 Map of the Auckland Islands showing the three survey sections in Port Ross. Inset shows the position of the Auckland Islands relative to mainland New Zealand.

distributions of calving and non-calving whales by conducting fine-scale species–habitat surveys in the Auckland Islands.

MATERIALS AND METHODS

Systematic, randomized surveys were carried out in and around Port Ross during annual, 3-week duration expeditions to the Auckland Islands in July and August 2010–2012. The survey platform was a 5-m aluminium research vessel powered by a 70-hp four-stroke outboard motor, with two observers onboard. Surveys were carried out at approximately 10 knots (18.5 km h^{-1}) in good visibility (> 10 km) at sea states of Beaufort 5 or less, in swell heights < 2 m. The survey area was divided into three sections: inner, middle and outer (Fig. 1). At the start of each day, a decision on which section to survey was made based on weather conditions in each section and the previous survey effort, in an attempt to survey the area as uniformly as possible. When conditions allowed, a zig-zag survey track was navigated through the section; otherwise we surveyed a line parallel to the sheltered coastline. Survey effort and sighting details were recorded on a palm-top computer (HP 200LX, Palo Alto, CA, USA) running custom-written software and interfaced with a GPS unit (Garmin GPS72, Olathe, KS, USA, or Lowrance HDS-5, Tulsa, OK, USA). A location fix was automatically stored every 30 s. One observer scanned from straight ahead of the vessel to 90° abeam on the port side, while the other performed a similar search pattern on the starboard side. When a group of whales was sighted, the vessel position at that time was recorded, then the survey vessel was slowed and directed towards the sighting. The sighting location was recorded when the vessel was as close as possible to the group's initial position (typically within 20 m). Where possible, radial distance to the sighting was estimated using the difference between the GPS location of the vessel recorded when the group was first sighted and the subsequent position of the group. Group composition was recorded for each sighting. Whales were considered part of the same group if they were consistently within one and a half body lengths of each other, and a calf was defined as a whale less than half the length of an accompanying adult (Carroll *et al.*, 2011; Rayment *et al.*, 2012). Young SRW calves typically remain submerged for less than 1.5 minutes while nursing (Thomas & Taber, 1984). It was therefore simple to establish whether or not a calf was present before continuing the transect, thus reducing time spent with each group and minimizing the risk of repeatedly counting individuals during the same survey. For this analysis, all individuals not confirmed as being a calf were classified as adults. Whale groups were classified as 'calf groups' if they contained at least one mother–calf pair, or 'non-calf groups' otherwise.

Pseudo-absence generation

The performance of species distribution models is typically improved by incorporating absence as well as presence data (Brotons *et al.*, 2004; Barbet-Massin *et al.*, 2011). While conducting whale surveys, we constantly collected absence data. However, these data were in the form of strip transect areas (see below), as opposed to whale sightings, which are point location data (Torres *et al.*, 2008). Furthermore, genuine absences are very hard to confirm (MacKenzie & Royle, 2005), especially for mobile, aquatic species. Therefore, to investigate distribution using binomial presence–absence data, we generated pseudo-absence points (Zaniewski *et al.*, 2002) in the surveyed areas where whales were not sighted (Torres *et al.*, 2008). For each day, the survey track was plotted in ArcGIS 10 (ESRI, Redlands, CA, USA), and a buffer corresponding to the median of the estimated radial sighting distance (350 m) was constructed around the survey track to produce a transect strip. Buffers of 350 m were also constructed around each whale presence location for that day and deleted from the transect strip. The resulting area was the region surveyed in which we were relatively confident we would have seen whales had they been present at the surface. Pseudo-absences were generated randomly in this area using the Data Management tools in ArcGIS 10. For each day, we generated the same number of pseudo-absences as there were presence locations, resulting in an equal weighting of presences and pseudo-absences in the species–habitat models, as recommended by Barbet-Massin *et al.* (2011). This method resulted in pseudo-absences being generated over the study area in proportion to survey effort, ensuring that areas which received less effort were not over-represented by absence data. This enabled the data to be modelled within a binomial framework, removing the need to subjectively divide the surveyed area into a grid in order to summarize effort.

Habitat variables

Factors that have been suggested to affect habitat selection by right whales on wintering grounds include water depth (Best, 1990; Elwen & Best, 2004a; Keller *et al.*, 2012), seabed slope (Elwen & Best, 2004a), protection from swell and wind (Elwen & Best, 2004a), distance from coast (Best, 1990), and sea-surface temperature (SST; Keller *et al.*, 2006, 2012). The effect of all these variables on SRW distribution in the Auckland Islands was investigated, except SST. Measurements of SST were made every 30 s while on survey effort using an echo-sounder (Navman Fish 4500, Auckland, New Zealand, or Lowrance HDS-5, Tulsa, OK 74128), which we calibrated daily against a calibrated thermometer. The range of SSTs encountered during the course of the study was very small (6.1–7.7 °C). Elsewhere, SSTs encountered in right whale wintering habitat are much higher and the range is much greater, e.g. 15–30 °C in South Africa (Elwen & Best, 2004a) and 9–21 °C in the south-eastern USA (Keller *et al.*, 2006). We considered the range of SST in the Auckland Islands to be unlikely to affect SRW distribution, and its inclusion to be of little value in predicting SRW habitat.

