INSIGHTS INTO BLAINVILLE'S BEAKED WHALE (*MESOPLODON DENSIROSTRIS)* COMMUNICATION

Charlotte Dunn

A Thesis Submitted for the Degree of PhD
at the
University of St Andrews

2014

Please use this identifier to cite or link to this item:
http://hdl.handle.net/10023/6542

Insights into Blainville's beaked whale (*Mesoplodon densirostris*) communication

Charlotte Dunn

This thesis is submitted in partial fulfilment for the degree of PhD
at the
University of St Andrews

December 2014

Two subadult Blainville’s beaked whales in 2005 in the Bahamas.

An adult male and adult female Blainville’s beaked whale in 2005 in the Bahamas.

A mother-calf pair of Blainville's beaked whales in 2012 in the Bahamas. The calf still has fetal folds.

A mother-calf pair of Blainville's beaked whales in the nursing position in 2013 in the Bahamas.

Candidate’s declarations

I, Charlotte Dunn, hereby certify that this thesis, which is approximately 40,000 words in length, has been written by me, and that it is the record of work carried out by me, or principally by myself in collaboration with others as acknowledged, and that it has not been submitted in any previous application for a higher degree.

I was admitted as a research student in October 2008 and as a candidate for the degree of Doctor of Philosophy in October 2008; the higher study for which this is a record was carried out in the University of St Andrews between 2008 and 2014.

1 December 2014

Charlotte Dunn

Supervisor’s declaration

I hereby certify that the candidate has fulfilled the conditions of the Resolution and Regulations appropriate for the degree of Doctor of Philosophy in the University of St Andrews and that the candidate is qualified to submit this thesis in application for that degree.

1 December 2014

Dr. Luke Rendell

Permission for publication

In submitting this thesis to the University of St Andrews I understand that I am giving permission for it to be made available for use in accordance with the regulations of the University Library for the time being in force, subject to any copyright vested in the work not being affected thereby. I also understand that the title and the abstract will be published, and that a copy of the work may be made and supplied to any bona fide library or research worker, that my thesis will be electronically accessible for personal or research use unless exempt by award of an embargo as requested below, and that the library has the right to migrate my thesis into new electronic forms as required to ensure continued access to the thesis. I have obtained any third-party copyright permission that may be required in order to allow such access and migration, or have requested the appropriate embargo below.

The following is an agreed request by candidate and supervisor regarding the publication of this thesis:
PRINTED and ELECTRONIC COPY
a) No embargo

1 December 2014

Charlotte Dunn

Dr. Luke Rendell

Collaboration statement

Some aspects of the work in this thesis involved collaborations and have resulted in a publication.

Dunn C., Hickmott, L., Talbot, D., Boyd, I. and Rendell, L. 2013. Mid-frequency broadband sounds of Blainville's beaked whales. Bioacoustics. doi:10.1080/09524622.2012.757540.

The work in Chapter Three was conceived by Dunn, Boyd and Rendell. Dunn was involved in all data collection. Data trawling was done by Talbot. Figure 4 in the publication was done by Hickmott. All other data analysis was done by Dunn. The thesis chapter and the resulting publication were written by Dunn. Boyd and Rendell commented on drafts of the publication. Rendell commented on drafts of the chapter.

Abstract

Lack of knowledge regarding beaked whale biology restricts our ability to evaluate their vulnerability to anthropogenic threats. This work addresses critical data gaps in Blainville’s beaked whale social structure and communication systems. Social analysis shows that Blainville’s beaked whales in the Bahamas exhibit group living through a harem structure characterised by a single male accompanying a group of females for up to a year. This study also reveals that females preferentially associate with conspecifics in the same reproductive state, remaining together for up to three years. I show what may be the first example of social philopatry in beaked whales, with adult males possibly providing protection for kin. Analysis of data from acoustic tags reveals previously undescribed sexually distinctive vocalisations. These sounds might serve a communicative function helping to form and maintain groups. Acoustic data also reveals a distinctive double click pattern in Blainville’s beaked whales that is likely physiological in nature. The same pattern is also shown in two other deep diving species, Cuvier’s beaked whales and sperm whales. Species differences in the frequency of production of these double clicks may be providing a window into the evolution of odontocete echolocation. Data from a bottom-mounted hydrophone array reveals a lack of sex and / or age specific information in this species’ echolocation clicks. Analysis of mother-calf pairs indicate calves from at least three months of age echolocate using clicks similar to those of adults. This work provides the first comprehensive study of possible communicative sounds in an elusive deep-diving cetacean species exhibiting a complex social structure that lies somewhere between stable groups and fission-fusion societies. Understanding the interaction between communication and social organisation enhances our ability to predict the effects of anthropogenic disturbance on this species.

Acknowledgements

I would like to thank Dr Lindsay Porter who enabled me to begin my journey from the computer systems of derivative trading floors, to communication systems of whales. So much more interesting! Always grateful to you Linds.

Beginning with my masters degree at St Andrews, there have been many ‘teachers’ that helped to guide me and shared their valuable time: Vincent, Doug, Jonathan, Patrick, Jonathan Kemp and Phil, thank you. I would also like to thank Peter McGregor and Peter Tyack, the examiners of this thesis, for their fascinating and knowledgeable discussion during the viva, providing plenty of ideas for the future of this work.

I began my PhD with both Ian Boyd and Luke as my supervisors, and thoroughly enjoyed the discussions in the early years that had no boundaries. From parrots to the Sistine chapel, these conversations began the development of my critical thinking mind, and my training as a biologist. Luke and I continued without Ian, following his move to government, and we have developed a unique and extremely fulfilling student-supervisor relationship. We shared a cupboard-sized office for much of the time, sometimes sharing too much information, and much to the alarm of Luke’s boss, Kevin. Luke’s brilliance as a scientist and sensitivity to my needs resulted in a training exercise that I do not believe I could have achieved with anyone else. Special appreciation for the discovery of Marialuisa Aliotta, a talented scientific writing tutor who made Luke and my final months a little smoother. In return I think I too may have provided a little training for him at the start of what I know will be a long and successful run of PhD supervision. Thank you for everything Luke, your patience, teaching, friendship, and of course humour!

And between all the intense study, of course there has been some wonderful time spent with special friends in St Andrews - many co-masters and PhD students - Kevin’s lab every Friday evening, and especially Monica, Lindsay & Gordon and my second family, Nic & Jules. Apparently Steph too, though these times, which I know must have been great fun, are less well remembered.

A longitudinal dataset such as the one used in this thesis is always the product of many people and their hard work. The data collected by the Bahamas Marine Mammal Research Organisation since 1991 is largely thanks to Diane Claridge and many colleagues and volunteers over the years. Special thanks goes to John Durban and Leigh Hickmott for data collection, analysis, collaborations and friendship. Kim Parsons has been involved with BMMRO for the duration and has been a great support during the thesis finale.

I would also like to thank Dave Moretti and his team for a lot of hard work getting me data from the AUTEC hydrophone array, particular thanks to Jess.

My friends and family in Abaco and across the world have supported me throughout my life transitions, special thanks to my brother and his family, and of course Caroline, Neva, Carole, Lila, Emily & Flip – thanks for everything. I would also like to thank Bette Claridge for her encouragement and belief in me, and my previous mother-in-law, Merle, who was an inspiring woman. My father has never waivered in his support of me, regardless of the next bombshell I delivered. Dad, thanks for your friendship, I love you. I would also like to thank Dianne for her on-going support.

The last months of writing up have been spent with Harry and Legacy Patterson, possibly the best companions I could have wished for, providing constant unconditional love.

Last but by no means least, I thank Di, to whom I owe so much. Of course sharing your life-long knowledge of the animals, but moreover sharing your life with me. You are my angel. With this thesis I hereby declare I am no longer your nurse. Can we study sperm whales now?

I dedicate this thesis to my late mother who instilled in me an appreciation of the water, and the importance of independence that could be achieved through education. My love, always.

TABLE OF CONTENTS

Chapter One

1 GENERAL INTRODUCTION

Beaked whales have been the focus of more dedicated research in the last decade than ever before, following a number of mass stranding events coincident with military naval exercises (Balcomb and Claridge, 2001; Van Bree and Kristensen, 1974; Cox *et al.*, 2006; Evans and England, 2001; Fernández *et al.*, 2005; Frantzis, 1998; Jepson *et al.*, 2003; Simmonds and Lopez-Juraco, 1991). They are one of the largest mammalian groups (Dalebout *et al.*, 2004), yet have been one of the least known (Wilson, 1992). This is in part because their behavioural characteristics make them difficult to study. They are typically found in small groups, are cryptic when at the surface, which is only ever for a brief period, and dive to great depths for extremely long durations making them difficult to detect (Barlow, 1999). This study focuses on Blainville's beaked whales, *Mesoplodon densirostris* (Blainville, 1817), also known as dense-beaked whales because of their dense skull structure.

Recent behavioural studies have focused primarily on beaked whales' responses to anthropogenic noise sources in order to quantify their movement away from potentially damaging sounds (Allen *et al.*, 2014; DeRuiter *et al.*, 2013; Tyack *et al.*, 2011). This is in contrast to earlier studies on the effects of anthropogenic noise on other marine mammals, which primarily focused on their communication systems. For example, ship noise reduces the distances over which blue (*Balaenoptera musculus*) and fin (*Balaenoptera physalus*) whales are able to communicate (Payne and Webb, 1971), and causes North (*Eubalaena glacialis*) and South Atlantic right whales (*Eubalaena australis*) to alter their call frequency (Parks *et al.*, 2007). Despite the recent interest in beaked whale biology, there is still no insight into beaked whale communication and the way it is affected by anthropogenic sounds. This lack of knowledge will inevitably hamper interpretation of behavioural response studies.

In this introductory chapter I present an overview of the way in which different animal species communicate and discuss how their social structures influence their communication. A brief review on what is currently known about Blainville's beaked whales will also be presented, together with an outline of the thesis.

1.1 Animal Communication

Communication is ubiquitous in the animal kingdom. Animal communication occurs either by non-voluntary cues, or by signals, and is widely agreed to involve the transfer of information between a sender and a receiver that on average benefits both (Bradbury and Vehrencamp, 1998). Cues are traits or behaviours that are obligate and inadvertent, and their emission does not generally benefit the producer, at least in terms of effects on other animals (Seeley, 1989); for example a mosquito can detect the cue of CO_2 exhaled from a mammal upwind, thus gaining information on the mammal's location, which the mammal surely does not benefit from.

Yet some obligate cues can benefit the producer; for example, a male lion's (*Panthera leo*) mane provides a cue of his fitness to female lions (Schaller, 1972), and the urine of female Asian elephants (*Elephas maximus*) provides a cue of their sexual receptiveness to male elephants (Rasmussen *et al.*, 1982). In the classical view of signal evolution, cues have been shown to evolve to become signals through ritualisation (Tinbergen, 1952), such as the canine behaviour of baring teeth. This cue, intimating the opponent to stay away, evolved from dogs baring their teeth immediately before biting, to get their lips out of the way (Krebs and Dawkins, 1984). The evolution of signals from cues is however limited by both physiological and ecological constraints (Arnold, 1992), which differ across species.

Signals, in contrast to cues, are deliberately given by a sender and have been selected for because of the effect they have on altering the behaviour of a receiver (Wilson, 1975). Signals evolve in line with the response and performance of the receivers. Studies of mate choice in fish through the evolution of colourful signals have also shown the removal of these signals in some cases due to local ecological conditions. Male sticklebacks (*Gasterosteus* spp.) in lakes that do not have clear water have lost their bright red marking on their underparts, and the females have lost their preference for the red marking and their sensitivity to red light (Boughman, 2001).

Signals can vary in form, function and benefit to the signaller. Forms include visual, acoustic, tactile and chemical. Functions include reproductive success through sexual advertisement and mate attraction; alarm calls to alert conspecifics to the presence of a predator; conflict resolution; individual identification, used commonly in mother-offspring recognition; and maintaining group cohesion. Additionally, bats and cetaceans use acoustic signals to detect and localise prey.

Visual signals can be used to attract females and also to deter predators or competing males by providing an indication of fitness and dominance. The Puerto Rican crested anole (*Anolis cristatellus*) displays its ability to escape a predator by the number of push-ups it can perform during certain predation events. This display benefits the anole by also acting as a signal to potential mates on the individual's quality (Leal, 1999). Another type of visual display is seen in bowerbirds (family *Ptilonorhynchidae*), in which sexual advertisement has evolved away from their own plumage to the elaborate decoration of the bowers they build. This evolution has enabled bower birds to indicate through the bower quality, their age, experience, and dominance to the females, as in order to produce the most elaborate bower, they will have had to steal and possibly destroy another male's bower (Pruett-Jones and Pruett-Jones, 1994).

Chemical signals are the oldest form of communication and they vary widely in form and function. A common use of chemical signalling is territorial defence through scent marking as seen in domestic dogs (*Canis familiaris*) (Lorenz, 1954). In general, the rate of marking is higher in males, with most of a female's urinations being simple elimination (Bekoff, 1979). Scent marking can also communicate dominance to other males, as found in wild brown bears (*Ursus arctors*) (Clapham *et al.*, 2012). Tactile signals have been studied extensively in primates and can provide benefit to the giver (sender) of the signal, as seen in chimpanzees (*Pan troglodytes*) that groom other individuals and are in turn given the benefit of food-sharing privileges with that individual (de Waal, 1989).

Finally, many animals produce a variety of acoustic signals that can be beneficial for conspecifics outside of visual, chemical or tactile range. Birdsong is widely used in territory defence and as a sexual advertisement by male birds to attract female mates (e.g., Catchpole and Slater, 1995). Similarly, mice (*Mus musculus*) have been shown to have a preference for non-kin male songs (Musolf *et al.*, 2010). Vervet monkeys (*Chlorocebus pygerythrus*) produce acoustic signals specific to the type of predator approaching; a ‘cough’ call indicates an aerial predator such as an approaching eagle prompting the monkeys to hide amongst vegetation as a response (Seyfarth *et al.*, 1980).

However, in the current literature, debate continues on whether animal signals provide information (Seyfarth *et al.*, 2010) or merely influence the receiver (Rendall and Owren 2013). This debate stems from a lack of definition of the term ‘information’ in the field of biology. For instance, Schaefer and Ruxton (2011) discuss whether there is an added factor of relevance in some signals, such as the elaborate plumage of a male sending an extraneous signal outside of the breeding season. In this case one could say that there is no information in the content of the signal, because there is no response from the receiver, and information should only be quantified in conjunction with the receiver’s response (Marler, 1961).

Rendall and Owren (2013) disagree with information-based definitions of signalling and communication. They point to the vervet monkey research as a catalyst to the direction that animal communication research has taken in recent decades, comparing signals to language and therefore attempting to understand what animals are saying. They argue that too often comparisons to human language are made, particularly in primate research, and that comparing a highly derived system of communication such as language to earlier simpler systems does not make sense. In addition, they state that there is no encoding within signals of certain information such as size, and in some cases individual identity, but that this information naturally occurs from a large vocal apparatus or characteristics of that apparatus (Fitch and Hauser, 1995; Rendall *et al.*, 1998). Thus, they argue, researchers should consider where information is intentionally encoded or a by-product of physiological factors.

Signals and / or cues can be exploited by an unintended receiver through ‘eavesdropping’ (Bradbury and Vehrencamp, 1998). Although some of these signals and / or cues have not been encoded, but are genetically pre-determined, they nevertheless still transfer information to the receiver. The word eavesdropping is defined as “standing beneath the eaves of a house or building to overhear a conversation”. In this paradigm it is often thought to relate to the acoustic medium, which is not always the case in the animal world. However, acoustic signals can be subject to pre-determined genetics that can provide useful cues for eavesdroppers. For example, knowledge of an animal’s size is often provided inadvertently through acoustic signals, and in some species this is also a cue to the signaller’s sex (*e.g.* sperm whales (*Physeter macrocephalus*), (Gordon, 1991) and age (*e.g.* giant panda (*Ailuropoda melanoleuca*), Charlton *et al.*, 2009). Occasionally, the size of the vocal folds is not correlated with body size but still informs sex (*e.g.* sheep (*Ovis aries*), Beckford *et al.*, 1985).

Eavesdropping is particularly useful for animals that spend the majority of their time in the dark and communicate acoustically, such as bats and deep diving cetaceans. Rough-toothed dolphins (*Steno bredanensis*) use eavesdropping when travelling synchronously in a group, using echolocation echoes from other group members to navigate (Götz *et al.*, 2006). This may be an energy-saving mechanism, or else one that aids in allowing fewer echoes to be processed without the backscatter that would occur if every dolphin were echolocating in the same direction. This type of eavesdropping may be part of a communication network where it is understood that signals can be received by multiple receivers, and these receivers can receive signals from several signallers at once (McGregor and Peake, 2000). However, it does not seem to fall either into the interceptive category or the social category of eavesdropping (Peake, 2005), as there is some shared click production occurring and therefore potential for co-operation.

Eavesdropping is commonly shown to be beneficial as an indicator of the presence of a predator. In some cases, prey have evolved to increase their eavesdropping opportunities. This can be seen in eight moth families who have evolved ears sensitive to ultrasonic calls used by bats to locate the moths and prey upon them (Miller and Surlykke, 2001). It is perhaps for this reason that bats do not echolocate in good lighting, for example a full moon night (Bell, 1985), therefore avoiding alerting moths to their presence through echolocation sounds. In other cases, predators have become savvy to their detection and altered their behaviour. For example, fish-eating killer whales (*Orcinus orca*), which presumably cannot be detected acoustically by fish, produce many more vocalisations during foraging attempts than mammal-eating killer whales (Barrett-Lennard *et al.*,1996). This is a useful tactic, as one of their known prey, harbour seals (*Phoca vitulina*), were shown not to respond to calls of familiar fish-eating killer whales, but respond strongly to both unfamiliar fish-eating killer whales and mammal-eating killer whales (Deecke *et al.*, 2002).

1.2 Cetacean social structure

Social structure is based on patterns of relationships between individuals. Following Hinde's (1976) framework, individuals build relationships through repeated interactions. The complexity of a social structure has been predicted to increase as the number of different contexts of interactions increase (Freeberg *et al.*, 2012). These contexts can include cooperative foraging, predator avoidance, reproduction and offspring rearing, and therefore contexts of interactions can change as social and ecological conditions demand (Dunbar, 1989).

Cetacean social structures vary widely in their complexities. Killer whales are at the top of the food chain and therefore their social structure has not evolved to include predator avoidance. Their marine mammal prey have been shown to include dolphins, porpoises, toothed whales and baleen whales (Jefferson *et al.*, 1991). Killer whales are typically found in pods containing maternally related individuals (matrilineal), with a mother’s offspring of either sex remaining with her for life. This is particularly the case with “resident” or fish-eating killer whales as opposed to “transient” or mammal-eating killer whales, whose members have been known to disperse from natal pods (Baird and Whitehead, 2000). Female sperm whales have similar stable matrilineal societies to killer whales, although male offspring leave the pod when they are subadults to travel to colder waters where prey is more abundant (Whitehead and Weilgart, 2000). Male sperm whales remain alone for the rest of their lives, returning to tropical waters to mate with females for only a few days a year. The females in sperm whale groups provide allocare to the young, the details of which vary between populations. In the Caribbean, allomothers do not nurse other females calves, whereas in the Sargasso Sea there are more allomothers per calf, and they also share in nursing (Gero *et al.*, 2009). Finally, small delphinids exhibit social organisation ranging from ephemeral groups where individuals have loose bonds, to long-term associations spanning multiple decades (Connor *et al.*, 2000).

Group living in cetaceans, presumably like all animals, is a trade-off between costs and benefits. Costs include increased susceptibility to predation purely because more animals are more likely to alert a predator to their presence. In addition, foraging efficiency can be reduced due to increased competition for resources. There is also increased competition for reproductive opportunities and finally, increased transmission of disease. Benefits on the other hand can include reduced predation, as the predator may likely take one of the other members of the group, enhanced detection and capture of prey, increased defence of resources and the transmission of information. Bertram (1978) stated that the matrix of cost-benefit ratios for an individual undertaking group living depends on its sex, reproductive state and ecology. Groups may therefore form for a specific timespan for a specific function, as seen in the yearly migrations of baleen whales to breeding grounds. These migrations are a possible strategy to avoid killer whales predating on vulnerable newborns, as there are fewer killer whales in tropical waters (Corkeron and Connor, 1999). Another example is gray whales (*Eschrictius robustus*) that gather to give birth in lagoons that may function as shelters from killer whales (Swartz, 1986).

Communication is fundamental in the establishment and maintenance of groups and therefore social structure (Baker, 1982), and its complexity depends on how much information is shared and in how many ways (Freeberg *et al.*, 2012). Freeberg *et al.* (2012) argue the existence of a ‘social complexity hypothesis’ whereby highly social animals require more complex communication systems, and cite passages from both Lamarck (1809) and Darwin (1872) supporting this view. Moreover, this connection between complex social relationships and complexity in communication has been suggested as a way to understand why only a few species, including humans and dolphins, have developed the ability to use learned vocalisations in social interactions (Janik, 2014).

1.3 Communication in cetaceans

Marine mammals produce acoustic signals to communicate. Baleen whales produce songs that are a reproductive advertisement display (Tyack, 1981), while pinnipeds use their contact call and bottlenose dolphins use their signature whistle for mother-offspring recognition. Marine mammals also produce cues as well as signals. For example, sperm whale echolocation clicks can be used to determine the size of the animal (Gordon, 1991). The constraints of the evolution of signals for deep diving marine mammals include a trade off between the need to communicate effectively with conspecifics, but avoid alerting acoustically sensitive predators.

There is some correlation between the way cetaceans organise themselves in societies and the kinds of communication they use. For example, sperm whales and killer whales who spend a lifetime in a stable group (Bigg *et al.*, 1987; Whitehead and Arnbom, 1987) have stable group-specific vocal repertoires. Killer whales produce discrete, pod-specific calls that are stable over years (Ford, 1991). These dialects are more similar between pods whose matrilines are closely related (Deecke *et al.*, 2010; Ford, 1991). Sperm whales use click vocalisations for both echolocation to find prey and communication. Patterns of clicks called codas function as communicative signals (Watkins and Schevill, 1977). Recently, codas have been shown to provide both group and individual recognition (Antunes *et al.*, 2011; Madsen, 2012). In addition, adult males produce slow clicks called clangs that may be used as sexual advertisement signals (Weilgart and Whitehead, 1988), although they are also recorded at latitudes where adult females are not found (Madsen *et al.*, 2002).

Bottlenose dolphins produce individually distinctive acoustic signals called signature whistles (Caldwell and Caldwell, 1965). These provide individual recognition (Sayigh *et al.*, 1999; Janik 2006) that presumably is required in their fission-fusion societies, and aid in maintaining group cohesion (Janik and Slater, 1998). It has been claimed that highly social species such as bottlenose dolphins require more complex vocal repertoires (Blumstein and Armitage, 1997; Seyfarth and Cheney, 1984) and that the complexity of that sociality may be driving the evolution of complexity in communication (Janik, 2014). In the case of dolphins, this includes dolphins copying signature whistles (King *et al.*, 2013). The complexity therefore is not the type of call, or that it has been learned, but that the dolphins are using it possibly to address one another. The most parsimonious explanation for this is that individuals have no stable group structure and track one another at the individual rather than group level, and therefore individual calls rather than group ones facilitate recognition.

1.4 Blainville's beaked whales

Blainville's beaked whales are in the family Ziphiidae, a highly speciose family for cetaceans. The genus Mesoplodon, to which Blainville's beaked whales belong, has 14 species currently recognised, and is the most speciose in the order Cetacea (Dalebout *et al.*, 2008). They grow to a maximum of 4.7 m in length (Pitman, 2002), and there is no known significant difference in body length by sex (MacLeod, 2006). All Mesoplodon have only one pair of teeth, and those in Blainville's beaked whales are located a few inches back from the tip of their rostrum. These teeth only erupt beyond the gum in males (McCann, 1963), and are used in male-male fights (Heyning, 1984; McCann, 1974; Mead *et al.*, 1982). The rostrum of a Blainville's beaked whale has the highest density (5.7 g/cm3) of any mammalian bone tissue measured (Zotti *et al.*, 2009), allowing the males to engage in intense head-to-head combat (Heyning, 1984). Battle scars from each other's teeth are extreme and remain visible on the whale throughout its life. Male-male combat is a common method to compete for females in mammals, seen widely in ungulates, the closest relatives of the Cetacea (Heyning, 1999).

Blainville's beaked whales are typically found in small groups (median = 4), containing a single male and a group of females and their calves, described as a harem structure (Claridge, 2006). It is presumed that the intense male competition is to gain access to these female groups. However, it is not known how stable these groups are, how they are formed, or how females within the groups are associated. Presumably, Blainville's beaked whales are predated upon by large sharks and killer whales and so group living may be a predation avoidance mechanism for this species.

Gathering data on Blainville's beaked whales is challenging as they exhibit extreme diving behaviour. They spend more than a third of their time in the dysphotic zone at depths greater than 200 m (Tyack *et al.*, 2006), and most of the remaining time perform shallow dives that last on average of 9-10 minutes, with very short surface intervals between dives to breathe (Tyack *et al.*, 2006). These dives are performed synchronously by all members of the group. They generate echolocation pulses for half the duration of their deep dives (Arranz *et al.*, 2011). Beaked whale echolocation pulses are regular, evenly spaced frequency-modulated clicks that are produced consistently throughout the base of a foraging dive and are thought to be associated with a prey-searching phase (Johnson *et al.* 2006). Beaked whales are thought to suction feed mainly on cephalopods (MacLeod *et al.*, 2003) and when prey has been detected, buzz clicks are produced, which occur as a rapid increase in click production at the end of click trains, thought to be associated with prey-capture attempts (Johnson *et al.* 2004, Johnson *et al.* 2006; Madsen *et al.* 2005).

There are only three sounds previously described from Blainville's beaked whales other than these two types of echolocation pulses. Caldwell and Caldwell (1971) described pulse-like sounds from a stranded animal in the surf that sounded like chirps or short whistles with frequencies around 1 kHz to around 6 kHz. Rankin and Barlow (2007) reported a 1.5 second whistle and three burst pulses between 6 and 16 kHz they recorded near a surface group of whales. Finally, Aguilar de Soto *et al.*, (2011) reported rasps (a series of frequency-modulated clicks with short inter-click-intervals) occurring on average twice per dive, and two whistles with fundamental frequencies around 12 kHz. Because beaked whales exhibit group living, and their synchronous diving behaviour, some kind of communication is likely occurring and may not be fully described as yet. In addition to the possibility of undescribed signals, cues may also exist.

In summary, clearly there is a link between communication and social structures, so it makes sense to study them together. For that reason this thesis first investigates Blainville's beaked whale social structure and then delves into aspects of their communication. Understanding of their communication system will advance our knowledge of their biology and conservation needs. In behavioural response studies, Blainville's beaked whales consistently move away from anthropogenic noise sources (Allen *et al.*, 2014; Tyack *et al.*, 2011). The population level effects of these movements are currently being investigated (New *et al.*, 2013), but we also need to understand how these movements might disrupt social systems or how the sound itself affects communication. In this study, I explore social structure, cues and signals using unique datasets from longitudinal studies to increase our understanding of Blainville's beaked whale communication and its potential role in their social structure.

1.5 Thesis overview

The social structure of Blainville's beaked whales has been described as a harem structure with a single adult male and a group of adult females. Yet the nature of the associations within these groups has not been described. In Chapter Two, I investigate the relationships of the females in these groups, the lengths of these associations, as well as how long a male remains with a group of females.

Earlier studies have found only a handful of non-echolocation sounds made by Blainville's beaked whales (Caldwell and Caldwell, 1971; Rankin and Barlow 2007; Aguilar de Soto *et al.*, 2011). In Chapter Three, I examine potential communicative signals used by all individuals on all their deep dives that have not yet been described for this species.

Animal vocalisations have been shown to hold information regarding the sender from sex to size and / or age. In Chapter Four, I investigate whether this type of additional information exists among Blainville's beaked whale's echolocation pulses.

Mother calf recognition is required across many taxa, and is managed using different communicative mechanisms. In Chapter Five, with scant data I investigate the ontogeny of Blainville's beaked whale clicks with the aim of understanding whether this requirement is somehow being met through the echolocation pulses of mothers and calves in this species.

Finally, in Chapter Six I describe a pattern in the echolocation pulses of three deep-diving odontocete species that appears to be physiological, and compare the difference in its production across the species.

In summary, the aim of this study is to provide an insight into Blainville's beaked whale communication to advance our knowledge and increase our understanding of the full effects of anthropogenic threats to this species.

Chapter Two

2 CONTRASTING PATTERNS OF SOCIAL BONDS BETWEEN THE SEXES IN BLAINVILLE'S BEAKED WHALES (*MESOPLODON DENSIROSTRIS*)

2.1 Introduction

Animal social structure reflects the relationships between individuals in a population, which are built on patterns of interactions between those individuals (Hinde, 1976). Studying these relationships can lead to a greater understanding of population biology (Wilson, 1975), and in turn aid in the management and conservation of a species (Sutherland, 1998). Studying animal societies can also help to understand the evolution of species-specific characteristics. For example, a study on sexual size dimorphism in primates (Lindenfors and Tullberg 1998) showed that both male and female size increased as the amount of polygyny increased, and the increase in size of the males was more pronounced than in the females. Moreover, extrinsic factors have likely driven the ways in which animals associate with one another, with pressure from predation and the need to forage affecting how animals, including cetaceans (Connor, 2000; Gowans *et al.*, 2007), organise themselves in social groups (Wrangham and Rubenstein, 1986). Therefore understanding animal societies may enable predictions of the effects that changes in environmental factors have on social organisations (Crook *et al.*, 1976). Social systems are often analysed by measuring how often two subjects, in this case whales, co-occur in time and space, rather than specifically measuring interactions – the so-called 'gambit of the group' (Whitehead and Dufault, 1999). Typically solitary animals do not have complex social structures, as they do not repeat interactions with individuals to form any type of relationship. However animals that live in a group clearly have relationships, which can vary according to the age, sex, dominance status and individual histories of the group members.

Gowans (2007) argued that complexity in social strategies evolves in line with foraging strategies, which seems to be the case in marine mammals, if one considers complex social strategies to be those that involve relationships with repeated interactions. There are a variety of social structures that exist amongst marine mammals. Migrating baleen whales do not generally have long-term bonds but can have some short-term bonds for the duration of a season (Clapham, 2000). The lack of associations among individual baleen whales may be due to not requiring coordinated foraging techniques when targeting large quantities of small prey, and likely being less pressured by predation due to their large size (Gowans *et al.*, 2007). There are exceptions of course, such as humpback whales (*Megaptera novaeangliae*), a migrating baleen whale that displays coordinated cooperative feeding on herring (*Clupea*) (Baker and Herman, 1984; D'Vincent *et al.*, 1985; Perry *et al.*, 1990), and have transferred the knowledge of lobtail feeding (Hain *et al.*, 1982) by social learning through a population (Allen *et al.*, 2013). In contrast, bottlenose dolphins (*Tursiops truncatus*) have both short-term associations that can last hours, as well as long-term bonds that can last decades, and use both cooperative and solitary feeding strategies (Connor *et al.*, 2000). Killer whales (*Orcinus orca*) also engage in cooperative hunting where multiple matrilines will forage together and share the prey (Baird, 2000), and the matrilineal pods can last decades (Baird, 2000). Although there have been many studies of marine mammal social structure, much of the focus on deep-diving odontocetes has been on sperm whales (*Physeter macrocephalus*). Female sperm whales live together for a lifetime (Christal *et al.*, 1998; Whitehead and Weilgart, 2000), whereas males leave the pod as teenagers and then live a solitary life (Rice, 1989; Richard *et al.*, 1996), visiting a pod for only a few days each year to breed (Best, 1979).

In contrast, little is known of other deep diving cetaceans. What is known of social structure in beaked whales comes from only two studies thus far. One study was on northern bottlenose whales (*Hyperoodon ampullatus*) in the Gully off Nova Scotia in Canada (Gowans *et al.* 2001), and the other study on Blainville's beaked whales (*Mesoplodon densirostris*) in the Bahamas (Claridge, 2006). Although these species of beaked whale are similar in some respects, such as observed group size (Benjaminsen and Christensen, 1979; Gowans *et al.*, 2001; Claridge, 2006), their social structure appears to be starkly different. Bottlenose whale groups are mixed sex, and there were no long term bonds observed, or any evidence for preferred associations, amongst females. However some male associations lasted up to a decade (Gowans *et al.*, 2001), comparable to male bonds in bottlenose dolphin alliances that last up to 20 years (Wells, 1991). These dolphin male pairs have been seen working together to isolate a female, presumably to increase mating opportunities (Connor *et al.*, 1992). Although male bottlenose whales are seen in pairs, they have also been seen head-butting each other shortly before one of the males was seen with a female (Gowans and Rendell, 1999). Therefore male bottlenose whale associations may be related to mating strategies, and involve aggression as well as affiliation.

In contrast to the bottlenose whales, adult male Blainville's beaked whales have never been observed associating with each other. However, extensive intra-specific scarring suggests that the male-male interactions that do occur are aggressive in nature (Claridge, 2006). Their social structure has been described as a "harem-like" mating system (Claridge, 2006), with a single adult male typically seen in a group with multiple adult females (Ritter and Brederlau, 1999). Claridge (2006) found the highest association indices were between adult females. Interestingly, and comparably to bottlenose whales, there was no evidence of baby-sitting in these groups, perhaps as both species' calves exhibited the capability of diving for similar durations as their mothers from birth (Gowans, 1999; pers. obs.). In contrast, sperm whale calves do not dive for the same length of time nor, presumably, to the same depths as adults (Whitehead, 2003), consequently a mother's female associates will often perform a baby-sitting function (Whitehead, 1996). Sperm whales may therefore have evolved to be a group living species in response to the risk of predation on calves (Whitehead and Arnbom, 1987).

Some studies have specified that the definition of group living is spending at least half of the time in that group (Bigg *et al.*, 1990; Sailer *et al.*, 1984). However I would define group living as individuals living with other individuals with whom they have relationships, and thus whose associations with one another are neither random nor driven by coincident external factors, such as ephemeral food patches. Therefore the nature of the interactions that have created the relationship are more important than the time spent together, since, for example, multiple animals could be following the same resources for extended periods of time, but not actually interacting. Although Blainville's beaked whales have been observed in harem-like group structures (Claridge, 2006), it is not known whether they are engaging in group living as defined above.

Both existing studies of beaked whale sociality are restricted, though in different ways. The Claridge (2006) study was somewhat limited in its sample size, because although it included seventy three well marked individuals, associations were calculated only for individuals seen two times or more (n=27). The Gowans *et al.* (2001) study was limited in its temporal effort distribution. The relatively high latitude Nova Scotia field efforts were restricted to summer months, with the longest field effort being three months and the shortest only a few days, although this may not have affected the analysis as the only long-term associations appear to be amongst males, who associated across years. However, both studies have contributed to our knowledge of deep-diving odontocete social structures and shown that foraging for similar prey, at similar depths, has not resulted in similarly organised societies. Sperm whales are known to dive to 1330 m (Watkins *et al.*, 2002), northern bottlenose whales to 1453 m (Hooker and Baird, 1999), and Blainville's beaked whales to 1885 m (Tyack *et al.*, 2006). Moreover, all three species feed on squid (Clarke *et al.*, 1993; Hooker *et al.*, 2001; Ross, 1984; MacLeod *et al.*, 2003). Clearly there are different factors driving each of the sperm whale, northern bottlenose and Blainville's beaked whale social organisations.
To understand what might be driving the strong associations between Blainville's adult females and whether or not Blainville's beaked whales are living in groups, I used a 16-year dataset detailing three generations of Blainville's beaked whales, with some females producing four calves during the study period, and added eleven more years of data to the five-year dataset analysed by Claridge (2006). Due to the longitudinal nature of this dataset, I was able to investigate timescales over which associations between whales were maintained, and whether associates were randomly chosen or not.

2.2 Methods

2.2.1 Field Methods

Photo identification data were collected during encounters with animals occurring on small vessel opportunistic surveys (Figure 2.1) off southwest Great Abaco Island in the Bahamas between 1997 and 2012 (Figure 2.2). From 1997 – 2001 photographs of whales were taken using black and white film with 35 mm SLR cameras and a 300 mm lens, and the negatives later examined over a light table to identify each individual in a group. From 2001 onwards, Nikon digital SLR cameras were used with either a fixed 300 mm or a 70 – 200 mm lens.

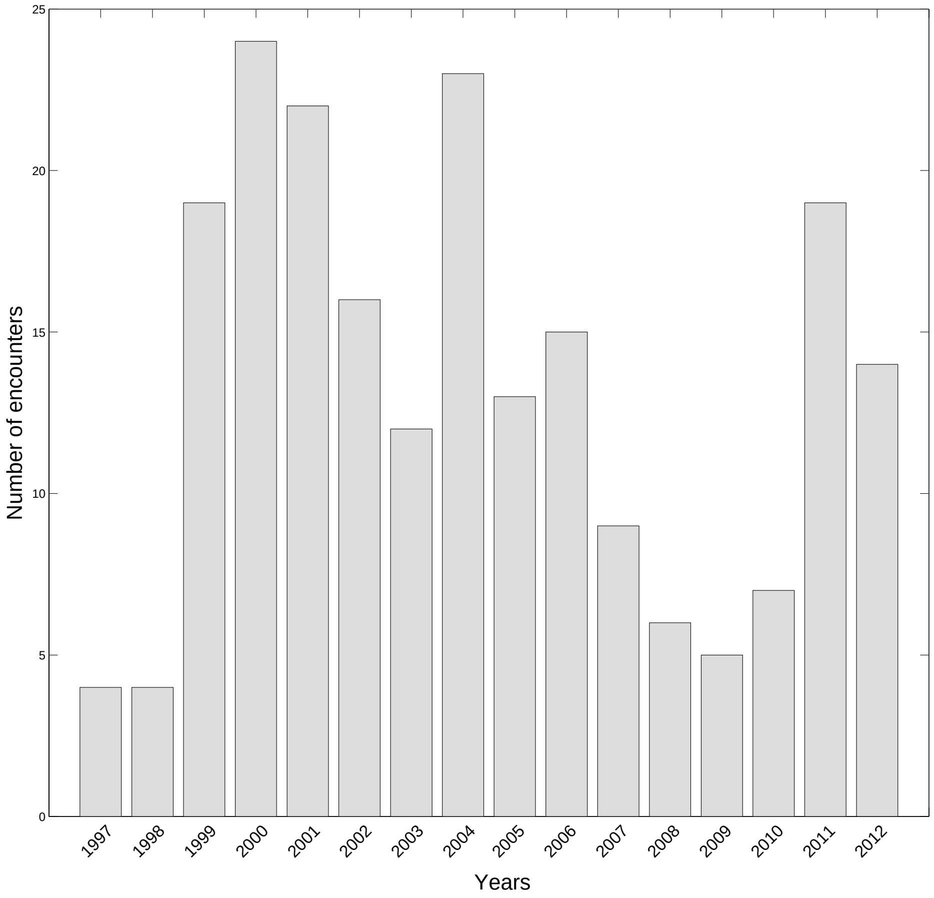

Figure 2.1. Number of Blainville’s beaked whale encounters by year for the duration of this study.

2.2.2 Photo identification analysis

All photos were matched and added to an existing photo-identification catalogue of Blainville’s beaked whales. I contributed to photo-identification from 2004 onwards, taking the photographs and either carrying out the matching myself, or confirming the matching performed by someone else. The photo-identification analysis also categorised individual whales into sex and age-classes using the following definitions and characteristics from Claridge (2013).

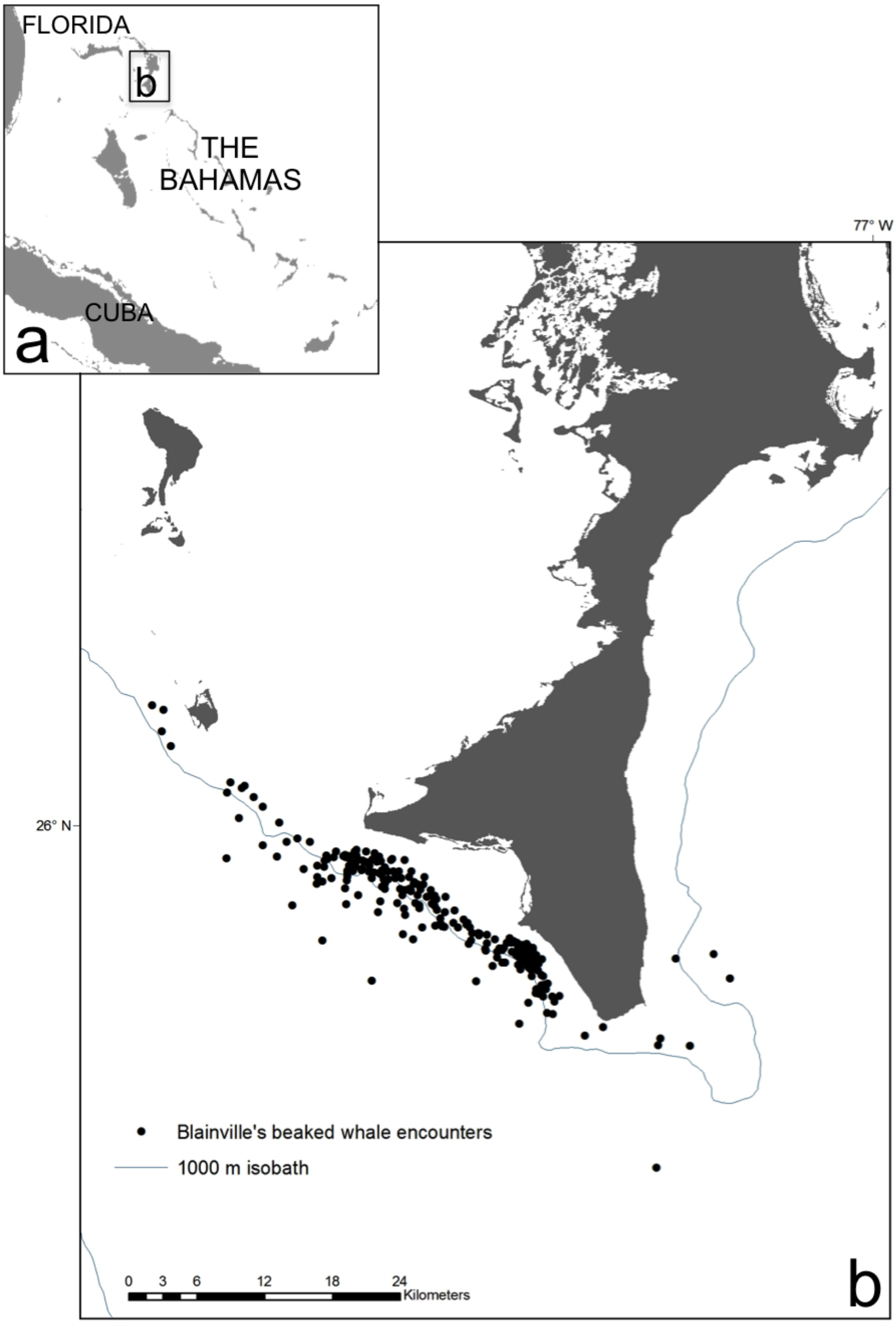

Figure 2.2. a) Map of the Bahamas, and b) locations of all Blainville’s beaked whale encounters from 1997 – 2012 off southwest Great Abaco Island.