Bathymetry data were obtained by digitizing the local nautical chart (NZ 2862) in ArcGIS 10. Rasters of depth and seabed slope with 50-m cell size were created by interpolation using the ArcGIS Spatial Analyst tools. Values of these rasters were extracted for each presence and pseudo-absence point, along with minimum distance to the nearest coastline (variables 'depth', 'slope' and 'dcoast', respectively).

Exposure to average wind conditions was summarized as a variable termed 'distance to shelter' ('dshelter'). Hourly wind observations (mean wind speed and direction) were obtained from the automated weather station on Enderby Island (50°28.98′ S, 166°18.00′ E; altitude 40 m) for July and August 2004–2011. We used the maximum number of years data were available in order to obtain the most complete picture of average wind conditions, but only used data from July and August to summarize wind conditions during the time of year of our whale surveys. Observations were summarized as a stacked histogram wind rose (see Appendix S1 in Supporting Information), from which it was clear that the prevailing wind direction was from the westerly quarter. A baseline composed of 100-m length segments was overlaid on the coastline of the study area. Segments facing between 45 °T and 135 °T were deemed to provide shelter from westerly wind and were extracted and merged to form a GIS line layer. Minimum distance to this layer was extracted for all sighting and pseudo-absence points in ArcGIS 10.

Average wave exposure was modelled using a SWAN wave model (http://www.swan.tudelft.nl/). The SWAN model takes into account effects of shoaling, cresting, reflection, refraction, diffraction and fetch to produce spatial estimates of wind waves and longer period swell. The model requires inputs of wind, wave and bathymetry data. Wind data were obtained from daily QuickSCAT satellite observations taken at the nearest grid point, approximately 40 km north of Enderby Island. The QuickSCAT wind observations were used in preference to the Enderby Island weather station data to avoid the influence of elevation and topographic effects, after verifying that the satellite data and weather station data presented a similar summary of wind conditions. Wave data were obtained from NOAA's WAVEWATCH III™ model (http://polar.ncep.noaa.gov/waves/wavewatch/) taken at forecast hour zero (i.e. the 'now forecast') every 12 h. Concurrent wind and wave data were available from 2004 to 2009. As above, we used data from July and August only. The weather data were split into 10° wide bins based on mean wave direction, and the historical data within those bins were averaged to produce a 'mean conditions' case for each bin. The model was then run for all 36 of these 'mean conditions' bins to give a long-term average of exposure from each direction. These data were combined into a single product using a mean weighted by frequency of occurrence. The result was a long-term average of wave exposure in July and August represented as a raster of significant wave height at 50-m grid resolution (Fig. 2). The value of the raster for each presence and pseudo-absence point was extracted (variable 'Hsig').

Collinearity among explanatory variables was investigated using Spearman rank correlation tests. No correlation coefficients exceeded 0.7, the critical threshold identified by Green (1979; see also Fielding & Haworth, 1995; Herrera *et al.*, 2014), so all variables were included in the species–habitat models.

Species–habitat models

Species–habitat modelling is now commonly used to quantify the relationships between a species and its environment (Redfern *et al.*, 2006). One approach is the generalized additive model (GAM; Hastie & Tibshirani, 1990), a flexible, data-driven approach particularly useful for identifying the nonlinear relationships typical in ecology (Torres *et al.*, 2008; Pirotta *et al.*, 2011). As an additive model, the effect of each

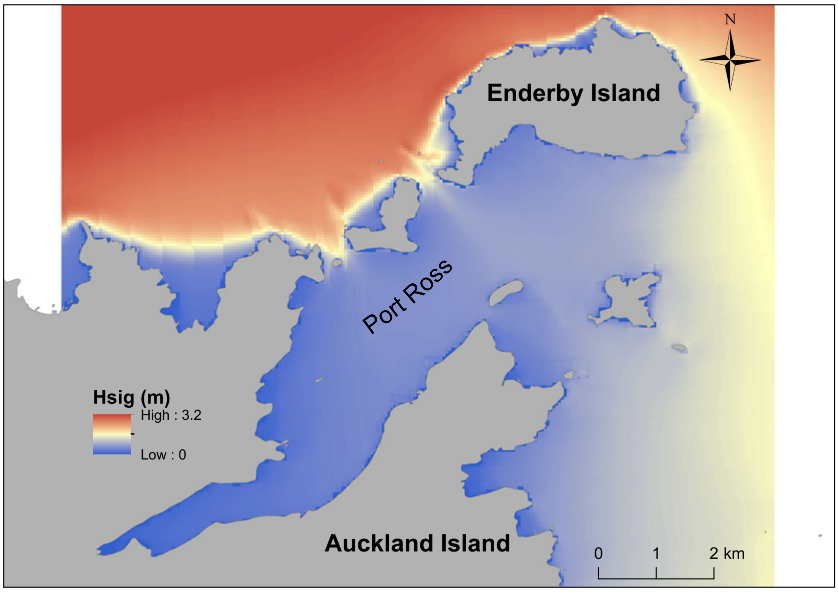

Figure 2 Modelled significant wave height (Hsig, 50-m horizontal resolution) during July and August for the northern region of the Auckland Islands.

variable on the response can be determined, while allowing for the effects of the other variables (Hastie & Tibshirani, 1990). The probability of whale presence was modelled with a suite of binomial GAMs with logit link functions, created in R 2.15.0 (R Development Core Team, 2012) using the MGCV package (Wood, 2011). We used thin-plate regression splines for smoothing, limited to a maximum of four degrees of freedom (e.g. Marubini *et al.*, 2009; Embling *et al.*, 2010) to reduce the risk of overfitting (Vaughan & Ormerod, 2005). GAMs were created with all first order combinations of independent variables as smooth terms. To facilitate interpretation of the fitted functions we did not include interactions among variables (Yee & Mitchell, 1991; Suárez-Seoane *et al.*, 2002); also, we saw no compelling biological reason to do so. The best models were chosen based on the lowest Akaike information criterion (AIC) score (Burnham & Anderson, 2002). To investigate the effect of reproductive status on distribution we created separate GAMs for calf groups and non-calf groups. Each of the three possible pairs of years (2010 and 2011, 2010 and 2012, 2011 and 2012) was used as training data to create predictive GAMs, with the other year used as an independent dataset to validate the model (see below). This enabled multi-fold validation as well as providing insight into temporal variation in distribution. Spatial autocorrelation was examined by plotting semivariograms of the residuals of the best fitting models using the GEOR package (Ribeiro & Diggle, 2001) in R 2.15.0.

Model validation

The GAMs built from each set of training data (i.e. each pair of years, for either calf groups or non-calf groups) were validated using the data from the third year. First, predictive maps of calf group and non-calf group distributions were generated based on the best GAMs. Each grid cell (50-m resolution) was assigned a predicted value of habitat suitability according to the model's fitted functions and the values of the habitat variables in each cell. The best GAMs were then used to generate predicted probabilities for each of the presence and pseudo-absence locations in the validation dataset. For validation purposes, the probability threshold was set at 0.5, as recommended by Lobo *et al.* (2008) for cases in which the training data contain equal numbers of presences and absences. We then calculated the true skill statistic (TSS; equation 1), a simple and intuitive measure of performance of species distribution models which is independent of prevalence (Allouche *et al.*, 2006). TSS ranges from −1 to +1, where +1 indicates perfect performance of the model and values of zero or less represent performance no better than random.

$$\mathrm{TSS} = \mathrm{sensitivity} + \mathrm{specificity} - 1 \tag{1}$$

where sensitivity and specificity are the proportion of correctly observed presences and absences, respectively (Allouche *et al.*, 2006). In order to compare the performance of the calf group models and non-calf group models, TSS was calculated separately for each day of validation data. A mean TSS was then calculated for each group, weighted by the number of presence locations per day, such that the contribution of the daily TSS to the mean was proportional to the number of validation opportunities.

For comparative purposes, we also assessed model performance using AUC (area under the receiver operating characteristic curve). AUC is a measure of a model's predictive power, ranging from 0.5 (no predictive power) to 1.0 (perfect prediction) and is widely used in studies of distribution (e.g. Torres *et al.*, 2013; Herrera *et al.*, 2014). While AUC provides information about the distribution of a species along the range of predictor conditions, it has been criticized for not being a good metric of model performance (Lobo *et al.*, 2008). Lobo *et al.* (2008) therefore recommend reporting AUC along with sensitivity and specificity, as achieved by the use of TSS.

RESULTS

Distribution surveys were conducted over 31 days from 2010 to 2012, resulting in 1399 km of survey effort, 462 sightings of SRW calf groups and 313 sightings of non-calf groups (Table 1, Fig. 3). Sightings of calf groups tended be concentrated in the western and northern regions of Port Ross (Fig. 3a), whereas sightings of non-calf groups were more evenly distributed throughout the survey area (Fig. 3b). Radial detection distances were estimated for 80 calf groups (median = 376 m) and 52 non-calf groups (median = 308 m). There was no evidence for a difference between the medians (Wilcoxon rank sum test; $W = 1265$, $P = 0.93$), so the pooled data (median = 350 m) were used to estimate the radial sighting distance for the GIS analyses.

GAMs

For calf groups, the best models (based on the minimum AIC score) were relatively consistent among the three sets of training data (Table 2). The full set of variables was included in one of the models, and only slope was excluded in the other two, with deviance explained ranging from 18.0% to 25.4%. Calf groups were typically seen in areas sheltered from swell (< 0.5 m significant wave height; Fig. 4a) and wind (< 1000 m to a sheltered shoreline; Fig. 4b), at shallow depths (5–20 m; Fig. 4c) between 200 and 1200 m from the coast (Fig. 4d). The precision of all the responses decreased

Table 1 Effort and sighting data during surveys of southern right whales at the Auckland Islands from 2010 to 2012.