Whales given an age-class of ‘calf’ are still in the same group as their mother, and presumably dependent upon their mother. ‘Subadults’ are weaned, but have few, if any, of the characteristics that distinguish adults, such as extensive cookie cutter shark (*Isistius sp.*) scars or erupted teeth. However, as subadult males mature they begin to show a high arch on their mandibles (lower jaw) and can be distinguished from subadult females around age 9 (Claridge 2013). Cookie cutter shark bites leave long-lasting scars that accumulate over the life of beaked whales (Walker and Hanson, 1999), as do intraspecific scars seen on males from aggressive interactions with other males (Heyning, 1984). ‘Adult’ females are either accompanied by a calf, or are larger than a subadult and have multiple cookie cutter shark scars but few intraspecific scars. Finally, ‘adult’ males have erupted teeth and numerous intraspecific and cookie cutter shark scars.

Photographs were given a quality (Q) grade ranging from 0 to 3 (3 being the highest quality photograph) based on the image size, focus, lighting, angle, and exposure of the photograph. In addition, individuals are given a certainty (C) grading (Figure 2.3) to rate the level of certainty of an animal’s sex/age-class. Ratings ranged from 0, not certain at all, to 3, very certain. All photo-identification analysis and categorisation was calibrated between individuals carrying out the analysis, through training by a member of the research team who was involved throughout the duration of the study (Diane Claridge).

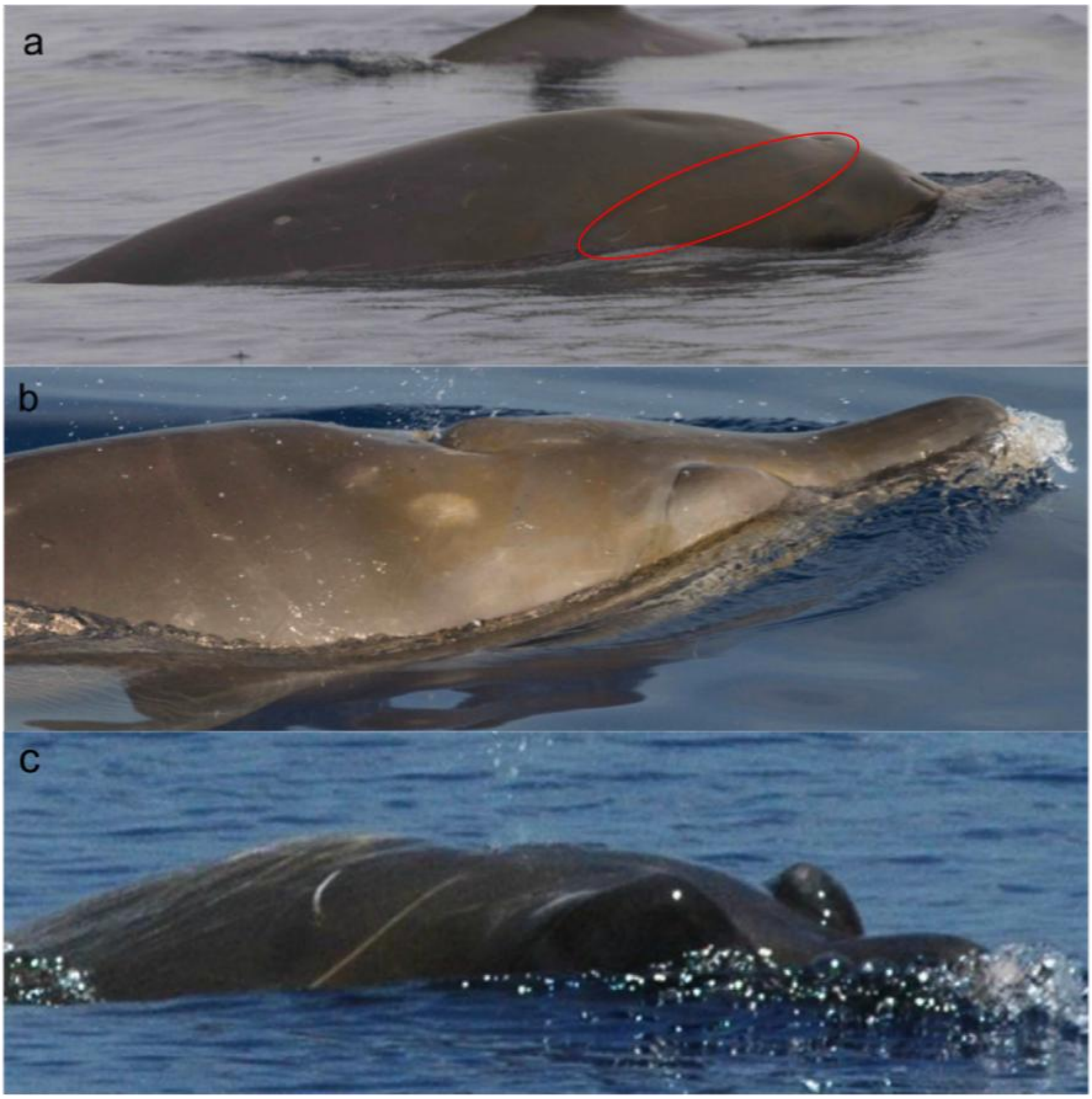

Figure 2.3. An example of certainty gradings for subadult males: (a) C = 1, based on an intra-specific linear scar behind the blow hole, circled in red (biopsy results later confirmed this animal is a male), (b) this animal is 8 years old and his mandibular arch is beginning to show, he was given a certainty rating of C = 2 and finally (c) the males teeth are just about to erupt, C = 3.

The data were organised into records containing the date of an encounter, the sequence number of that encounter within that day (to separate multiple encounters in the same day), the identification of each animal present, as well as the quality of the best photograph of that animal taken during that encounter. For each encounter, if an individual had left and right photos taken, the photo with the best quality was used.

2.2.3 Association analysis

Animals were considered to be associated if they were photo-identified in the same encounter. An encounter was defined as all animals seen no more than ten body lengths apart from each other, diving in synchrony, as long as the closest animal was within 500 m of the survey vessel. Encounters ended when the vessel left the animals, either because identification photographs of all animals in the encounter had been obtained, the weather had deteriorated, or the onset of darkness made photography impossible.

I used SOCPROG 2.5 (Whitehead, 2009) for Matlab R2014a (8.3.0.532) to analyse associations between whales. I used a sampling period of 1 day for all analyses except the investigation into preferred or avoided associations. Association was defined by membership in the same encounter, and only individuals seen in more than three days were included in the analysis, to ensure associations were meaningful. Only photographs with Q > 1 and animals with C > 1 were used, therefore some associations may have been missed due to poor quality pictures of an individual in an encounter, i.e. Q = 0 or 1. Supplementary data describing the individuals were organised with a single record for each individual with its most recent sex/age-class an indicator as to whether it changed age-class during the study, and, if it did, the date(s) it changed, therefore allowing age-class analysis. Some animals changed age-class more than once during the study, for example from ‘calf’ to ‘subadult’ and then to ‘adult’.

I chose the simple ratio association index $(x/(x + y_{AB} + y_A + y_B))$, as recommended by Ginsberg and Young (1992), and Whitehead (2009). x is the number of sampling periods in which A and B were observed associated, y_A the number of sampling periods A was identified without B, y_B the number of sampling periods B was observed without A, and y_{AB} the number of sampling periods A and B were both observed but not associated with each other (in this case, zero, because if both animals were observed in the same encounter, they were defined as associated).

2.2.3.1 Accuracy and variability of the analysis

I measured the accuracy of the social representations that association indices can provide with this dataset by calculating the correlation coefficient (*r*) between the actual time pairs of whales were observed associating with one another, and the estimated time, the association indices (α_{AB}): $r = S/CV(\alpha_{AB})$. *r* ranges between 0 and 1 and the closer to 1, the better the representation of the sociality of the dataset (Whitehead, 2008). In order to calculate *r*, one must first calculate social differentiation, *S*, which is the coefficient of variation (CV) of the observed proportion of time that dyads are associated. Social differentiation indicates the variability of association indices within a population. If social differentiation is less than about 0.3, then associations are homogenous and if *S* is greater than about 2.0 then association strengths are highly variable within the population (Whitehead, 2008).

2.2.3.2 Associations between classes

Using the simple-ratio association index, I calculated the mean and maximum association indices within and between all sex and age-classes. I used Mantel permutation tests to test correlations between association matrices and 1/0 matrices that indicated whether pairs of individuals belonged (1) or did not belong (0) to the same sex/age-class. Rejecting the null hypothesis of no correlation in these tests would show that individuals were more (or less, in the case of significant negative correlations) likely to associate with others of the same age-sex class than expected by chance. These tests were run with 10,000 permutations using a two-tailed significance test.

2.2.3.3 Associations over time

I used standardised lagged association rates (SLARs) to look at the probability that individuals seen together at a given time would still be associated at some time lag (τ) in the future (Whitehead, 1995, 2008). Standardising the lagged association rate accounts for the possibility that not all associates of an individual, for a particular sampling period, are included in the dataset. The analysis was carried out for all individuals in the population, as well as for adult female associations with other adult females, and adult male associations with adult females, to provide some idea of the timespans of these bonds. A null association rate, the association rate expected if there were no preferred associations, was also calculated to compare to the observed SLARs, and a jackknife process estimated the precision of the SLARs (Whitehead, 1995, 2007). Models were fit to the SLARs of how an association rate changed with time (Table 2.1), and the model with the best fit was chosen using the quasi-Akaike Information Criterion (QAIC) (Whitehead, 2007). The model with the lowest QAIC was selected as the best model (Burnham and Anderson, 2002), and ΔQAICs between each model's QAIC value and that of the best model were calculated to measure model selection uncertainty (where ΔQAIC from 0 to 2 indicates neither model can be preferred with certainty; ΔQAIC from 4 to 7 shows some uncertainty and ΔQAIC > 10 indicates considerable certainty in the preference of the model with the lower QAIC value).

Table 2.1. Models fit to SLARs by the SOCPROG software (Whitehead, 2008).

Model name	Model	Description
1. Preferred companions	$g(\tau) = a$	Association rate between individuals that does not change over time
2. Casual acquaintances	$g(\tau) = a \bullet e^{-b\tau}$	Short term associations *a*, for the duration 1/*b*
3. Preferred companions + casual acquaintances	$g(\tau) = a + c \bullet e^{-b\tau}$	Short term associations (*a* + *c*), for the duration 1/*b*, levelling off at association rate *a*
4. Two levels of casual Acquaintances	$g(\tau) = a \bullet e^{-b\tau} + c \bullet e^{-d\tau}$	Short term associations (*a* + *c*), with different durations (1/*b* and 1/*d*)

2.2.3.4 Testing for non-random associations

To investigate whether associations between individuals were different from random, I created association matrices for a set sampling period, and assigned a 1 for each pair of whales that were associated within the period, and a 0 for those that were not. The sampling period was chosen as the time when the SLARs began to decline. This allowed enough time for group compositions to switch, and different associations to occur, as well as associations across sampling periods to be meaningful. These matrices were permuted by inverting the association values between randomly chosen rows, whilst keeping constant both the number of identified individuals in a group, and the number of groups in which each individual was observed (Bejder *et al.*, 1998). A Mantel test was run to determine the similarity of the matrices with the null hypothesis that associations between sampling periods were no greater or less than random. The number of permutations was chosen when *p*-values indicating the test significance become stable (Whitehead *et al.*, 2005).

The analysis for preferred or avoided associations used adults only, as the subadult age-classes had only a small number of whales (<5), and calf preference will obviously be for their mother. I tested for long-term companionship by permuting associations within samples, as recommended by Whitehead (2009), testing whether individuals associated in different sampling periods more than would be expected by chance. Preferred long-term associations would be represented by significantly high standard deviations (SD) of the real association indices (Whitehead *et al.*, 2005), and evidence of avoidance indicated if the proportion of zero association indices was higher in the real dataset than the randomised version.
Where there was evidence for preference or avoidance from significant *p*-values, I ran Mantel permutation tests to compare between 1/0 matrices that indicated whether a group had a calf (1) or did not (0), and matrices detailing the measured distances (in kilometres) between these groups. Rejecting the null hypothesis of no correlation in these tests would show that groups with a calf were more (or less, in the case of significant negative correlations) likely to be sighted in a similar area. These tests were run with 10,000 permutations using a two-tailed significance test. This Mantel test for location preference was performed on matrices using the ‘ape’ package (Paradis *et al.*, 2004) in the statistical software R software version 3.0.3 (R Development Core Team, 2012), with all other tests having been performed using Matlab as part of the SOCPROG software package.

2.3 Results

The dataset comprised 16 years of photo-identification data, resulting in 167 individual whales identified from 250 encounters (Figure 2.4).

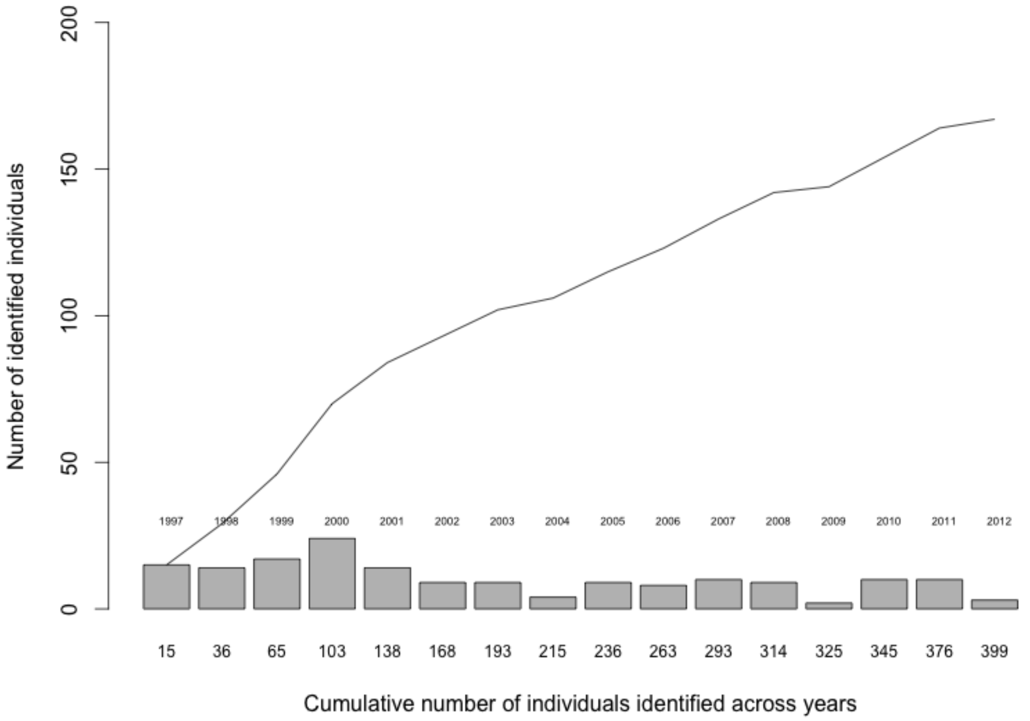

Figure 2.4. A discovery curve for photographically identified Blainville's beaked whales (1997-2012), showing a total of 167 individuals, with the number of new individuals identified each year shown by the histogram bars, and the number of all animals identified over the years shown on the x axis.

For most of the analyses, the dataset was then filtered to include only animals seen on more than three days, and with pictures Q > 1 and individuals C > 1, resulting in 51 individuals (Table 2.2).

Table 2.2. The dataset after filtering for high quality photographs (Q > 1), sex/age-class assignments with high certainty (C > 1), and individuals seen in more than three days (displaying an individual's current age-class).

Class	# Individuals
Adult Female (AF)	20
Adult Male (AM)	11
Calf (C)	11
Subadult Female (SF)	4
Subadult Male (SM)	4
Subadult Unknown (SU)	1

Analysis of group composition included only the 86% of all encounters where every individual in a group was identified, resulting in 62 different group sex/age-class compositions observed in a total of 216 encounters. With an additional eleven years of data since the Claridge (2006) study, the median group size found here (4) was exactly the same, with group sizes in the range 1-11.

Of the 62 variations in group sex/age-class composition, the top eleven group compositions accounted for more than 60% of the encounters and each occurred more than six times (Figure 2.5). I observed strong support for the harem group structure described by Claridge (2006), where more than one female accompanies a single adult male. The composition of a single adult male accompanied by two adult females and their calves was by far the most common composition, observed almost three times more than the next most common. Seven of the eleven most commonly observed compositions, representing 73% of all observed groups, contained a single adult male with one or more adult females with or without calves.

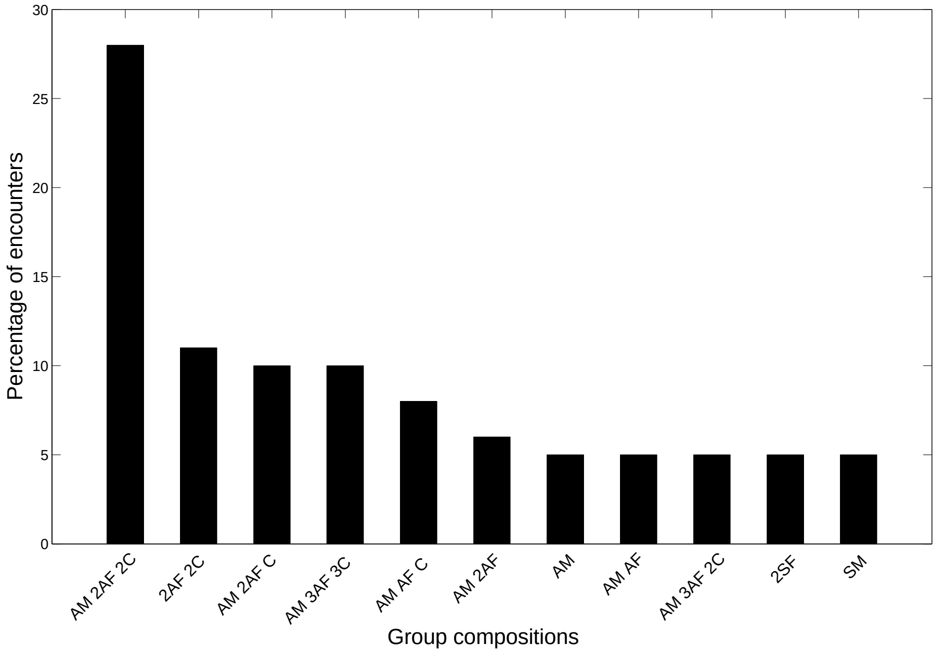

Figure 2.5. The eleven most frequently observed group compositions, comprising 60% of encounters where all individuals in the group were identified.

2.3.1 Association analysis

For the measure of the accuracy of the social representations of this dataset, the correlation coefficient (*r*) between the true and estimated associations was 0.407 (standard errors (SE) = 0.014), and the social differentiation (S) of the dataset was 1.107 (SE = 0.029). The mean number of observed associations per dyad was 0.77, more than double the suggested 0.3 (Whitehead, 2008). Therefore I am confident that the analysis of estimated association indices is reasonably representative of the population of whales in this dataset.

2.3.1.1 Associations between classes

The mean association of whales (and their SD's) within sex/age-classes was slightly higher between classes, 0.04 (SD = 0.05), compared to within, 0.03 (SD = 0.02), suggesting some difference in association preference between sex/age-classes (Table 2.3). However the results from the Mantel test did not provide a basis to reject the null hypothesis of intraclass and interclass association indices having the same mean (t=0.70, p=0.24).