Year	No. survey days	Survey effort (km)	No. calf groups	Calf group size (mean; SD)	No. non-calf groups	Non-calf group size (mean; SD)
2010	9	461	108	2.48; 1.38	110	1.86; 1.27
2011	8	264	138	2.28; 0.80	51	1.61; 0.90
2012	14	674	216	2.24; 0.73	152	2.03; 1.58

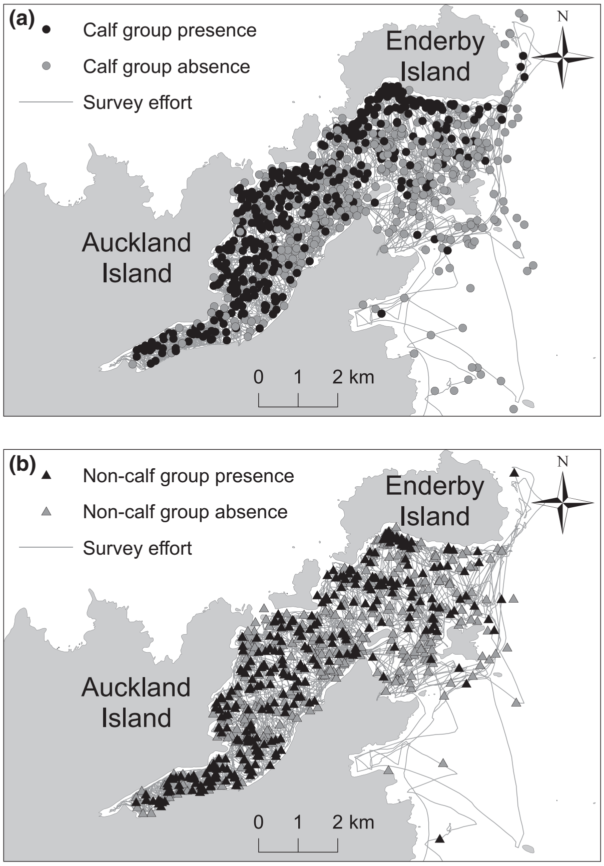

Figure 3 Survey effort in and around Port Ross, Auckland Islands, during winters of 2010, 2011 and 2012, showing sightings and absence locations for (a) southern right whale calf groups, and (b) southern right whale non-calf groups.

as the number of observations decreased at larger values of the predictor variables.

For non-calf groups, different sets of training data resulted in different best models (Table 3). Each explanatory variable was retained in at least one best model, but only wave exposure and distance to coastline appeared in all three. Deviance explained was very low, ranging from 4.2% to 8.4%. The responses to the explanatory variables were also more variable and more difficult to interpret. The best model from the 2011 and 2012 training data (that which explained the greatest deviance) suggested that non-calf groups were found in habitats sheltered from wave exposure (< 0.4 m significant wave height; Fig. 5a), between 400 and 800 m from a sheltered shoreline (Fig. 5b) and 200–400 m, or greater than 700 m, from the coast (Fig. 5c).

Semivariograms of the residuals suggested no evidence of spatial autocorrelation in the best models for calf groups and non-calf groups (see Appendix S2).

Model validation

The best models were used to create predictive surfaces of habitat suitability. For calf groups, the models from each set of training data consistently predicted that the most suitable habitats would be in the inner regions of Port Ross and close to shorelines sheltered from the prevailing westerly winds (Fig. 6). The multi-fold validation method provided three opportunities for validating the model predictions. The mean TSS ranged from 0.338 to 0.442, and the 95% confidence interval around the estimates never included zero, indicating that all the models had useful predictive power (Table 2). The estimates of AUC were similarly consistent, ranging from 0.712 to 0.800 (Table 2).

For non-calf groups, the predicted probability surfaces were more variable among the training sets. The most suitable habitats were always predicted to be in inner Port Ross, but they were less well defined and also included areas in the outer part of the study site, farther from shelter (Fig. 7). The non-calf models performed poorly compared to the calf models, with mean TSS ranging from 0.064 to 0.177 (and confidence intervals including zero) and AUC ranging from 0.544 to 0.633 (Table 3).

DISCUSSION

In and around Port Ross, groups of SRWs containing calves were consistently present in nearshore habitats sheltered from prevailing wind and swell. Our modelling of wave exposure and inclusion of local wind data in the habitat models represent a significant advance in understanding distribution of organisms at a vulnerable life-history stage in a high energy environment. In contrast, the same suite of physiographic variables explained the distribution of groups without calves far less effectively. This indicates that presence of calves drives subtle but important differences in

Table 2 Best logistic generalized additive models to explain presence of southern right whale calf groups at the Auckland Islands, and metrics of model performance.

Training data	Validation data	Best model	Adjusted R^2	Deviance explained %	Weighted mean TSS (95% CI)	AUC (95% CI)
2010, 2011	2012	Hsig + depth + slope + dcoast + dshelter	0.203	18.0	0.442 (0.353–0.530)	0.800 (0.759–0.842)
2010, 2012	2011	Hsig + depth + dcoast + dshelter	0.289	25.4	0.338 (0.187–0.489)	0.712 (0.652–0.772)
2011, 2012	2010	Hsig + depth + dcoast + dshelter	0.230	19.8	0.426 (0.262–0.590)	0.788 (0.726–0.849)

Hsig, modelled significant wave height; dcoast, distance to nearest coastline; dshelter, distance to nearest coastline sheltered in prevailing wind; TSS, true skill statistic; AUC, area under receiver operating characteristic curve; CI, confidence interval.

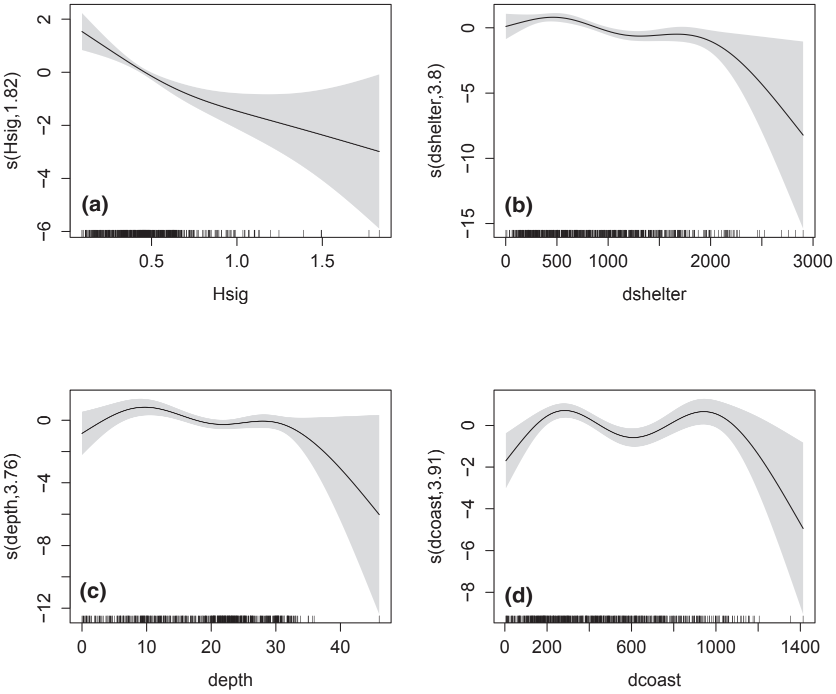

Figure 4 Effect of explanatory variables from logistic generalized additive model on presence of southern right whale calf groups in the Auckland Islands using training data from 2010 and 2012. Shaded area is 95% confidence interval of the response. The *y*-axes show the smooth function of each variable, with the estimated degrees of freedom. (a) Modelled significant wave height (Hsig, m), (b) distance to nearest coastline sheltered in prevailing wind (dshelter, m), (c) water depth (depth, m), (d) distance to nearest coastline (dcoast, m).

Table 3 Best logistic generalized additive models to explain presence of southern right whale non-calf groups at the Auckland Islands, and metrics of model performance.

Training data	Validation data	Best model	Adjusted R^2	Deviance explained %	Weighted mean TSS (95% CI)	AUC (95% CI)
2010, 2011	2012	Hsig + depth + slope + dcoast	0.066	6.14	0.086 (−0.050–0.221)	0.568 (0.503–0.632)
2010, 2012	2011	Hsig + dcoast	0.046	4.24	0.177 (0.054–0.299)	0.633 (0.526–0.741)
2011, 2012	2010	Hsig + dcoast + dshelter	0.086	8.41	0.064 (−0.094–0.222)	0.544 (0.467–0.620)

Hsig, modelled significant wave height; dcoast, distance to nearest coastline; dshelter, distance to nearest coastline sheltered in prevailing wind; TSS, true skill statistic; AUC, area under receiver operating characteristic curve; CI, confidence interval.

distribution of SRWs on their wintering grounds in the Auckland Islands, and highlights the need to account for reproductive status in species–habitat models.

Among the Cetacea, differences in distribution according to reproductive status have been observed for SRWs in Argentina (Payne, 1986) and South Africa (Elwen & Best, 2004b), and for humpback whales (*Megaptera novaeangliae*; Craig & Herman, 2000; Ersts & Rosenbaum, 2003; Félix & Botero-Acosta, 2011; Craig *et al.*, 2014) and dusky dolphins (*Lagenorhynchus obscurus*; Weir *et al.*, 2008). Two, possibly complementary, explanations have been suggested for these differences. First, baleen whale calves are comparatively weak swimmers in the first few weeks postpartum (Thomas & Taber, 1984). Growth and survival of neonates are potentially compromised in the rough seas characteristic of southern high latitudes and therefore parturient females may select sheltered habitats to reduce the energy expenditure by their calves (Corkeron & Connor, 1999; Ersts & Rosenbaum, 2003). Larger, more experienced individuals presumably need sheltered habitat less, resulting in differences in distribution determined by reproductive status. Second, the choice of shallow, inshore habitats by mothers and calves has been hypothesized to reduce harassment by conspecifics (Elwen & Best, 2004b), particularly males seeking mating opportunities (e.g. dusky dolphins, Weir *et al.*, 2008; humpback whales, Félix & Botero-Acosta, 2011; Craig *et al.*, 2014). That mortality rate of SRW neonates in South Africa is higher in regions with a greater proportion of non-calf groups supports this idea (Elwen & Best, 2004b). Again, the active choice of specific habitats by females with calves could result in the observed differences in distribution.