Table 2.3. Mean (a) and maximum (b) simple ratio association indices and their SD's (in parentheses) for dyads among different sex/age-classes. (This table is not symmetrical as sex/age-classes have different numbers of individuals.)

(a) Mean association indices

	Female	Male	Calf	SF	SM
Female	0.04 (0.02)	0.04 (0.02)	0.04 (0.03)	0.01 (0.01)	0.00 (0.01)
Male	0.04 (0.01)	0.00 (0.00)	0.03 (0.02)	0.01 (0.02)	0.00 (0.01)
Calf	0.04 (0.02)	0.03 (0.02)	0.02 (0.02)	0.00 (0.01)	0.00 (0.01)
SF	0.01 (0.01)	0.01 (0.01)	0.00 (0.00)	0.05 (0.05)	0.02 (0.03)
SM	0.00 (0.00)	0.00 (0.00)	0.00 (0.00)	0.02 (0.04)	0.17 (0.14)

(b) Maximum association indices

	Female	Male	Calf	SF	SM
Female	0.24 (0.09)	0.17 (0.08)	0.38 (0.26)	0.02 (0.03)	0.00 (0.01)
Male	0.19 (0.09)	0.00 (0.00)	0.21 (0.12)	0.03 (0.08)	0.01 (0.02)
Calf	0.42 (0.21)	0.17 (0.11)	0.51 (0.19)	0.01 (0.03)	0.01 (0.02)
SF	0.04 (0.05)	0.09 (0.11)	0.07 (0.05)	0.13 (0.11)	0.07 (0.10)
SM	0.02 (0.01)	0.05 (0.04)	0.05 (0.04)	0.07 (0.13)	0.33 (0.29)

The constant association of calves with their mothers could have affected this result therefore I re-ran the test without calves. This resulted in mean associations within the same classes of 0.04 (SD=0.06) compared to 0.02 (SD=0.01) between classes being similar (Mantel test: t=1.44, p=0.07); therefore the null hypothesis was again not rejected. Therefore testing the correlations of matrices of association indices and classes did not show any preference for associations of individuals within versus between classes.

There are also other notable features of the associations between and within classes to consider. Adult males never associated with one another, while subadult males associations with one another had by far the highest mean association index. Additionally, subadult males and females were notably not associating with adults. Therefore the results of the test between classes may not be for a representative summary of the entire population, but very informative by class (Table 2.3).

2.3.1.2 Associations over time

The standardised lagged association rate (SLAR) calculated for the entire population was higher than the null association rate for time periods up to approximately three years (Figure 2.6).

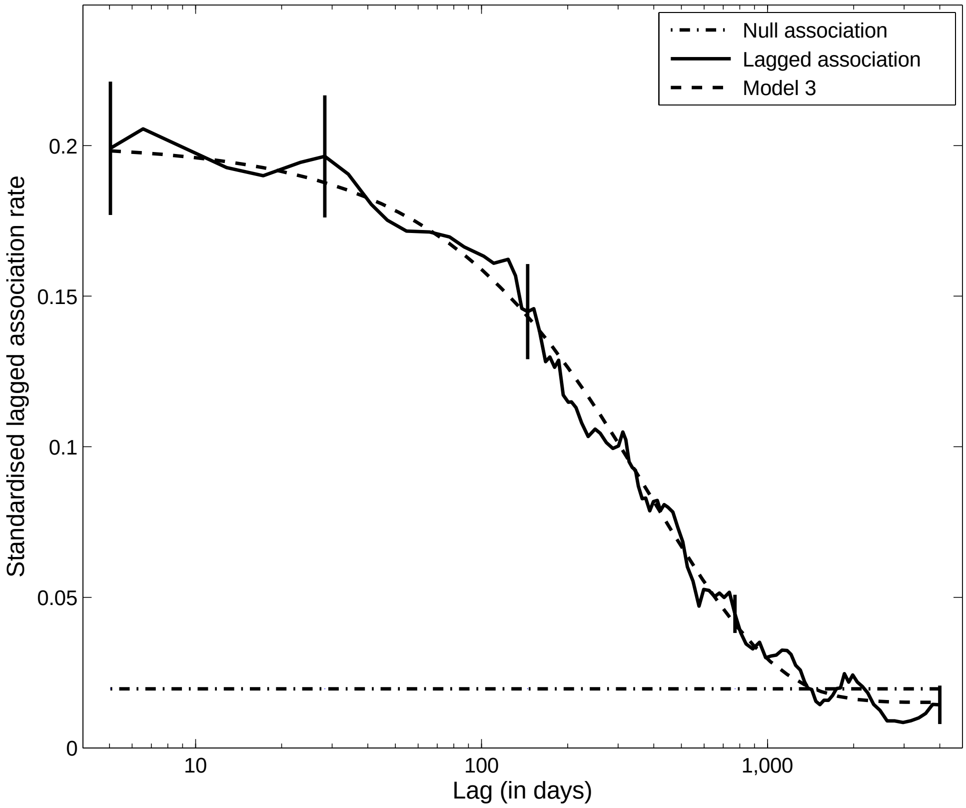

Figure 2.6. Standardised null and lagged association (SLAR) rates for all individuals, showing the best-fit model, model 3, ‘preferred companions and casual acquaintances’ (Table 2.4). Vertical error bars represent temporal jackknife standard errors.

The best model for the SLAR for adult females was the same model that best fit the dataset of all individuals (Table 2.5), model 3: preferred companions and casual acquaintances, with virtually no support for the next best model, which had a ΔQAIC of 34. As the name implies, this model accommodates two levels of associations of different durations (Whitehead, 2008). To investigate which individuals might be driving the longer term associations, I looked at the life history of the most frequently sighted adult female in the catalogue, Md076, to relate her associations to the suggested model. She had an almost three year (March 2000 to August 2002) apparently continuous association with another adult female, Md141, but also had shorter, repeated associations (maximum five months), with periods up to three years of separation, with the adult female, Md106, over a decade, from August 1998 to May 2010. Therefore in keeping with the suggested associations from the model name (preferred companion and casual acquaintances) with a longer association with Md141 who is perhaps a preferred companion, and shorter associations with Md106 who may be a casual acquaintance.

Table 2.5. Model selection for the SLAR of adult females.

Model	QAIC	ΔQAIC	Comments
1. Preferred companions	3313	496	no support
2. Casual acquaintances	2854	37	no support
3. Preferred companions + casual acquaintances	**2817**	**0**	**best model**
4. Two levels of casual acquaintances	2851	34	no support

The calculated SLAR for adult males associating with adult females was higher than the null association rate for time periods up to approximately a year (Figure 2.8), with association rates beginning around 0.35. However, it is interesting that the line of lagged association rate crosses the horizontal null association rate twice.

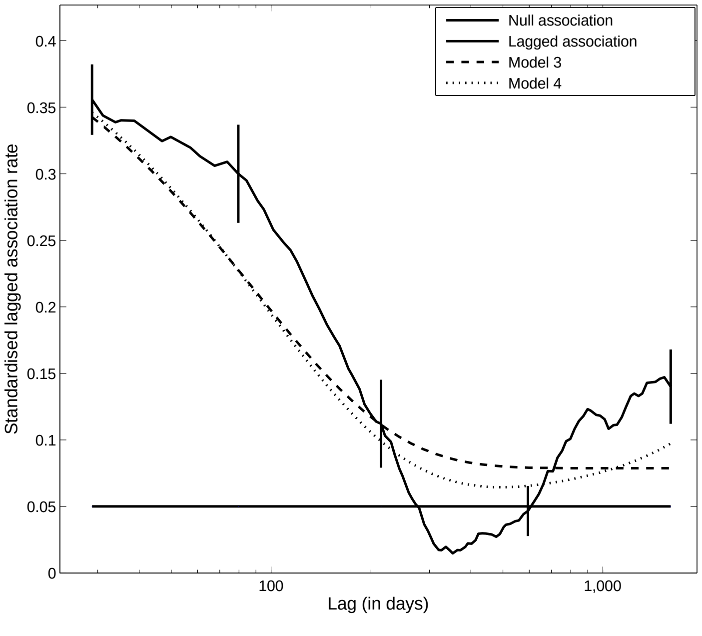

Figure 2.8. Standardised null and lagged association (SLAR) rates for adult males associating with adult females, showing the best-fit models, model 3, ‘preferred companions and casual acquaintances’, and model 4, ‘two levels of casual acquaintances’ (Table 2.6). Vertical error bars represent temporal jackknife standard errors.

For male associations with females, there were two models with an almost identical QAIC, models 3 and 4 (Table 2.6).

Table 2.6. Model selection for the SLAR of adult males associating with adult females.

Model	QAIC	ΔQAIC	Comments
1. Preferred companions	437	43	no support
2. Casual acquaintances	429	35	no support
3. Preferred companions + casual acquaintances	395	1	well supported model
4. Two levels of casual acquaintances	**394**	**0**	**best model**

Although I found associations between adult males and females remained above random for lags of up to a year, single adult males were rarely observed associating with the same females more than once during the study period. The adult male Md075, however, associated with Md076, an adult female, four separate times over a 13-year timespan, for periods up to five months (6 associations over 172 days). Therefore Md075's repeated associations over such a long timespan may have caused the lagged association rate to re-cross the null association rate (Figure 2.8). By removing Md075 from the dataset, the calculated SLAR for adult males associating with adult females remained higher than the null association rate for time periods of approximately a year (Figure 2.9), however the association probabilities were lower, beginning around 0.28, due to the fact that Md075, who had repeated associations, was now removed.

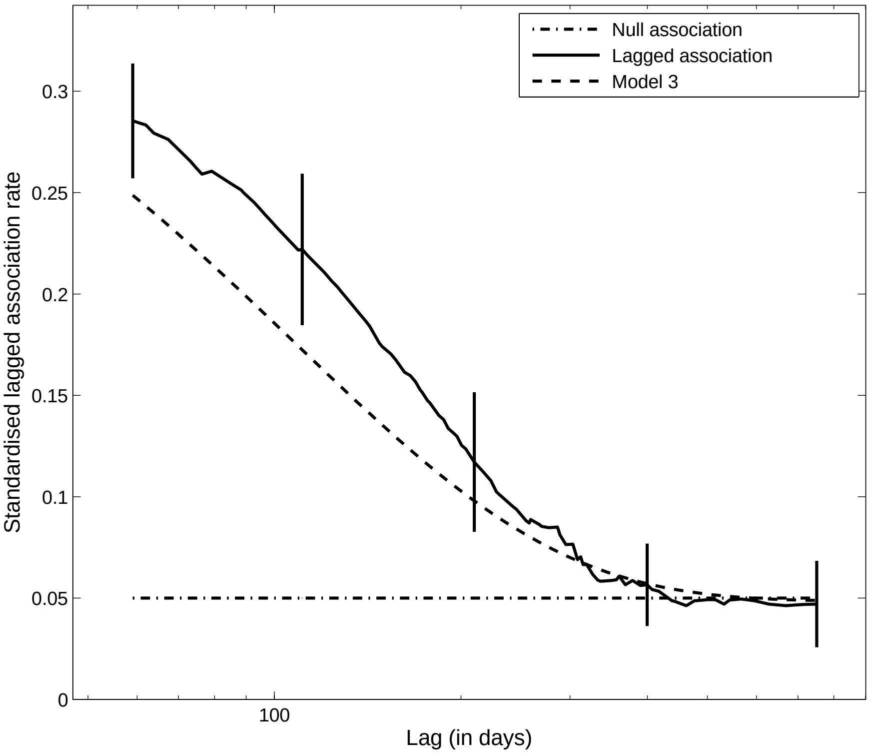

Figure 2.9. Standardised null and lagged association (SLAR) rates for adult males (except Md075) associating with adult females, showing the best-fit model, model 3, 'preferred companions and casual acquaintances' (Table 2.7). Vertical error bars represent temporal jackknife standard errors.

The best model describing male associations with females, with Md075 removed from the dataset, was again model 3 (Table 2.7). Therefore I concluded that the selection uncertainty between models 3 and 4 when Md075 was included in the dataset (Table 2.6) was driven by this individual's repeated associations with Md076, and that this single individual might not be representative of the general pattern in the population.

Table 2.7. Model selection for the SLAR of adult males associating with adult females, with Md075 removed from the dataset.

Model	QAIC	ΔQAIC	Comments
1. Preferred companions	277	30	no support
2. Casual acquaintances	260	13	no support
3. Preferred companions + casual acquaintances	**247**	**0**	**best model**
4. Two levels of casual acquaintances	272	25	no support

For each dataset except the adult males to adult females with Md075 included in the dataset, the SLARs were best fitted with the ‘preferred companions and casual acquaintances’ model ($g(\tau) = \mathrm{a} + \mathrm{c} \cdot e^{-b\tau}$). The model parameters can be interpreted as the proportion of preferred companions (a), the proportion of casual acquaintances (c), and the disassociation rate $1/b$. For all cases, casual acquaintances took up the majority of the proportion of acquaintances (Table 2.8).

Table 2.8. Estimated model parameters (a = proportion of preferred companions, c = proportion of casual acquaintances, $1/b$ = disassociation rate), for the ‘preferred companions and casual acquaintances’ model, describing temporal association patterns amongst all individuals in the population, between adult females, and between adult males associating with adult females (with Md075 removed from the dataset).

Associations	***a*** **(SE)**	***c*** **(SE)**	**1/*b*** **(SE)**
All-all individuals	0.02 (0.01)	0.19 (0.02)	391.47 (0.001)
Female-female associations	0.04 (0.23)	0.50 (5.05)	504.13 (3.34)
Male-female associations	0.05 (0.07)	0.35 (0.07)	107.99 (0.01)

2.3.1.3 Testing for non-random associations

The SLARs began to decline after a period of 100 days for the entire population (Figure 2.6), so a sampling period of 100 days was used for the preferred / avoidance tests, to look for associations between periods of 100 days. The number of random permutations was set at 10,000, as increasing this number did not affect the resulting p-values. The results for preferred and avoided associations were not different from random expectations for all except adult female associations with one another (Table 2.9). The SD of adult females’ mean association index was significantly higher in the observed dataset than the randomly permuted data. Additionally, the proportion of non-zero association indices was significantly lower in the observed dataset than the random (having many more zero association indices than would be expected). These results suggest that adult female Blainville’s beaked whales have both preferred associates and individuals they avoid among members of their own age/sex class, between periods of 100 days. Performing the same tests for a sampling period of a year produced very similar results.

Table 2.9. Permutation tests for long-term preferred associations and avoidances, with a sampling period of 100 days, and 10,000 random permutations.

	Long-term preferred associations? (SD)			**Avoided associations? (proportion of non-zero)**		
Class	**Real**	**Random**	***p*-value**	**Real**	**Random**	***p*-value**
AM -> AF	0.0806	0.0801	0.4139	0.3333	0.3339	0.4718
AF -> AM	0.0806	0.0789	0.2990	0.3333	0.3319	0.5478
AF -> AF	0.0845	0.0684	<0.0001	0.3072	0.3620	0.0002

To further investigate the adult female preferred associations and avoidances, I used an association matrix for the 15 adult females in the population that were seen on more than 10 days. The pair of females with the highest association index (0.38) was Md076 and Md141 (Table 2.10). Md076 is the most frequently sighted individual in the catalogue (49 sightings) and as a case study I examined her association history over the 14-year period across which she had been sighted. I detailed her preferred and avoided associations with other females through three different calving cycles as her reproductive state changed over the study period. This revealed an apparent preference to associate with other females in the same reproductive state; i.e. when she had a calf, she associated with other mother-calf pairs, and when she was without a calf, she associated with other females also without calves.

Table 2.10. Association indices of 15 adult females seen on at least 10 days. Dyads with association indices at least double the mean simple ratio association index (0.038) are shown in bold, and indices of 0 shaded in grey. ID's of an individual's calf, if it has become an adult and seen on more than ten days, are shown in parentheses. Standard errors (SE) for these association indices ranged from 0.14 to 0.02.

Md070	1.00														
Md076 (190)	**0.13**	1.00													
Md078 (135)	0.02	0.02	1.00												
Md079 (134)	0.00	0.04	**0.35**	1.00											
Md091	0.00	0.00	0.00	0.00	1.00										
Md094	**0.13**	0.05	0.04	**0.10**	0.04	1.00									
Md106 (107)	**0.14**	**0.26**	**0.08**	0.05	0.00	0.03	1.00								
Md107	0.00	0.04	0.00	0.00	0.00	0.00	0.00	1.00							
Md121	0.03	0.02	0.00	0.00	0.00	**0.09**	0.00	**0.13**	1.00						
Md134	0.00	0.00	0.00	0.00	0.00	**0.12**	0.00	0.00	**0.14**	1.00					
Md135	0.03	0.00	0.00	0.00	0.00	0.02	0.00	**0.15**	0.06	0.00	1.00				
Md139	0.00	0.00	0.00	0.00	**0.22**	0.04	0.00	0.00	0.11	0.00	0.00	1.00			
Md141	**0.16**	**0.38**	0.00	0.00	0.02	0.06	**0.16**	0.00	0.02	0.00	**0.10**	0.04	1.00		
Md190	0.00	0.00	0.00	0.00	0.00	0.00	0.00	**0.14**	0.00	0.00	0.00	0.00	0.00	1.00	
Md196	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	**0.25**	0.00	0.00	0.00	0.00	0.00	1.00
	Md070	Md076	Md078	Md079	Md091	Md094	Md106	Md107	Md121	Md134	Md135	Md139	Md141	Md190	Md196

To test whether Md076's associations were representative of a general pattern, I carried out further analysis just on adult females and their calves. For this analysis, the data were not filtered by Q or C values, nor by a minimum number of sighting days, in order to include all females who have had a calf in the population. This resulted in three generations of individuals including 27 females with documented calves (range 1 to 4 calves). I found that females with dependent calves were much more likely to associate with other female–calf pairs, while females without dependents prefer to associate with one another (Figure 2.10). The mean association index of dyads in different reproductive classes was 0.0089 (SD 0.018), whereas it was twice as much, 0.0173 (SD 0.021) for animals in the same reproductive class (Mantel test: t=2.13, p = 0.01).

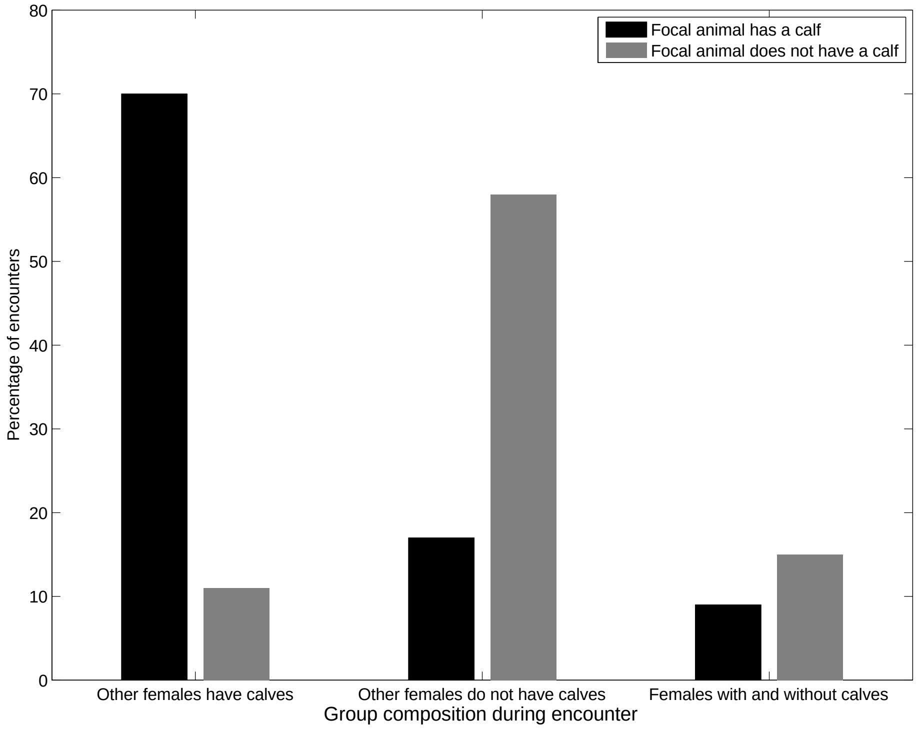

Figure 2.10. Group compositions showing when the focal adult female is with and without a calf, in three different group compositions; groups which include only other females with calves, groups which include only other females without calves, and groups which include other females both with and without calves.

2.3.2 Female associations and foraging overlap

To investigate whether adult female preferred / avoided associations were related to an overlap in foraging area rather than individual association preference, I plotted the sighting locations for Md076 and Md091. Md091 was one of the females with whom Md076 had a mean association index of 0 (Figure 2.11). There were three individuals who were sighted more than Md091 during the study, who also had an association index of 0 with Md076, however they were born in 1998 and 2003. Conversely, Md076 and Md091 were both first sighted as adults in 1997 and 1998 respectively, making them in the same age-class throughout the study. During the study period, Md076 had four calves, and Md091 had three.