We have no evidence that groups of SRWs with calves select inshore habitats to avoid harassment by conspecifics. Indeed, female SRWs are unlikely to be sexually receptive immediately postpartum (Best, 1994; Cooke *et al.*, 2003; Brandao *et al.*, 2010) and hence accompanying males may not be seeking to mate. We did, however, observe that groups of SRWs containing calves were more commonly found in inshore habitats protected from wind and swell. A preference for sheltered calving habitat by SRWs has been suggested previously. Elwen & Best (2004a) used categorical metrics of exposure to show that cow–calf pairs in South

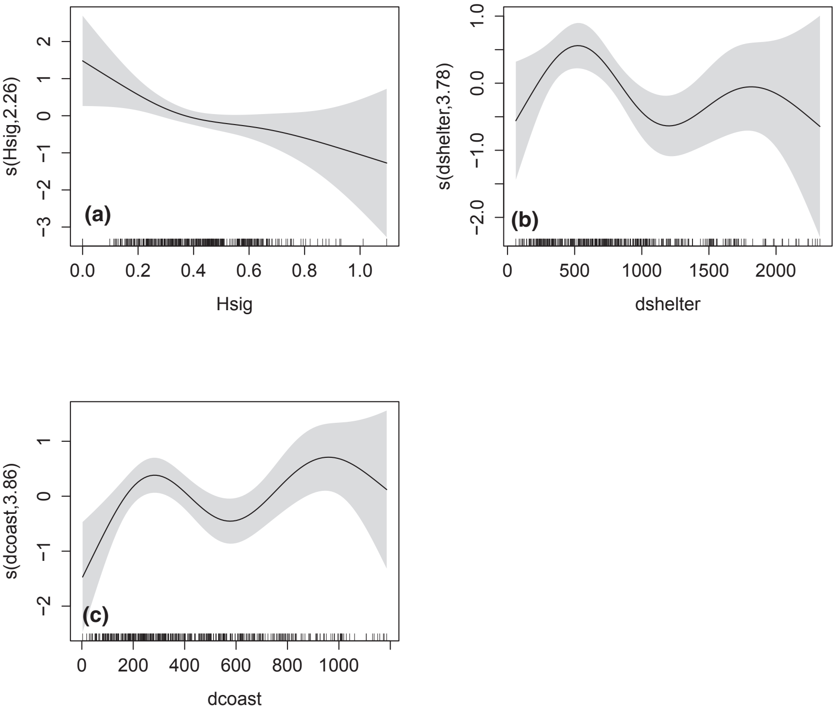

Figure 5 Effect of explanatory variables from logistic generalized additive model on presence of southern right whale non-calf groups in the Auckland Islands using training data from 2011 and 2012. Shaded area is 95% confidence interval of the response. The *y*-axes show the smooth function of each variable, with the estimated degrees of freedom. (a) Modelled significant wave height (Hsig, m), (b) distance to nearest coastline sheltered in prevailing wind (dshelter, m), (c) distance to nearest coastline (dcoast, m).

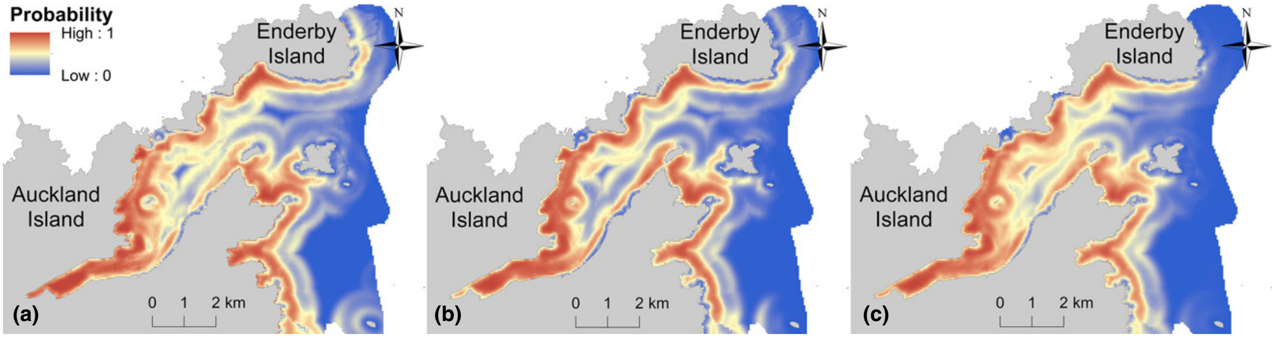

Figure 6 Predicted habitat suitability for southern right whale calf groups during winter around Port Ross, Auckland Islands. Habitat suitability based on predictions from logistic generalized additive models using training data from (a) 2010 and 2011, (b) 2010 and 2012, (c) 2011 and 2012.

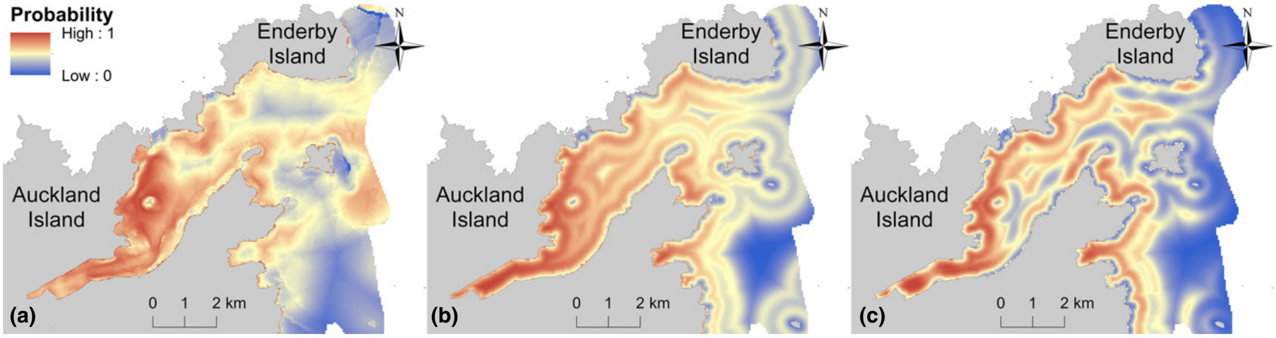

Figure 7 Predicted habitat suitability for southern right whale non-calf groups during winter around Port Ross, Auckland Islands. Habitat suitability based on predictions from logistic generalized additive models using training data from (a) 2010 and 2011, (b) 2010 and 2012, (c) 2011 and 2012.

Africa preferred habitats protected from open ocean swells and prevailing winds. To our knowledge, however, our study is the first to use measured or modelled wave conditions to quantify the effect of average swell height on distribution of cetaceans. The results provide conclusive evidence that female SRWs select sheltered, inshore habitats during the early stages of nursing while their calves are presumably at their most vulnerable. While calf groups favoured nearshore areas, presumably because these are consistently sheltered from wind and swell, very shallow waters (< 5 m depth) within 200 m of the coastline appeared to be less suitable habitat. Potentially there is an increased risk of stranding or injury due to contact with the substrate in these areas. Our general conclusions are supported by historical records of SRWs in New Zealand waters during the whaling period in the 19th century. The majority of whales taken from the inshore grounds were mothers and calves captured in shallow, sheltered bays (Richards, 2002).

The nature of species–habitat relationships is strongly dependent on the resolution at which the dependent and independent variables are measured (Cushman & McGarigal, 2004), with the accuracy of model predictions generally increasing at coarser spatial scales (e.g. Block *et al.*, 1994; Karl *et al.*, 2000). The effects of environmental features on distribution of SRW calf groups at the Auckland Islands were evident even at the very fine spatial scale of the study. Using accurate locations for the sighting data, and independent variables with minimum resolution of 50 m, we were able to describe and predict variations in distribution over tens of metres. The mean TSS for the best calf group models was greater than zero for each set of data, and each AUC score exceeded 0.7, demonstrating the models had utility (e.g. Boyce *et al.*, 2002). Nonetheless, the calf group models explained only between 18% and 25% of the deviance, suggesting there were substantial influences on distribution that we did not account for.

The fact that model predictions are often most useful at fine scales provided the impetus for the approach taken in this study. The performance of the habitat models may have been compromised, to some extent, by the fine scale of the sighting data and the mobility of the study species. Furthermore, our analysis approach was relatively conservative and we used average conditions for exposure to wind and swell, rather than using real-time conditions, which may have explained whale distribution more effectively. We chose to use average conditions because it allowed us to survey, during periods of good weather, areas which are typically exposed to high winds and swells. Effectively, this permitted inclusion of a greater range of habitat conditions in the models. We also acknowledge that by surveying the same areas on separate days we ran the risk of sampling individuals repeatedly during the study period. However, SRWs are highly mobile and redistribute themselves over relatively short periods in this habitat. For example, during a shipboard line-transect survey of the study area in winter 2011, 73 SRWs were counted in and around Port Ross (Rayment *et al.*, 2012). In contrast, over a 3-week period overlapping the line-transect survey, the mark–recapture estimate for the number of whales using the same surveyed area was 291 (coefficient of variation = 0.12; W. Rayment, unpublished data). Even though the line-transect count is not corrected for whales which were present but not detected, the disparity between the figures suggests a high rate of turnover of individuals and a reduced risk of encountering the same individuals on multiple occasions.

Both validation metrics, along with the very low deviance explained, show that the non-calf group models performed poorly compared to the calf group models, indicating that non-calf groups are less dependent on the range of habitat features included in this study. This is unsurprising. Adult male and juvenile whales must have different motivation for travelling to the calving grounds compared to parturient females. Adult males are likely to be seeking mating opportunities (Patenaude *et al.*, 1998; Best *et al.*, 2003), although because most female SRWs are not seen on the calving grounds in the year prior to giving birth, doubt exists as to where the majority of effective mating actually occurs (Payne, 1986; Best *et al.*, 2003). It is less clear why juvenile whales would migrate to calving grounds rather than stay in areas with greater foraging opportunities. It may be to gain social experience; for example, Best *et al.* (2003) noted that the majority of courtship behaviour by SRWs in South African calving areas was focused on juvenile females. Furthermore, proximity to other whales was a significant factor determining distribution of SRWs in southern Australia (Pirzl, 2008). Explaining the distribution of non-calving whales in the Auckland Islands would therefore require additional variables not related to habitat, but perhaps to social organization and concurrent distribution of conspecifics. Combining the environmental features of a habitat with its suitability due to social factors represents a significant challenge for species–habitat modelling.