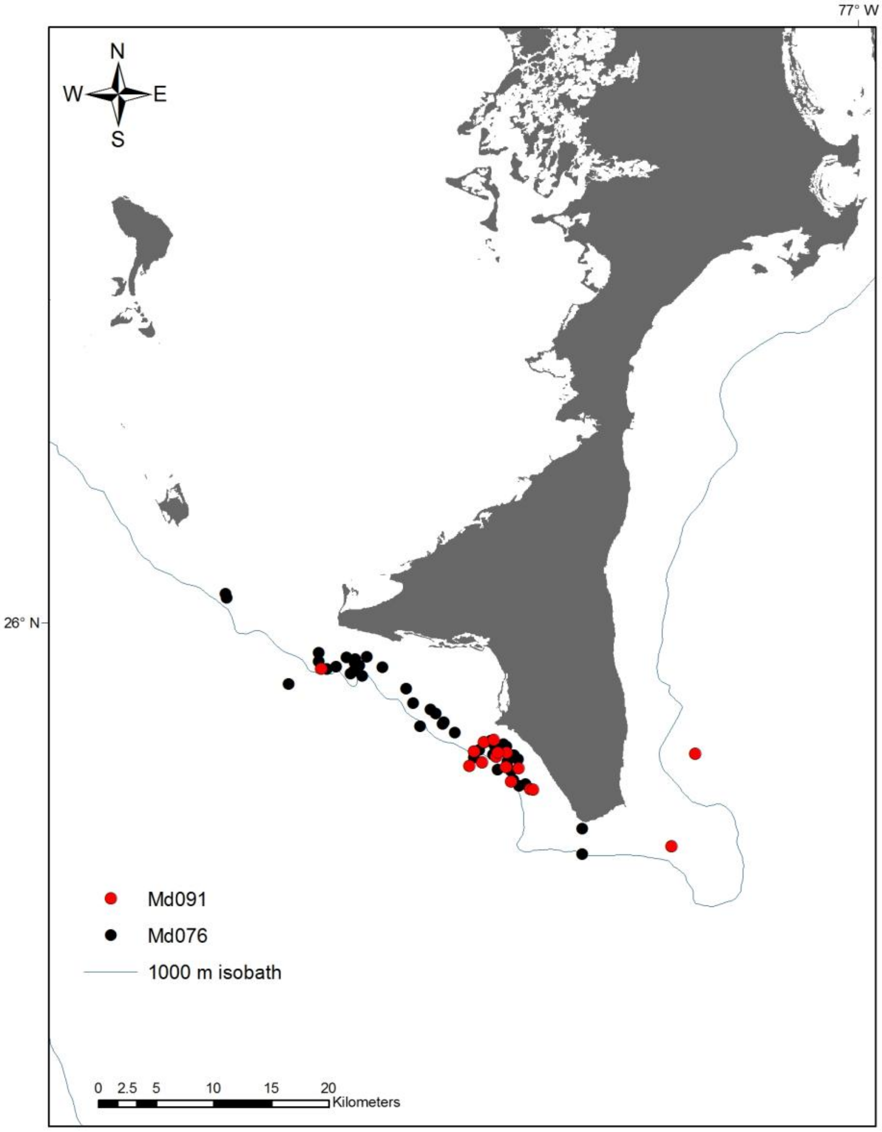

Figure 2.11. Map of the sighting locations for adult females Md091 (red) and Md076 (black).

During the study, there is overlap of sighting locations (Figure 2.11) for these two animals suggesting that their apparent avoidance is not attributed to different habitat preference. Notably, Md091’s calving cycle was asynchronous to Md076’s, further suggesting that these two individuals may be avoiding one another because they were not in the same reproductive state. However, to confirm habitat was not a driver of the avoidance of these two animals, I again plotted the sightings of Md076 and Md091, this time differentiating which sightings they were with and without a calf (Figure 2.12), in case there is preferred habitat for either state.

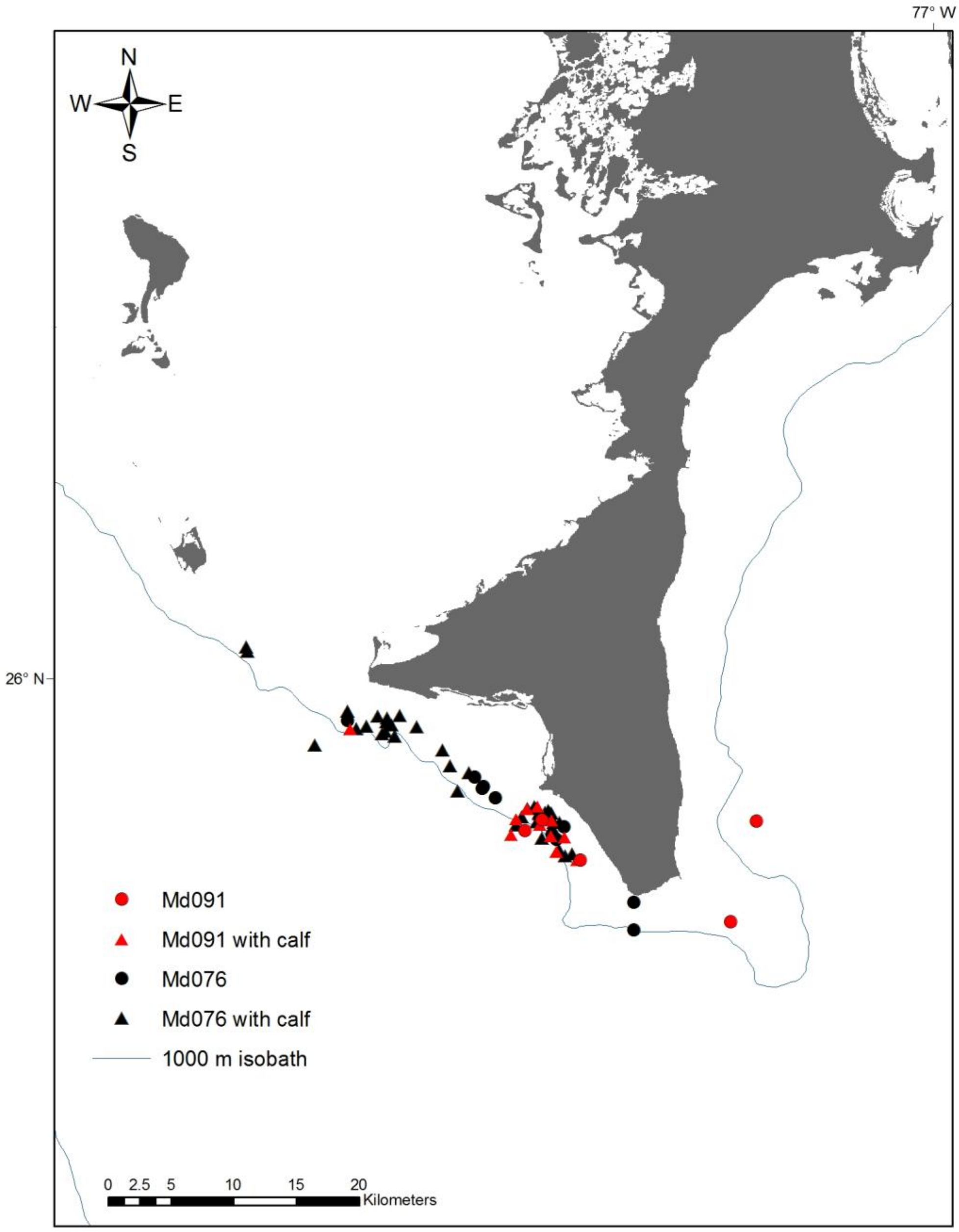

Figure 2.12. Map of the encounter locations for Md091 (in red) and Md076 (in black), when they had a calf (triangles), and without a calf (circles).

The map shows for these two animals at least, there does not appear to be preferred habitat that is dependent on reproductive state. To quantify this and expand the question to more than these two females, I created two symmetric matrices for all encounters in which there was an adult female present. One matrix detailed whether a calf was present or not in either encounter (1/0) and the other matrix had the distances between each encounter. The Mantel test did not reject the null hypothesis that there was no correlation between these two datasets (p=0.5, 10,000 permutations, Z-statistic=11718957), further suggesting that there is no general difference in habitat preference when a female is with or without a calf. If there had been preferred habitat when one was with a calf, the matrices would have correlated with shorter distances between sightings with calves.

2.3.3 Male associations with kin

There were four males in the dataset whose mothers are known, so their associations with their mothers and their siblings could be investigated. I found that with one exception, all of these males had an association index of 0 with both their siblings (n=8, range 2 to 4) and their mothers post weaning. The single exception was Md143 who was seen as an adult with his oldest sibling Md107 three times while she was nursing her first calf, resulting in an association index of 0.11. None of the other males had reached adulthood by the end of the study period, and none of their siblings have had calves to date.

2.4 Discussion

From this study we now know that adult female Blainville's beaked whales remain with other adult females in the same reproductive state for up to three years while males conform to the harem structure, a single adult male with one or more adult females. Notably, sperm whale groups were initially described as being structured in harems, because groups with more than one mature male were almost never observed (Tomilin, 1967). However, Best (1979) illustrated large males remained with groups of females for only days at a time, and it was later agreed, when photo-identification results also became available, that sperm whales did not in fact display a harem social structure, because males continuously rove between groups of females (Whitehead and Waters, 1990). In contrast to male sperm whales, which leave their natal group and move to higher latitudes at or near the onset of sexual maturity, male Blainville’s beaked whales do not leave on reaching maturity, but display philopatry, as seen by Md143 who was born during this study, and is now an adult male.

The female Blainville’s beaked whales in any given harem were shown to usually be in the same reproductive state, and have associations with one another for up to three years, about the same time it takes for their calves to wean (Claridge, 2013). Thus females’ associations with each other were typically longer lasting than with any individual male. Females were shown to have preferred associates among other females, and to avoid others, and according to my definition are exhibiting group living because they are having repeated interactions, and therefore forming relationships.

Harems are usually correlated with breeding. Male greater spear-nosed bats *(Phyllostomus hastatus)* can remain with their harem for more than three reproductive cycles, and sire over 50 offspring during their lifespan, whereas males who reach adulthood and do not acquire a harem, fail to reproduce (McCracken and Bradbury, 1977). Harems in Blainville’s beaked whales however appear to be an exception, as they are certainly not correlated solely with breeding. Blainville’s beaked whale males join and leave groups of females when the females have young calves and are most likely lactating, and therefore not available for mating. Despite the male remaining with these lactating females for up to a year, Blainville’s beaked whale calves are not weaned for approximately three years. So why does a male invest in the same female group for such a long time when he obviously has no mating opportunity?

While males associate with groups of females for access to mating, I have two hypotheses why a male might have long-term social associations with females with dependent calves. The first is that the male is the father of one or more of the calves in the group. Temporal gaps in the effort timeline in this study make it challenging to fully address this possibility. If a male was not seen associating with a female before she had a calf, it does not mean they did not associate, just that it was not observed. Moreover, it cannot be proven that a particular adult male has or has not sired a certain females' calf using photo identification techniques alone, as this can only be confirmed through genetic testing – a clear next step towards investigating this paternal hypothesis. However, there is no known case of paternal care in any cetacean, with the possible exception of another Ziphiid, Baird's beaked whale (*Berardius bairdii*) (Kasuya *et al.*, 1997), which makes this hypothesis, although possible, a priori unlikely.

An alternative hypothesis is that the males are not the fathers of the calves in their harems. One explanation for this could be social philopatry, with males associating with their mothers or female siblings when they have calves, as has been shown in killer whales (Baird, 2000). This may be a similar strategy to that suggested by Kasuya *et al.*, (1997) for Baird's beaked whales, where confidence of paternity may be low and therefore males invest in the care of close relatives by remaining with them. This could also explain why an adult male, Md143, was observed associating with his sibling only once she had a calf. Although based on a single related pair, this study may have revealed the first evidence of social philopatry in Blainville's beaked whales.

Adult male Blainville's beaked whales in this population show lower site fidelity than adult females (Claridge, 2013), and likely have a larger range. This suggests that the function of harems is a female defence by the males as opposed to a resource defence, i.e., the males are not defending a particular area, as this would have resulted in higher site fidelity. The evolution of beaked whale tusks as 'battle teeth' (Heyning, 1984) gives them effective weapons to defend a group of females, and polygynous males who compete for mates, particularly harems, are said to have the biggest weaponry of all, with bigger teeth than females (Lincoln, 1994). Therefore having paternity of one or more of the calves in a harem seems plausible. However, the cost of the frequent fighting the males may have to undergo to maintain and protect these harems is unknown, but may lead to a lower adult male survival (Claridge, 2013).

Although it is not known why males choose particular harems, this study has given some understanding regarding the female associations within harems. Here, due to the extreme sexual dimorphism in Blainville’s beaked whales, I was able to distinguish between adult females and subadult males, therefore allowing the adult females to be assigned to a distinct age and sex class. This was a constraint in Gowans (2001) study of northern bottlenose whales, as subadult males and adult females of that species cannot be distinguished in the field, therefore limiting some sex/age-class analyses.

Females within some mammal harems are related, as in gelada baboons (*Theropithecus gelada*), which have such strong bonds that they control a male’s access to a female, allowing access when the female shows a preference for a certain male (Dunbar, 1984). Alternatively in hamadryas baboons (*Papio hamadryas*), the males kidnap and herd the females to form their harems, therefore the females are unrelated and affiliate more with the harem male than the other females (Abegglen, 1984). Other mammal harems contain females of differing reproductive states. In plains zebra *(Equus burchellii),* the lactating females in the harem are the ones that drive movement (Fischhoff *et al.*, 2007), as presumably they have the greatest motivation to move to increase foraging opportunities and find water. In the zebra harems however, there are no consistent leader positions as there is no history of relationships (Fischhoff *et al.*, 2007). Choices of associations with harems can therefore vary dramatically and can be driven by extrinsic environmental and social factors.

The females in Blainville’s beaked whale harems are not apparently forced into the harem, and there is no evidence they are close relatives, although the sample sizes and genetic analyses to date have been limited (Phillip Morin, SWFSC, U.S.A, pers. comm.). According to my results, females appear to choose their associates based on shared reproductive state rather than relatedness. Both the anecdotal case of Md076 and the analysis comparing dyads in different reproductive classes suggest this to be the case. Females may associate in a group with others in the same reproductive state because they share similar requirements for food and protection (Connor *et al.*, 2000). Dolphins appear to be one of only a few species that form groups based on shared reproductive state, with common bottlenose dolphins (*Tursiops truncatus*) and Indo-Pacific bottlenose dolphins *(Tursiops aduncus),* both apparently influenced by reproductive state in their associations (Wells *et al.*, 1987;

Möller and Harcourt, 2008). However these groups are not harems, as they do not contain males.

Group living is expected to evolve when the benefits outweigh the costs. There is evidence that some delphinids prey on different food items in different reproductive states, with pan-tropical spotted dolphins (*Stenella attenuata*) preferring flying fish during lactation but squid during pregnancy (Bernard and Hohn, 1989). Therefore if lactating Blainville's beaked whales have prey preferences specific to their reproductive state, the combination of being in a group and also foraging in synchrony, may be benefit enough to select for group living. Additionally, single adult females who associate with mother-calf pairs may incur an energetic cost by not foraging at optimal times, or for optimal durations (Conradt and Roper, 2000). Therefore grouping with females in the same reproductive state could maximise foraging efficiency for that state, without being constrained by individuals in a different state. This idea could be tested using field methods capable of estimating the girth of all females in a harem group using laser measurements (Durban and Parsons, 2006) or aerial photogrammetry (Perryman and Lynn, 1993); I would expect female girth to be more similar intra-group than inter-group.

All four calves that became adult females during the study period had, as adults, association indices of zero with their mother (Table 2.10). However, in all cases, by the time the calves had reached sexual maturity, their mothers had either died or emigrated from the study site. A slight caveat to this was Md106 and her calf Md107. The last day Md106 was sighted was the same day Md107 was first seen as an adult female, however they were not sighted in the same group. Given that emigration of adult females has been shown to be extremely low for this population (Claridge, 2013), this pattern could suggest that female Blainville's beaked whales do not have long post reproductive lives.

These results suggest Blainville's beaked whales have a social strategy not observed in other marine mammals thus far. Group living in this species may result from possible variation in foraging tactics with reproductive state, and the advantages of avoiding predation by being in a group. It may also be driven by the ability of their young to dive immediately for relatively long durations (discussed further in Chapter Five). Although this study identified multi-year temporal bonds and some understanding of those bonds amongst females, genetic studies are necessary to advance our understanding of the role males play in Blainville's beaked whale harems.

The hypothesis that social complexity is a driver for communication complexity across taxa (Freeberg *et al.*, 2012), these results could suggest that communication signals serving to indicate sex, possibly fitness of males to attract females to form a harem, and to warn off other potential competitor males might be selected for. Additionally, there may be a cue that indicates the reproductive state in females, and even a cue to indicate relatedness to aid in avoiding inbreeding or in reuniting with relatives to provide care for related calves. For these reasons, the rest of this thesis is dedicated to the investigation of communication in Blainville's beaked whale vocalisations.

Chapter Three

3 ATYPICAL BROADBAND SOUNDS PRODUCED BY BLAINVILLE'S BEAKED WHALES (*MESOPLODON DENSIROSTRIS*)

3.1 Introduction

Blainville's beaked whales (*Mesoplodon densirostris*) spend large amounts of time submerged at depths where visibility is very limited (Tyack *et al.*, 2006; Baird *et al.*, 2008). They dive in small groups, (mean group size = 4.1, standard deviation = 1.9, Claridge, 2006) and have an unusual social structure (Chapter Two). Some cetacean species, such as killer (*Orcinus orca*) and sperm (*Physeter macrocephalus*) whales have a stable matrilineal social structure, preserving associations for decades (Whitehead, 2003). In contrast, smaller dolphins have a fission-fusion social structure (Connor *et al.*, 2001), where associations can change minute by minute. Both types of social structure are apparently mediated by acoustic communication signals that vary in conjunction with that social environment, namely group dialects and individual signatures for these two cases (Tyack and Sayigh 1997). Maintaining group cohesion over timescales of months and years as Blainville's beaked whales are capable of doing, would likely require some mechanism for remaining in contact outside visual range. The most likely candidate for maintaining group cohesion is some form of acoustic communication, given its ubiquitous occurrence in other odontocetes.

3.1.1 Beaked whale vocalisations

All odontocetes make echolocation sounds, but non-echolocation sounds have rarely been described for Blainville's beaked whales (Caldwell and Caldwell, 1971; Rankin and Barlow 2007; Aguilar de Soto *et al.*, 2011; for similar reports in Baird's beaked whales (*Berardius bairdii*) see Dawson *et al.*, 1998). Most recently Aguilar de Soto *et al.*, (2011) reported 'rasps', a series of frequency-modulated clicks with short inter-click-intervals (ICI) occurring on average twice per dive, and two whistles, from a sample of 102 hours of acoustic data recorded from digital recording tags placed on seven Blainville's beaked whales in the Canary Islands, Spain.

This chapter identifies sounds produced by Blainville's beaked whales that are plausible candidates for communication signals as they are used by all individuals studied and on all their deep dives, unlike rasps (Aguillar *et al.*, 2011) which are not ubiquitous to all deep dives and therefore may be used for a more specific function.

3.2 Methods

3.2.1 Data collection

Acoustic recording tags (DTags; Johnson and Tyack, 2003) sampling at a rate of 192 kHz were attached using suction cups to five free-ranging Blainville's beaked whales during five separate encounters between 2006-2007, at the Atlantic Undersea Testing and Evaluation Centre (AUTEC) test range in the Tongue of the Ocean (TOTO) off Andros Island in the Bahamas. The five encounters consisted of three different group compositions; one group comprised two adult females, a subadult and a calf, another encounter consisted of a single adult female, and three encounters involved two adult females and an adult male, resulting in four tags on adult females and one tag on an adult male (Table 3.1). The five tags recorded 89.46 hours of acoustic data that were visually and aurally processed by two independent observers using Adobe Audition CS6 and Matlab R2014a (8.3.0.532).

Table 3.1. Details of tag deployments. The catalogue number, with age/sex class in brackets (AM = adult male, AF = adult female, SA = subadult).