Our characterization of the winter habitat of SRWs was based on static (depth, slope and distance from coast) and persistent environmental features (average wave exposure and distance to shelter). While we would caution against applying model predictions to other locations (e.g. Randin *et al.*, 2006), these environmental features could be used to make inferences about potentially suitable habitat elsewhere. While SRWs face no known anthropogenic threats around the uninhabited Auckland Islands, they will undoubtedly experience a range of impacts around the New Zealand coast as they recolonize their former range (Carroll *et al.*, 2014). Elsewhere, right whale populations have suffered significant human induced mortality due to ship strike and entanglement in fishing gear (Kraus *et al.*, 2005; Campbell-Malone *et al.*, 2008; Knowlton *et al.*, 2012) and sub-lethal effects from many sources including anthropogenic noise (Parks *et al.*, 2007; Hatch *et al.*, 2012; Rolland *et al.*, 2012). Our study has provided insights into the habitat features which influence the distribution of SRWs at a particularly vulnerable life stage. It is a useful first step in identifying where conflicts with anthropogenic impacts might occur as recolonization of the mainland progresses.

ACKNOWLEDGEMENTS

We thank those who assisted with data collection: Liz Slooten, Anthony Davidson, Lucy Rowe, Richard Kinsey, Kath Blakemore, Tim Cole, Tim Lever and Sophie Fern. We are hugely grateful to the crew of R/V Polaris II (Bill Dickson, Phil Heseltine, Steve Little and Evan Kenton) for delivering us safely to and from the Auckland Islands, and for supporting our daily fieldwork. Thanks to Laura Boren, Doug Veint, Pete McLelland, Gilly Adam, Jo Hiscock and Sharon Trainor (Department of Conservation) for assisting with permitting and procedures. We sincerely thank Leigh Torres for help and advice with survey design and analysis, Hamish Bowman for building the wave model, Simon Childerhouse for discussions on project planning, and Gary Wilson for help and advice with logistics. The work was conducted under Department of Conservation permit 2010/05 issued to W.R. and S.D. Funding was provided by the Foundation for Research, Science and Technology (FRST), University of Otago, New Zealand Whale & Dolphin Trust, and Otago Museum. W.R. was supported by a FRST post-doctoral fellowship and T.W. by a University of Otago PhD scholarship. The manuscript was greatly improved by comments and analysis suggestions from three anonymous referees and the handling editor, Alistair Crame.

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SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article:

Appendix S1 Summary of Enderby Island wind data 2004–2011.

Appendix S2 Semivariograms of the residuals of the best logistic generalized additive models.

BIOSKETCHES

William Rayment is a lecturer in the Marine Science Department at Otago University. His research is focused on the ecology of marine fauna and the design of marine protected areas.

Steve Dawson is a Professor of Marine Science at Otago University specializing in conservation biology of marine mammals.

Trudi Webster is a PhD student at Otago University studying acoustics of southern right whales.

Author contributions: W.R., S.D. and T.W. designed the study and carried out the fieldwork. W.R. led the analysis and writing.

Editor: Alistair Crame

APPENDIX C

Summary of the acoustic recordings used to determine acoustic repertoire

Recording date and time	Recording length minutes	Recording location
100801_062547	50	Laurie Harbour
100802_061845	60	Erebus Cove
100802_221847	60	Erebus Cove
100803_061233	80	Erebus Cove
100804_061840	70	Erebus Cove
100804_100744	30	Erebus Cove
100804_113641	20	Erebus Cove
100804_171308	30	Laurie Harbour
100805_061753	60	Terror Cove
100805_173249	20	Erebus Cove
100806_061421	80	Erebus Cove
100806_114819	30	Laurie Harbour
100806_175511	30	Shoe Island
100807_061636	70	Erebus Cove
100807_164226	20	Shoe Island
100807_172209	40	Laurie Harbour
100808_064051	60	Erebus Cove
100808_175215	40	Laurie Harbour
100809_061653	65	Erebus Cove
100810_061305	80	Erebus Cove
100813_062023	65	Erebus Cove
100814_061547	72	Erebus Cove
100814_132830	62	Erebus Cove
100815_061410	71	Erebus Cove
110722_070400	49	Erebus Cove
110723_140030	44	Erebus Cove
110724_135946	12	Laurie Harbour
110724_225939	137	Erebus Cove
110725_021805	62	Erebus Cove
110728_130537	63	Erebus Cove
110728_151512	80	Laurie Harbour
110728_221536	43	Erebus Cove
110729_034152	34	Erebus Cove
110729_163257	39	Erebus Cove
110801_141818	55	Sandy Bay
110801_161229	46	Deas Head
110801_225407	70	Erebus Cove

Recording date and time	Recording length minutes	Recording location
120726_211009	97	Erebus Cove
120726_225135	40	Erebus Cove
120727_234234	60	Erebus Cove
120728_135702	40	Terror Cove
120728_150619	16	Laurie Harbour
120728_154002	75	Laurie Harbour
120729_135020	108	Erebus Cove
120731_062937	5	Erebus Cove
120731_140914	58	Laurie Harbour
120801_035549	53	Erebus Cove
120802_062805	41	Erebus Cove
120803_221617	121	Laurie Harbour
120804_024849	24	Laurie Harbour
120805_061107	20	Laurie Harbour
120807_042830	19	Laurie Harbour
120807_222648	46	Laurie Harbour
120808_013749	35	Laurie Harbour
120809_060902	15	Laurie Harbour
120810_033623	16	Laurie Harbour
120810_063103	16	Laurie Harbour
120811_050913	38	Erebus Cove

Table C.1 Summary of the acoustic vocalisation recordings used to determine the acoustic repertoire of southern right whales at the Auckland Islands. Recording date, time, length and locations for recordings made between 2010 and 2012.