Tagged animal	Others in group	Date	Recording duration (hh:mm:ss)	Number of Dives >100m
Md539 (AM)	AF+AF	5-Sep-2007	17:36:41	4
Md518 (AF)	AF+SA+calf	23-Oct-2006	19:23:20	4
Md524 (AF)	None	15-Aug-2007	17:23:18	4
Md515 (AF)	AF+AM	2-Sep-2007	17:28:32	4
Md527 (AF)	AF+AM	5-Sep-2007	17:35:31	6

3.2.2 Data processing

Sounds were identified from spectrogram visualisations of the acoustic records and their times of occurrence used to extract corresponding depth data from the tag records. All sounds with the exception of regular echolocation sounds, buzz clicks (a series of clicks with extremely short ICIs and little frequency modulation), and rasps (Aguilar de Soto *et al.*, 2011), were noted (all data trawling was carried out by D. Talbot). As the DTags had two hydrophones, the time difference of arrival of sounds at the two receivers was used to calculate the angle of arrival of acoustic signals at the tag (Johnson *et al.*, 2009; Jensen *et al.*, 2011). Consistency in the direction a sound is arriving from helps determine whether the sounds are coming from the tagged animal. The angle-of-arrival was measured for each sound where possible. Overlapping sounds (conspecific echolocation sounds or flow noise) or a poor signal-to-noise ratio (SNR) meant it was not possible to obtain this measurement for every sound of interest. Additionally, I accessed archive data recorded during the dive times of the tagged whale groups from 82 bottom-mounted hydrophones on the AUTEC tracking range (Moretti *et al.*, 2006), to search for detections of other cetacean species within an approximate six nautical mile radius (three hydrophone range) of the tagged whale group. I used the Raven software (version 1.4, Cornell Lab of Ornithology, 2005), with spectrogram settings of 1024 point FFT, Hamming window and a 512 point overlap, to measure the features of sounds recorded by the tags directly from the spectrograms. The highest frequency with significant energy (‘high frequency’ in Raven, henceforth called maximum frequency, in kHz), duration in seconds, and the ICI from the start of one click to the start of the next click, where clicks could be clearly identified in the signal waveform, were measured for each sound. Tag flow noise at low frequencies (Johnson *et al.*, 2009) overlapped the lower end of the signals’ bandwidth, which prevented me from making sensible bandwidth, mean and minimum frequency measurements of the signals. Finally, I measured the root mean square (RMS) received levels of the sounds in Matlab. Apparent source levels of the sounds were calculated following the method of Aguilar de Soto *et al.*, (2011) where “apparent source levels were back-calculated from the signal at the tag assuming spherical spreading over the 2 m separation between the tag and the sound source” (page 10). This method only measures apparent levels in one direction from the sound source, and I was therefore unable to assess whether the production of the sounds was omnidirectional or otherwise.

3.3 Results

3.3.1 Sounds identified

I identified four different types of sounds in the recordings that were not previously described echolocation sounds, buzzes or rasps, comprising 146 sounds in total. Two types, A and B, were produced by the adult male (Figure 3.1), and two others, C and D, by the adult females (Figure 3.2). Type A sounds are broadband signals with strong amplitude modulation and a sharp onset, with most energy below 15 kHz, (Figure 3.1.i). Type B sounds have an increasing bandwidth and are a set of clicks, on average nine, with a large ICI (0.17 s) relative to buzzes (0.012 s; Johnson *et al.*, 2008). Type C sounds are broadband with amplitude modulation, with the pulses having apparent energy peaks at approximately 5 kHz, 20 kHz and 45 kHz. Finally, type D sounds are similar to type A sounds, but with approximately a third of the bandwidth and with almost all energy during the first half of the sound, and below 30 kHz.

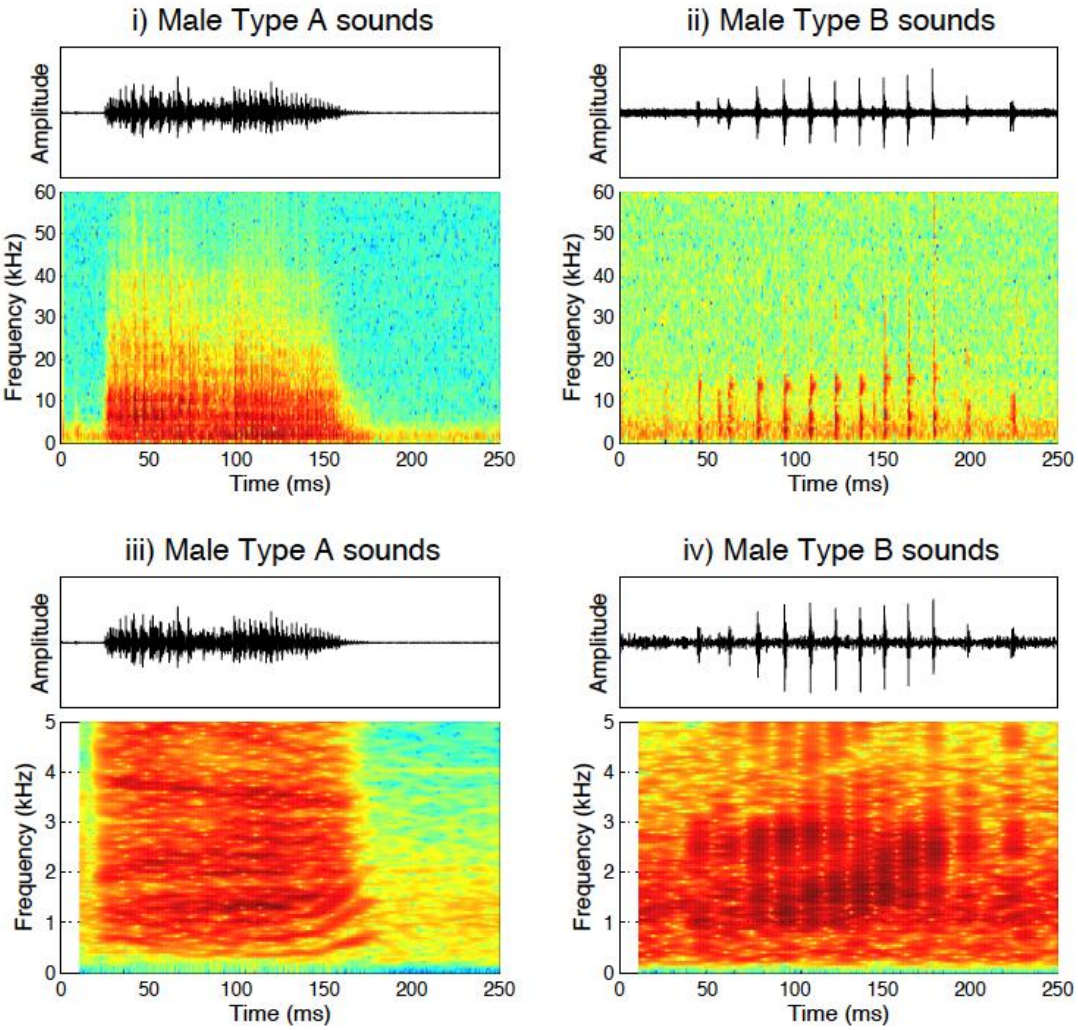

Figure 3.1. Waveforms and spectrograms for both the male’s sounds, A and B, showing both the full frequency bandwidth with a highpass filter of 1kHz for each of the sounds; i) Male Type A sound and ii) Male Type B sound (Hamming 256 FFT, 64 overlap, 192kHz sample rate), and showing only the frequency bandwidth between 1kHz and 4khZ; iii) Male Type A sound and iv) Male Type B sound (Hamming 4096 FFT, 4000 overlap, 192kHz sample rate).

The pulses that make up these sounds show very different frequency content, with little or no frequency modulation, compared to regular echolocation pulses as recorded on the tags (Figure 3.3). They were also an order of magnitude lower in amplitude than the regular echolocation pulses, though Figure 3.3 has a high pass filter at 1 kHz.

Evidence that the tagged animals were the source of these sounds was derived from both the angle-of-arrival results and the fixed AUTEC hydrophone records from the area. The angles of arrival for all the sounds that were measured were highly consistent with each other and with other sounds from the tagged animal. 80% of type A and 100% of type B sounds had an angle-of-arrival within 15º of the mean for each of these types. 80% of type A and 83% of type B sounds also fell within 15º of the mean of the tagged animals’ echolocation sounds, of which five were selected from the first bout of echolocation recorded during each dive. The sounds were therefore consistently arriving from the same direction throughout. The mean angle-of-arrival for both type A and B sounds also fell within 1º of the mean angle-of-arrival for a random selection of echolocation buzzes and rasps from the tagged animal. One of the female tags had only one working hydrophone channel, therefore making it impossible to analyse the angle-of-arrival of sounds from that tag. However, 75% of all type C sounds where the angle-of-arrival could be measured arrived within 15º of the mean of those sounds, and the angle-of-arrival measurements of all type C sounds were within 2º of the closest measurable tagged animal sounds. Type D sounds had too low a SNR to measure the angle-of-arrival accurately. Interestingly, 77% of D sounds were followed by C sounds with an average delay of only 1.2 seconds, suggesting some relationship between these two sounds.

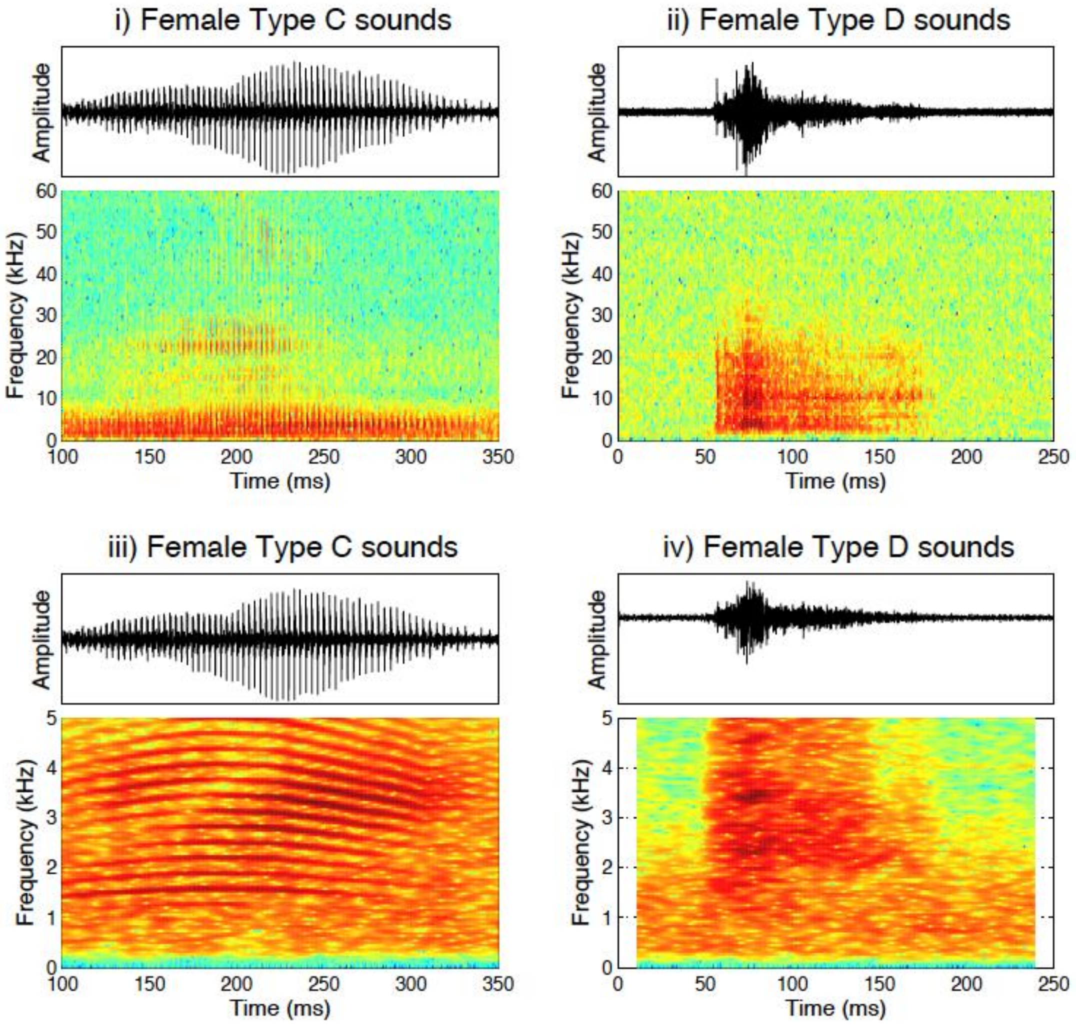

Figure 3.2. Waveforms and spectrograms for both the females sounds, C and D, showing both the full frequency bandwidth with a highpass filter of 1 kHz for each of the sounds; i) Female Type C sound and ii) Female Type D sound (Hamming 256 FFT, 64 overlap, 192 kHz sample rate), and showing only the frequency bandwidth between 1 kHz and 4 khZ; iii) Female Type C sound and iv) Female Type D sound (Hamming 4096 FFT, 4000 overlap, 192 kHz sample rate).

On three of the four tagged male dives, delphinids were detected within an approximate six nautical mile range on the AUTEC hydrophones (Appendix 3.1). These detections were purely acoustic, and no species confirmation was obtained visually, so it was not possible to accurately locate or identify the source groups. No characteristic delphinid signals (tonal whistles or broadband echolocation clicks) were detected either aurally or visually on any of the tag recordings analysed. Furthermore, on one of the male’s dives, there were no delphinids detected within six nautical miles, but both type A and B calls were recorded on this dive at the same amplitude as the other dives. During 13 of the 18 tagged female dives there were no other species detected within 6 nautical miles of the tagged group on the AUTEC hydrophones. On the remaining five dives, delphinids were detected within an approximate six nautical mile range on the AUTEC hydrophones (see Appendix 3.1), but C and D type sounds were recorded at similar amplitudes on dives with and without overlapping delphinids, so there was no pattern of heterospecific presence consistent with them being the source of the sounds I describe.

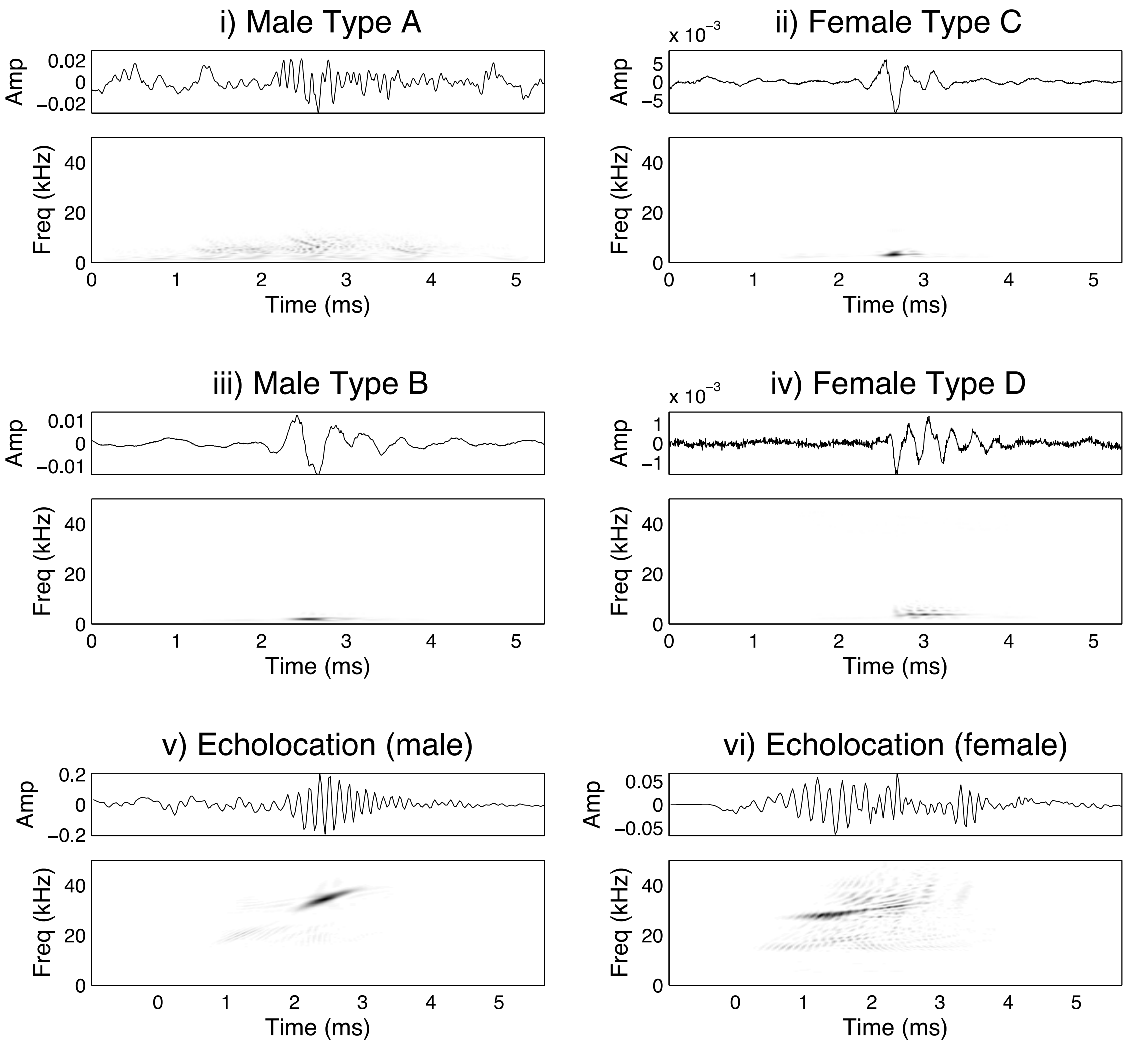

Figure 3.3. Waveforms and wigner plots for all four sound types, A, B, C and D, showing a single pulse from each sound, and a single click from a male and female, with a highpass filter of 1 kHz for each of the sounds; i) Male single pulse from Type A sound, ii) Female single pulse from Type C sound, iii) Male single pulse from Type B sound, iv) Female single pulse from Type D sound, v) Male single echolocation pulse and vi) Female single echolocation pulse.

A further possibility is that the sounds represent flow noise associated with the animal making sharp manoeuvres in the water. The tags have an accelerometer that records the animal’s movement on three orthogonal scales: pitch, roll and heading (Tyack *et al.*, 2006). Inspection of the dive time-depth profiles of each animal during production of these sounds however showed no relationship between occurrence of the sounds and strong variation in the animal’s pitch, roll or heading (Figure 3.4.iii, iv).

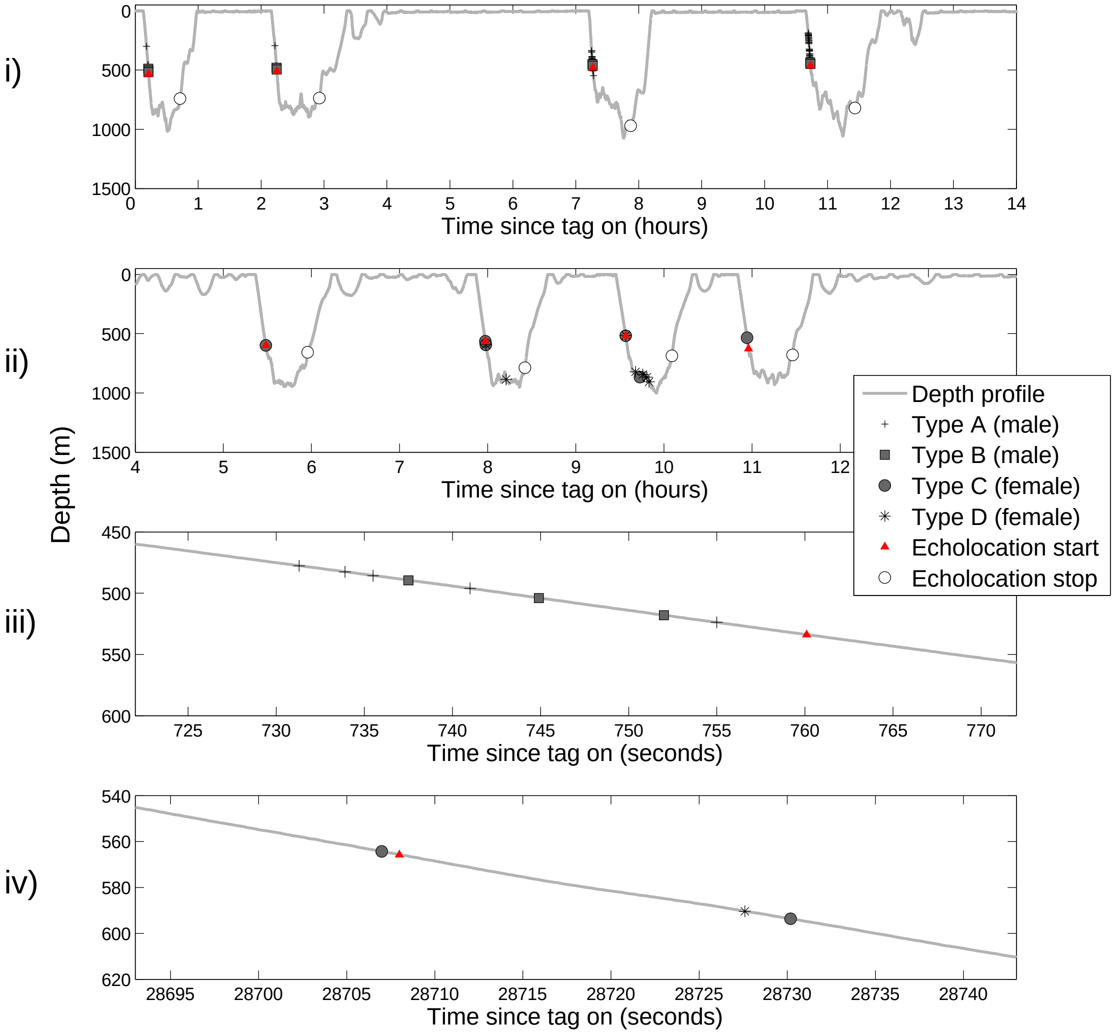

Figure 3.4. Time-depth profile plots showing the distribution of sound production for (i) the adult male (Md539, tag attachment at 14:31:23 local time), (ii) one of the adult females (Md527, tag attachment at 09:55:17 local time), and (iii) and (iv) fine-scale plots of the first dives by the (i) male and (ii) female respectively. (This figure prepared by L. Hickmott)

Of the sounds recorded, 96% of those from the male and 42% of those from the females were recorded before the onset of regular echolocation, and the remainder were made between series of echolocation sounds during the foraging phase of the dives (Table 3.2). The sounds I report occurred between 109 and 1289 m of depth, and always on the descent phase before the deepest point of the tagged animal's dives.

Table 3.2. Number of each sound type produced, by animal, relative to the commencement of regular echolocation clicking.

Tagged animal	**Sound type**	**# before clicking commences**	**# after clicking commences**	**Total**
Md539 (AM)	A	63	3	66
	B	9	0	9
Md518 (AF)	C	3	0	3
	D	1	0	1
Md524 (AF)	C	6	12	18
	D	8	11	19
Md515 (AF)	C	4	7	11
	D	3	3	6
Md527 (AF)	C	4	2	6
	D	1	6	7
TOTAL		**102**	**44**	**146**

The male produced 66 type A sounds and 9 type B sounds over four dives. The four females produced a total of 38 type C and 33 type D sounds over 18 dives (Table 3.3). The highest broadband RMS apparent source level for type A sounds, the loudest of the four types recorded was 132 dB re 1µPa @ 1m, and 130 dB for sound type B. The broadband RMS apparent source level for the type C sound was 124 dB, and 125 dB for sound type D. These levels should be regarded as indicative only, as there is no information available on signal directionality, and low frequency water-flow noise from the tag itself (Johnson *et al.*, 2009) overlaps the frequency bandwidth of the signals. These sounds do not correspond to the rasps or whistles described by Aguilar de Soto *et al.*, (2011), as they are much shorter in duration (mean duration 0.23 s versus rasp mean duration of 0.6 s), and have distinctive frequency content, although they are similar in being broadband and amplitude-modulated. I did not detect any whistles in the recordings.

Table 3.3. Summary of call parameters and production depth by animal and sound type, showing standard deviations (sd) for each in the same units.

Tagged animal	Sound Type	Maximum freq. (kHz) / (sd)	Duration (s) / (sd)	Mean ICI (s) / (sd)	Mean Depth (m) / (sd)
Md539 (AM)	A	60.3 / (17.4)	0.14 / (0.05)	-	298 / (118)
	B	53.2 / (20.4)	0.16 / (0.03)	0.017 (9) / (0.002)	417 / (99)
Md518 (AF)	C	74.0 / (8.9)	0.33 / (0.05)	-	475 / (121)
	D	40.3 / (n/a)*	0.14 (n/a)	-	533 / (n/a)
Md524 (AF)	C	54.9 / (17.4)	0.47 / (0.12)	-	522 / (99)
	D	30.2 / (7.5)	0.16 / (0.04)	-	509 / (107)
Md515 (AF)	C	37.8 / (20.7)	0.27 / (0.06)	-	751 / (224)
	D	21.9 / (6.8)	0.18 / (0.06)	-	803 / (296)
Md527 (AF)	C	63.4 / (16.1)	0.36 / (0.10)	-	612 / (129)
	D	25.8 / (12.9)	0.09 / (0.03)	-	776 / (156)

- Only one D sound was recorded from this animal

3.4 Discussion

I have described four distinct types of sounds recorded from tags placed on free-swimming Blainville’s beaked whales. The first question to address is whether these sounds were produced by the tagged animal, by other beaked whales or by heterospecifics. The angle-of-arrival analysis shows that the sound sources were at a consistent angle relative to the axis of the two fixed tag hydrophones, which was also consistent with other tagged animal sounds (identifiable because echolocation calls from tagged animals typically contain low frequency energy from tissue transmission that is not present in calls received from non-tagged animals; Johnson *et al.*, 2006). Although some of the recordings were made when delphinids were detected in the same area by other hydrophones, the pattern of their presence in relation to the occurrence of the sounds is incompatible with the notion that the sounds came from the delphinids, and I did not detect any other characteristic delphinid sounds on the recordings. I am therefore confident that these sounds were made by the Blainville’s beaked whales that carried the recording tags.

It is unlikely that these sounds are related to foraging, which is known to rely on echolocation sonar signals, as the majority of the male sounds and almost half of the female sounds fell outside of the regular echolocation period, and none of the sounds resemble any known biological echolocation signal. The functions of all beaked whale sounds are subject to speculation to some extent. However, for previously described beaked whale vocalizations, that is regular and buzz clicks, echolocation is highly likely to be the function. The recording of echoes from presumed prey items and a temporal production pattern homologous with echolocation in captive dolphins and bats (Au, 1993; Griffin, 1958), where direct observation of foraging is possible, provide a high level of confidence that echolocation to find prey is the primary function of most beaked whale signals studied to date (Johnson *et al.*, 2004). The function, if any, of the sounds I report is unknown. It is possible that they are purely physiological rather than communicative in nature and may be related to pressure changes experienced as the animal dives, or the movement of air within the nasal passages in preparation for producing echolocation signals. This seems plausible for the female type D sounds that have a low SNR, occur just prior to type C sounds and aurally sound like recycling of air similar to that observed in sperm whales (Norris and Harvey 1972). I consider this unlikely however for the other three sound types because production begins beyond the region of the water column where pressure changes are greatest, and because there is no reason, under this hypothesis, to predict the differences between the male and females that I observed. Therefore I argue it is most likely that these sounds have a communicative function, although the data I present here cannot prove this. Of course sounds with a physiological origin can still have a communicative function, serving as cues and raw material for signal evolution. These hypotheses need not be mutually exclusive either, as the sounds could have multiple functions, i.e. physiological and communicative (Gould and Lewontin, 1979). As shown in Chapter Two, Blainville’s beaked whales maintain stable small groups for up to years at a time, and they also forage together, diving and surfacing in synchrony. They may however display some special separation during actual foraging, and it may be that regular foraging echolocation sounds hold enough information to maintain group cohesion once foraging has commenced, and therefore additional communication would happen largely outside the foraging period. The female with a subadult and calf produced far fewer calls per dive (on average one per dive compared to an average of five per dive for the other tagged females), possibly because any separation between her and her calf during a dive would be limited, and therefore the need to produce communicative sounds reduced. Additionally, it may be prudent for an adult female with a calf to make fewer sounds if there was any possibility of being tracked by a predator.

Much of the behavior of beaked whales suggests that they minimize, to the extent possible in an air-breathing mammal, the amount of time they spend close to the surface. Neither do they appear to forage in the top 200 m (Johnson *et al.*, 2004). This can be understood by considering beaked whale diving behavior as an optimization across a 3-way trade-off between the risks of oxygen starvation, predation and nutritional starvation. The temporal patterns of occurrence of signalling in birds exemplified by the dawn chorus have been similarly attributed to higher energy levels in individuals at dawn (Whitten, 1982), optimal sound propagation circumstances due to lower temperatures at dawn (Brown and Handford, 2003), and taking advantage of a time when it is too dark to forage or to be located by predators (Catchpole and Slater, 1995). Overall therefore, dawn may be a good time to sing because it simultaneously minimises risk of predation and lost foraging opportunities while taking advantage of the behavioural flexibility offered by relatively high energy levels. Based on these considerations, I can ask the question where in space and time would it make sense for beaked whales to produce communicative sounds? It is reasonable to expect beaked whales to organise signal production according to similar principles: when energy or oxygen levels are high, outside of a foraging period, and at depths that are sufficient to avoid predation. Blainville's beaked whales only produce regular echolocation signals at depths below 200 m (Johnson *et al.*, 2004), possibly because this is the only region in which these animals can forage successfully, but also as an anti-predation precaution, because the signals are potential cues for killer whales and sharks in the upper water column (Madsen *et al.*, 2005, Morisaka and Connor, 2007).

The sounds observed in the present study occurred at a point within the dive cycle when all of these risks were likely to be minimized simultaneously. The whales showed little evidence of deviation in the dive profile associated with signal production (Figure 3.4.iii, iv) and they were produced at depths where the animals were too deep for their sounds to be a useful cue for predators at the surface. They also occurred in the descent phase of their deep foraging dives, when these animals have greater surplus oxygen reserves than at the equivalent depth on the ascent, and thus the largest margin for behavioural flexibility, even if sound production itself is not demanding on oxygen supplies. During the ascent animals were likely not vocalizing due to trade-offs between the risks of predation and hypoxia. Ascending to replenish oxygen would not be a time to alert a predator to their presence, given the response options for avoiding the predators are more limited because of the risk of hypoxia. Consequently, I suggest that if vocal communication was to occur among beaked whales then it would most likely happen between the depth that is likely to represent a limit for surface dwelling predators and the depth at which there is greatest prey density, i.e. during the descent phase of foraging dives. The sounds observed in the present study fit this prediction.

Finally, although I sampled one male only, it is clear that this animal made many more sounds than the females, and the sounds made by the male in the study were louder, particularly type A, than those made by the females. Aguilar de Soto *et al.*, (2011) also reported whistles only made by a male. Future work could attempt to ascertain whether this is a genuinely sexually dimorphic pattern, and try to document these sounds in a broader range of group contexts, in order to work toward testable hypotheses for their function.

The remainder of this thesis investigates the possibility of a communication role in Blainville’s beaked whale echolocation clicks.

Chapter Four

4 DO BLAINVILLE'S BEAKED WHALE (*MESOPLODON DENSIROSTRIS*) CLICKS VARY BETWEEN ANIMALS OF DIFFERENT SEX AND AGE?

4.1 Introduction

Communication is necessary for an individual's success as it provides information to aid in mating, foraging and avoiding predation and can influence other individual's behaviour in advantageous ways (Bradbury and Vehrencamp, 1998). Communication involves the production and reception of signals. Although the sounds that are described in Chapter Three are plausibly communicative signals produced by Blainville's beaked whales (*Mesoplodon densirostris*), the distance at which they are likely to be detectable by other whales is limited compared to the range beaked whale echolocation clicks can be detected (6500 m, Ward *et al.*, 2008). Additionally, the associations outlined in Chapter Two suggest the ability to identify at least the sex and age of another individual should be important, which leads me to question whether these whales produce other cues? Therefore this chapter introduces cues in animal behaviour to this thesis, with a view to the possibility of finding cues of sex and / or age in Blainville's beaked whale clicks that may provide information at greater ranges than the sex-specific sounds already described.

4.1.1 Use of cues in animal behaviour

In the study of animal behaviour, cues are traits or actions that provide a piece of information to an observer or listener whose production does not necessarily benefit the emitter, and has not been selected for because of the effects on others (Seeley, 1989). However cues in the animal world can change the knowledge state of receivers, and are therefore providing information, so can be perceived as communication (Wilson, 1975). There is an alternative view that states cues can only be communicative if the receivers responses are on average beneficial to the signaller (Owren *et al.*, 2010). Therefore this chapter will investigate whether Blainville's beaked whale echolocation clicks contain sufficient information to be considered cues of the age and / or sex of the producing individual, and not whether those cues are indeed communicative.

Cues are not intentional, for example a lizard that rustles leaves is inadvertently advertising its presence to predators. Moreover, cues attached to other behaviours happen each and every time that behaviour occurs. Wolves (*Canis lupus*) for example howl to inform the pack where to meet, and alert non-group members to stay away, however their howls also include the identity of the individual, its pack and its current state of arousal (Harrington and Asa, 2003). Similarly, bat echolocation pulses used for foraging can provide information about the identity and the sex of the animal producing the pulses (Yovel 2009). Although bats produce calls with a large overlap in frequencies between sexes, several studies have been able to show sex differences in the frequency content of a call (Guillén *et al.*, 2000; Jones, 1995; Neuweiler *et al.*, 1987). Recently an age cue was identified from acoustic parameters in African elephants' (*Loxodonta Africana*) rumbles. This cue is partly due to the relationship between the size of the elephant and the frequency it produces (Stoeger *et al.*, 2014).

In some cases cues attached to a behaviour can be highly relevant to that behaviour, for example female copulation calls made by Barbary macaques *(Macaca sylvanus)* contain information on the reproductive state of the calling female (Semple and McComb, 2000). It seems reasonable to posit the existence of such cues in female Blainville's beaked whales since they prefer to associate with other females in the same reproductive state (Chapter Two), and would therefore find it useful to identify such potential associates from a distance. It is worth noting that the majority of studies that can discriminate information from animal cues show that the information is distinguishable by the researchers, and presume therefore it is also distinguishable by the animals – experimental testing of this presumption is more difficult and therefore rarer than demonstrating the existence of a cue.

This is also true in marine mammal research. For instance, researchers can determine the size of a sperm whale (*Physeter macrocephalus*) from its clicks, using the inter-pulse-interval (IPI) of a click. A sperm whale click is multipulsed, caused by the click reflecting within the head of the whale, and therefore the IPI represents the time the click takes to travel the length of the head. The head measurement is extrapolated using historical stranding and whaling data to provide an estimate length for the whale (Gordon, 1991; Rhinelander and Dawson, 2004). However this does not tell us whether sperm whales themselves are also gleaning information regarding the size of the animal that is producing the clicks.

The exploitation of cues by a receiver is termed 'eavesdropping' (Bradbury and Vehrencamp, 1998) and is used by marine mammals both in captivity and in the wild. A bottlenose dolphin (*Tursiops truncatus*) in captivity was able to recognise a target while its melon was out of the water from another dolphin's echolocation on the target (Xitco and Roitblat, 1996). Additionally wild rough-toothed dolphins (*Steno bredanensis*) echolocated less during synchronised travel, indicating eavesdropping on accurate echoes from echolocation of a few members of the group on targets ahead of the group (Götz *et al.*, 2006). Therefore we can presume that marine mammals are informed by these conspecifics cues.

A common cue given by odontocetes (and bats) who echolocate to find food is the production of a buzz. On final approach to a prey item, echolocating animals typically increase their click repetition rate so that the click train gives the aural impression of a buzz – this is thought to provide higher resolution information to the echolocating animal during the final approach to prey. These buzzes are therefore inadvertent cues of prey encounter and capture attempts, often used by researchers (beaked whales, Johnson *et al.*, 2006; sperm whales, Miller *et al.*, 2004). Buzzes may therefore be a cue alerting eavesdroppers to the presence of prey, but their role as cues has not been explored by looking for responses of other animals to their production. Cues have not been looked for in beaked whale clicks thus far.

4.1.2 Beaked whale vocalisations

All beaked whales echolocate using clicks produced in at least partially ultrasonic frequency bands. Blainville's beaked whales produce echolocation pulses for half the duration of their deep dives (Arranz *et al.*, 2011). Two types of clicks have been described from recordings obtained with acoustic and movement suction cup tags (DTags; Johnson and Tyack, 2003) attached to individuals in the Canary Islands (Johnson *et al.*, 2004). 'Regular clicks' are evenly spaced frequency-modulated (FM) clicks made consistently throughout the base of a foraging dive and thought to be associated with a prey-searching phase (click duration = 250 μs, ICI = 200-400 ms, -10 dB bandwidth = 25-51 kHz). 'Buzz clicks' occur as occasional brief bursts of clicks with no obvious FM structure, and have a short click duration of 100 μs, and a large bandwidth of 55 kHz at -10 dB (Johnson *et al.*, 2006). These buzz clicks occur as a rapid increase in click production at the end of click trains, *ca.* 250 clicks s^{-1}, and are thought to be associated with prey-capture attempts (Johnson *et al.* 2004, Johnson *et al.* 2006; Madsen *et al.* 2005). The existing literature on beaked whale vocalisations has resulted from two different recording methods thus far, (i) towed hydrophone arrays from a research vessel (Baumann-Pickering *et al.*, 2010, 2012, 2013, 2014; Gillespie *et al.*, 2009), and (ii) DTags (Johnson and Tyack, 2003). However both methods have their own drawbacks.

Hydrophone arrays towed behind a moving vessel may only ever detect a small selection of clicks from beaked whales. This is because Blainville's beaked whales produce clicks with a narrow beam of 13° and a high directivity index of 23 dB (Shaffer *et al.*, 2013), and are constantly sweeping their head from side to side (+/-10°) whilst traveling in search of prey. Moreover, towed arrays are often used in conjunction with a survey that has particular objectives to fulfil once animals have been detected. In some cases these objectives may result in either the towed array being retrieved from the water once animals have been detected, or the ship with the towed array staying a certain distance from the animals to allow a smaller vessel to approach the group for individual animal data collection such as biopsy sampling.

In contrast, a DTag attached to an animal records every sound that animal makes. Tags are usually placed in front of the dorsal fin on a part of the animal that is likely to break the surface, allowing real-time VHF radio tracking of the animal. Because of the physical attachment, some of the sound energy received by the tag travels backwards from the sound production site in the head to the tag via the animal’s tissues. This transmission of sound through tissue means the sound the tag records is not necessarily the same sound the animal emits into the water - it will be absent of the effects of filtering or beam forming that affects the sound energy emitted in front of the animal, and contain additional low frequency energy that only transmits via the animal’s tissues. Therefore DTag recordings are distorted and not representative of a far-field recording of a click whose spectrum, duration and waveform are a more reliable representation of what another animal would hear (Johnson *et al.*, 2009).

This study took advantage of an opportunity to analyse far-field beaked whale recordings of known individuals from multiple stationary hydrophones at the Atlantic Undersea Testing and Evaluation Centre (AUTEC) range in the Tongue of the Ocean (TOTO), Bahamas (Figure 4.1). Previous studies of Blainville’s beaked whales using these sensors include a density estimate calculation which mapped acoustic detections of beaked whales and applied estimates of average group size (Moretti *et al.*, 2006); the calculation of detection and localisation capabilities using the time-difference-of-arrival of clicks on the sensors from a DTagged animal (Ward *et al.*, 2008); monitoring the displacement of whales during multi-ship military exercises and correlating the cessation and recommencement of foraging clicks on the sensors with the exercise activities (McCarthy *et al.*, 2011); monitoring movements of whales during both multi-ship military exercises and simulated naval sonar using satellite tags and DTags to track whale movements (Tyack *et al.*, 2011); and estimating the effective beam width (13°) of beaked whale clicks using clicks from DTagged whales recorded on far field sensors (Shaffer *et al.*, 2013). However, there has not yet been a study that has looked for potential cues in beaked whale echolocation clicks.

To investigate for cues, click parameters were chosen by examining the literature on cues from bat vocalisations, and the literature that has determined species-specific differences in beaked whales, to look for parameters that may also provide cues to conspecifics. The -3 dB and -10 dB bandwidths, duration (as measured within the -10 dB bandwidth) and peak frequency (the frequency band containing the most energy) parameters have been used to distinguish between Cuvier’s (*Ziphius cavirostris*), Gervais (*Mesoplodon europaeus*) and Blainville’s beaked whales (Zimmer *et al.*, 2005; Gillespie *et al.*, 2009; Johnson *et al.*, 2004). Frequency parameters have also been shown to correlate with sex and age differences in the rufous horseshoe bat (*Rhinolophus rouxii*) (Jones *et al.*, 1992; Neuweiler *et al.*, 1987). The sweep rate (the rate at which a click gets from it’s lowest to highest frequency) differentiates individuals in greater mouse-eared bats (*Myotis myotis*), and the initial frequency of their echolocation pulses also resulted in a better than chance classification of individuals (Yovel 2009).

The potential presence of identity, size, sex and / or age-class cues in beaked whale clicks is biologically interesting as it could provide a greater understanding of how the whales are forming and maintaining stable groups over periods of years. Cues could potentially inform an adult male not only if another male is accompanying a group of females that he is detecting, but also the size and/or fitness of that male. Cues could aid in avoiding inbreeding in a population exhibiting natal philopatry, as the Blainville’s beaked whales do (Claridge, 2013). Cues could also be the key to adult females finding other adult females in the same reproductive state, with whom they prefer to associate (Chapter Two). Additionally, cues from echolocation clicks that can be picked up using passive acoustic monitoring tools would be very useful in population assessments. They could allow for a reliable classification of vocalising individuals into age, sex or even reproductive state classes. This information would give a much more detailed picture of a populations’ status, and also aid in direct mitigation of anthropogenic impacts. As studies continue to investigate the consequences of noise on this species, with displacement from preferred foraging areas already a known result (McCarthy *et al.*, 2011; Tyack *et al.*, 2011), mitigation could be modified real-time with information from cues. If a mother calf pair is present, for example, mitigation could be severely increased and some noise productions stopped and postponed.

4.2 Methods

4.2.1 Field methods for data collection

All data for this study were collected at the AUTEC range. Groups of beaked whales were detected and tracked acoustically on the AUTEC hydrophone array by the Marine Mammal Monitoring on Navy Ranges group (M3R). M3R is a U.S. Office of Naval Research funded program that carries out marine mammal monitoring on United States navy ranges, employing a variety of sound engineers, biologists and physicists. On the AUTEC range, the M3R group use an energy detector based on the fast Fourier transform (FFT) to identify beaked whale clicks on one or more hydrophones (Ward *et al.*, 2008). The detector uses a 2048 point FFT with 50% overlap, giving a frequency resolution per bin of 46.875 Hz and a time resolution of 10.67 milliseconds (ms). The magnitude of each bin of the FFT is compared to the noise varying threshold for that bin, and a detection is reported if the magnitude is greater than the threshold (Ward *et al.*, 2008). The hydrophone array consists of 82 sensors spaced roughly 4 km apart (Moretti *et al.*, 2006), with a mean depth of 1630 m (Ward *et al.*, 2011). These hydrophones cover an area of approximately 1500 km^2, and are single channel, with a sampling rate when digitised of 96 kHz. Sixty eight of the hydrophones have a usable bandwidth from 50 Hz to approximately 48 kHz, and the remaining fourteen have a smaller bandwidth from 8 kHz to around 50 kHz (Ward *et al.*, 2008). The M3R group was housed on shore with the ability to track whales on all 82 hydrophones, and conveyed locations of groups of whales via VHF radio to the field research team who were on a small (5.5 m) rigid hull inflatable boat.

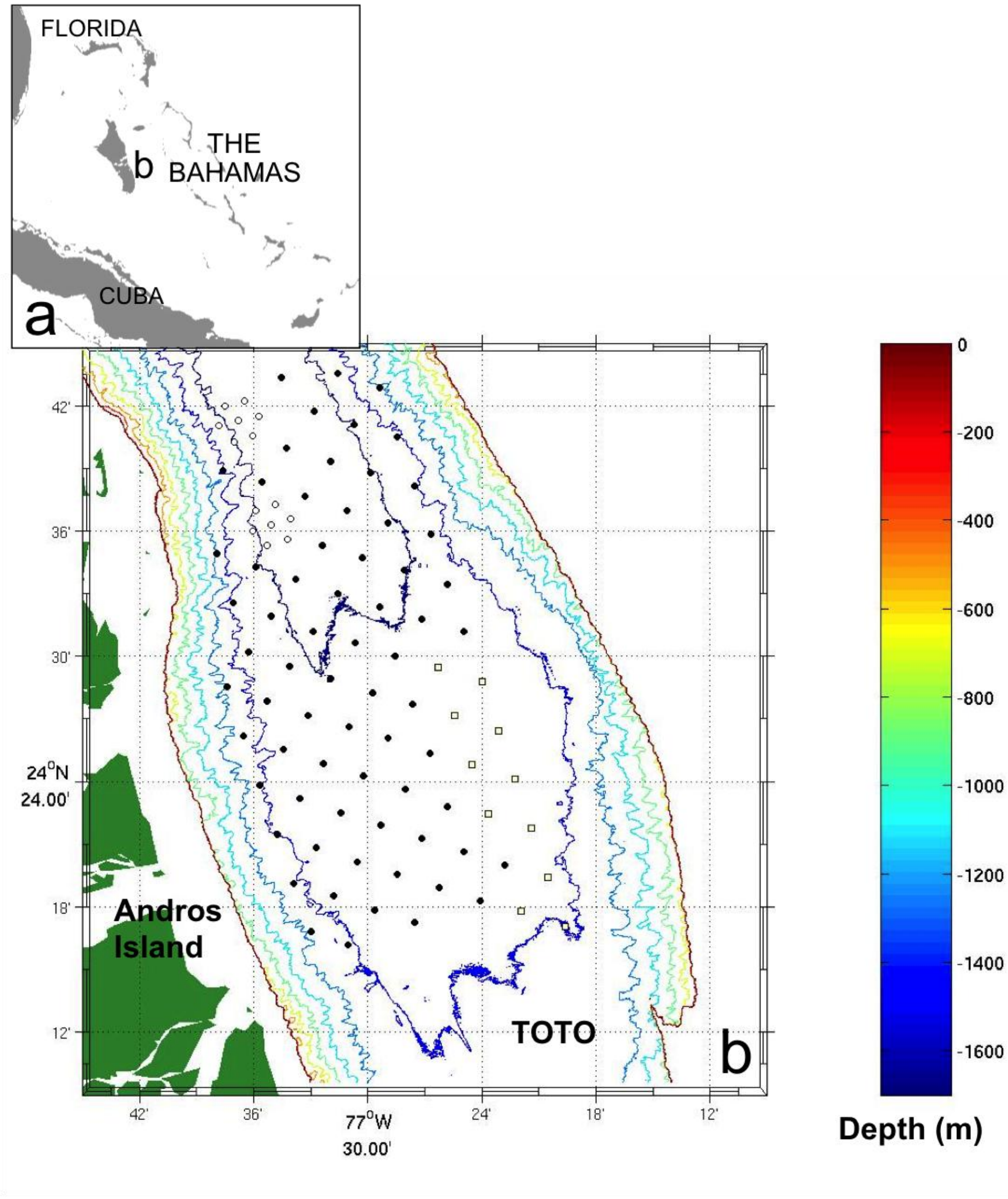

Figure 4.1. (a) Map of the Bahamas archipelago showing the study area, (b) TOTO, its bathymetry, and the AUTEC hydrophone range, with each dot representing one of the 82 hydrophones spaced over 1500 km^2.

Beaked whales click for approximately 20-30 minutes per dive (Madsen *et al.*, 2005; Tyack *et al.*, 2006), and typically surface ten minutes after they stop clicking (Arranz *et al.*, 2011; Tyack *et al.*, 2011). The boat team was informed by the M3R group when beaked whales they were detecting on one or more hydrophones ceased clicking, and were provided the last location where clicking had been detected. The whales were typically sighted on the surface of the water by the boat team approximately ten minutes after the cessation of clicking, within a mile of the last location provided by the M3R group. Blainville's beaked whales spend on average 92 minutes between deep foraging dives carrying out several shallow dives (Tyack *et al.*, 2006). During this period, the focal whales were approached and photo-identification photos were taken using Nikon D200 digital SLR cameras with a fixed 300 mm or a 70–200 mm lens.

Acoustic recordings were made from the hydrophones that detected clicks from the group of whales the boat team had visual encounters with. These recordings were attributed to the whales that were visually sighted because of the correlation between clicking and surfacing times. As well as surfacing ten minutes after the cessation of clicking, the whales begin clicking within approximately ten minutes of commencing a foraging dive. Prior to a foraging dive, beaked whales remain on or near the surface for a longer duration than previous inter-shallow dive surfacings, and swim non-directionally (sometimes termed 'milling'). The whales then begin their foraging dive by exhibiting a noticeably stronger exhalation, and leave the surface with their body arching high out of the water. This behaviour allowed the boat team to inform the M3R group ashore of the time and location that the whales dove, prompting them to monitor nearby hydrophones for the start of clicking.

As a second measure of confidence that the acoustic recordings were from the whales that were visually sighted, all marine mammal detections from nearby hydrophones were provided by the M3R group. When there was another group of beaked whales detected by M3R from hydrophones adjacent to the ones being used for this analysis, the recordings were not used for the duration of the temporal overlap, removing any possibility of analysing clicks from whales other than those visually identified.

Each group of whales may have been recorded on more than one hydrophone during each of their foraging dives. The animals produce their clicks in a narrow 13° wide beam centred on the main anterior-posterior axis of the animal, in which the majority of the click energy is concentrated. Typically, such 'on-axis' sound levels are 23 dB greater than levels recorded outside the main beam (Shaffer *et al.*, 2013).

The animals also move their head and therefore this beam, -10° to + 10° throughout their foraging dives (Shaffer *et al.*, 2013), so the actual recording aspect within which the high sound levels may be received is wider than 13°. Therefore different clicks in a dive will be picked up on different hydrophones, depending on the direction the whale is pointing. On-axis clicks of Blainville's beaked whales can be detected on the AUTEC hydrophone array at ranges of up to 6500 m (Ward *et al.*, 2008), however the probability of detecting off-axis clicks is reduced to less than 0.2 for distances greater than 3000 m (Ward *et al.*, 2011). Therefore there may be a small number of cases within the dataset analysed here where the same click is being compared to its own off-axis version. However, animal receivers hear clicks from different orientations, therefore clicks produced at an off-axis orientation to the receiver should still contain information if reliable cues exist (Soldevilla *et al.*, 2008). Therefore my hypothesis that cues exist to sex, age or individual identity in these clicks requires, if they are to be generally usable by listeners, that these cues be largely invariant to recording aspect, and therefore both on and off-axis clicks from the same individual should be representative of that individual. However, much of the data is filtered to remove more off-axis clicks to aid in detecting cues, although this filtering is not rigorous to just leave purely on-axis clicks, i.e. those with sound levels 23 dB greater than other clicks (Shaffer *et al.*, 2013).

4.2.2 Data selection

4.2.2.1 Photographs

This analysis only used acoustic recordings that were coincident with visual encounters with whales in which every individual in the group was photo-identified. There were at least three observers on the boat all agreeing on group sizes, which are typically small (median = 4; Chapter Two), and animals remain relatively close together at the surface, within ten body lengths of each other. Group size estimates confirmed with photo-identification are therefore almost always accurate.

The photo-identification analysis categorised individual whales into sex and age-classes (Claridge, 2013), and all photographs were matched and added to an existing photo-identification catalogue (see Chapter Two for further details on these methods). Only groups where all individuals in the group had a certainty grading >1 and a photograph from that sighting with a quality grading >1 were used.

The analysis of clicks between animals of differing sex was carried out on adults only, which avoided confounding a possible sex cue with an age cue. However, because there were not enough sub-adults in the dataset, analysis of clicks between adults and subadults for an age cue included both sexes.

4.2.2.2 Acoustic recordings

The acoustic recordings were received from the M3R group in WAV format, and processed through the default beaked whale click detector in the PAMGUARD software (www.pamguard.org, Gillespie *et al.*, 2008). A threshold trigger selected sounds significantly greater than background noise (>10 dB signal-to-noise ratio (SNR)), and a frequency based bandwidth classifier selected clicks with energy concentrated in the 25-40 kHz band. A detection was registered when the SNR exceeded the threshold parameter. Having a relatively high threshold trigger of 10 dB helped to remove extremely off-axis clicks from the dataset that would be subject to off-axis attenuation which could cause click characteristics to vary sufficiently for the detector not to detect the click anyway.

A receiver operating characteristics (ROC) analysis was carried out comparing manually selected detections of beaked whale clicks by a human observer to the output of the PAMGUARD automatic detector. Each acoustic file that had more than 100 clicks detected by PAMGUARD was analysed manually for one percent of the file’s duration. Manual detection consisted of visually examining waveform and spectrogram views in Adobe Audition CS6 (4096 point FFT with a 75% overlap and Hamming window). Indicators of a true or false beaked whale click included start frequency (e.g. 20-30 kHz), inter click interval (e.g. 200-400 ms), frequency modulation (e.g. 25-51 kHz), and a good visual SNR within the 25-50 kHz energy band. Within each file, manual detection started from the first set of clicks with a good SNR identified by the observer, and lasted for one percent of the file’s duration.

In addition to this dataset, two whales, a single adult male and a single adult female, were tagged in TOTO in 2007 with DTags (Johnson and Tyack, 2003), and their clicks were simultaneously recorded on the AUTEC hydrophone array. Clicks on the hydrophone array were attributed to each whale using the time of emission of each click from the DTag (Shaffer *et al.*, 2013). This method thus provided examples of clicks recorded by the AUTEC hydrophone array from animals of known age class and sex (Figure 4.2), and the clicks from the hydrophones for both whales were provided to me by the M3R group.

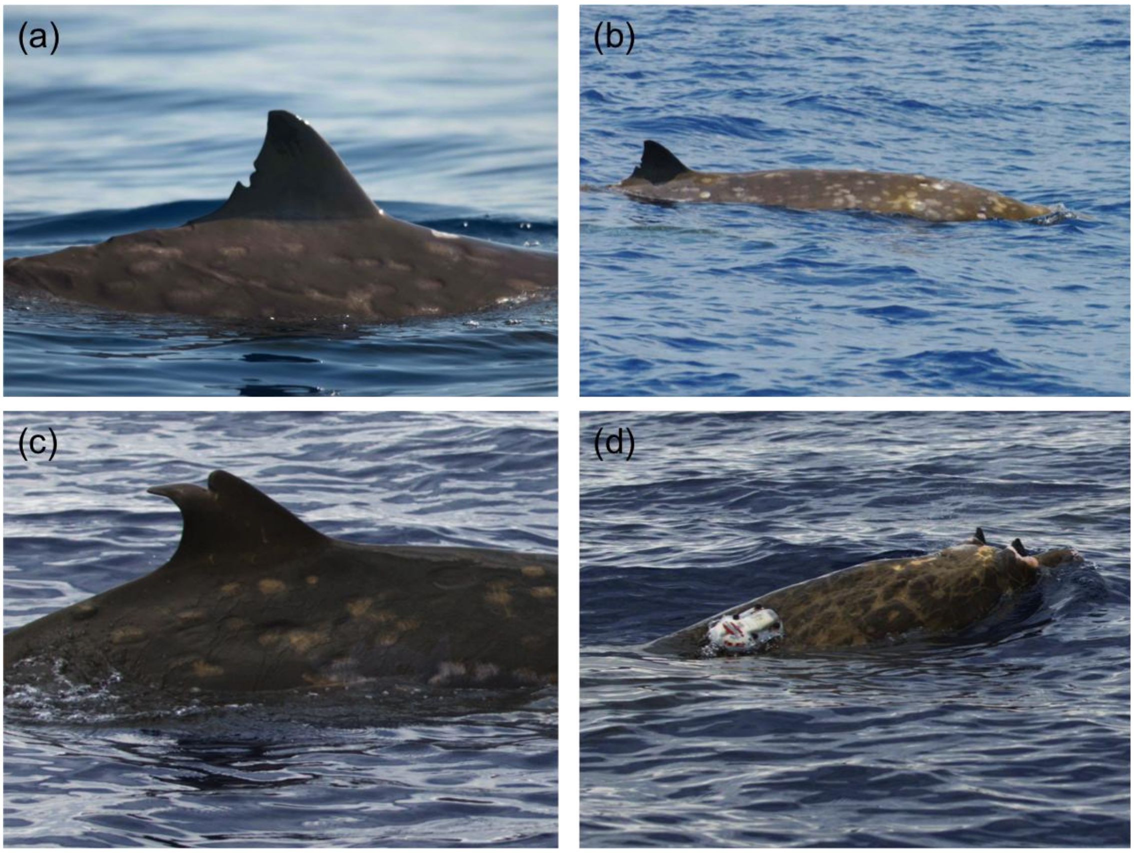

Figure 4.2. Identification photographs of an adult female showing her distinctive fin (a) and head (b), and an adult male with a distinctive fin (c) and a shot of his head with erupting teeth confirming his sex, as well as showing the DTag (d).

4.2.3 Click measurements

For all the clicks that were detected by PAMGUARD or provided by the M3R group, several parameters were measured using a Matlab R2014a (8.3.0.532) script. These were the -3 dB and -10 dB bandwidths, duration, peak frequency, sweep rate, and the starting frequency of the click.

The -3 and -10 dB bandwidths were calculated with respect to the peak frequency of the signal (Figure 4.3).

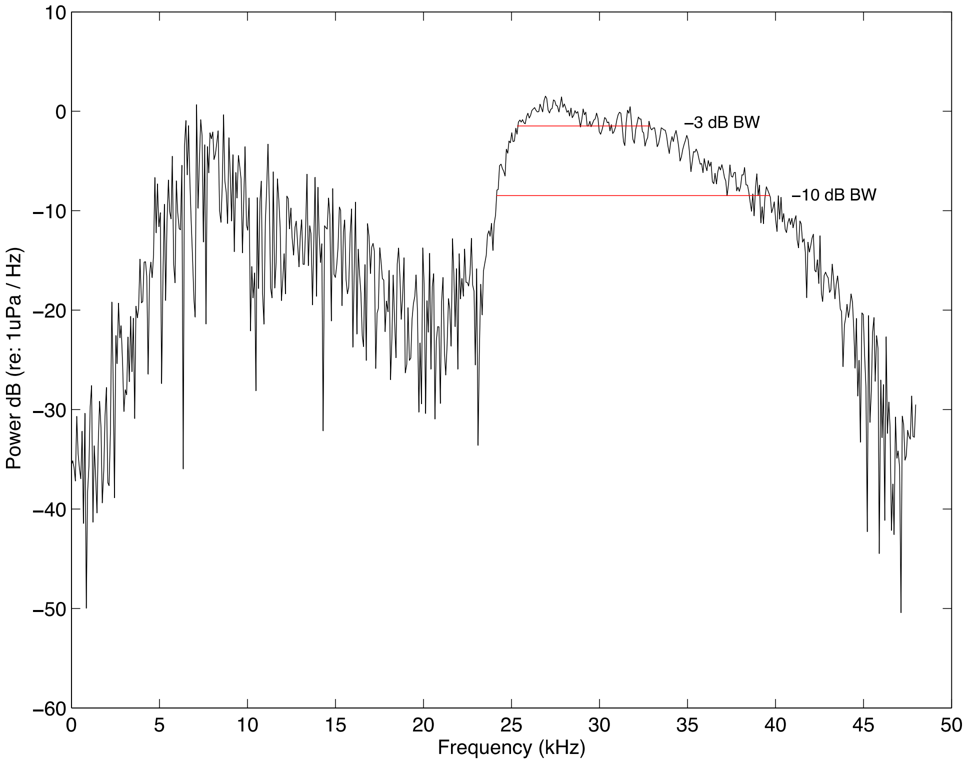

Figure 4.3. The relative power spectrum of a Blainville's beaked whale click generated from an FFT of the length of the click (1255). The -3 dB and -10 dB bandwidths are shown in red.

The duration of the signal was calculated using the D duration as recommended by Madsen and Wahlberg (2007). This is calculated as the duration in μs between the -10 dB points relative to the peak of the envelope of the waveform, and has been used to measure narwhal (*Monodon monoceros*) click durations (Mohl *et al.*, 1990). Since the signal is digitally sampled, the precise point at which the envelope drops to -10 dB almost always falls between samples. Therefore, I used linear interpolation between sample points to estimate the time at which the envelope passed through the -10 dB level (Figure 4.4).

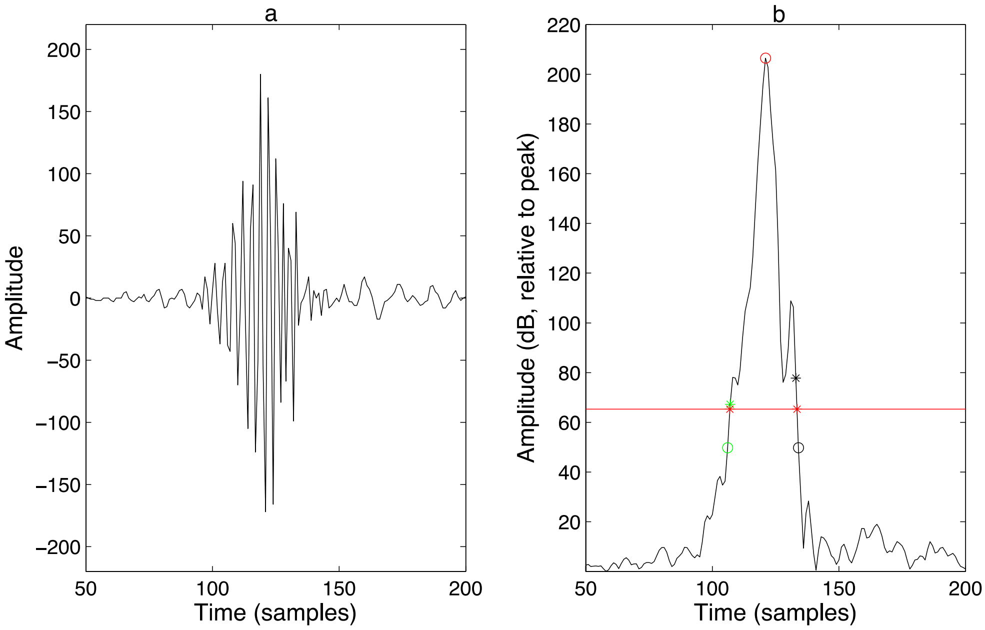

Figure 4.4. The waveform (a) and Hilbert transform envelope (b) of a click showing the -10 dB line in red, the peak frequency (red circle), and the interpolated start and end points of the signal (red stars) at the -10 dB (red) line. The time between the red stars was calculated as the signal duration. The green and black marks are the actual sample points within the envelope between which the -10 dB points were interpolated. (Sampling rate 96 kHz; 50 samples = 521 μs)

The sweep rate was calculated by fitting the line of best fit using a linear model through the frequency points from the start of the -10 dB duration period to the highest energy in the spectrogram of a click, producing a kHz/ms rate (Figure 4.5). Due to the low sampling rate relative to the frequency of the clicks, the spectrogram has to have a small window size (24) in order to achieve enough resolution to measure the clicks' sweep. Clicks with negative sweep rates were discarded from the dataset. Finally, to ascertain the starting frequency, a spectrogram was created with a 50% overlap and Hamming window. The first element from the array containing frequency values for the click was used as the starting frequency.

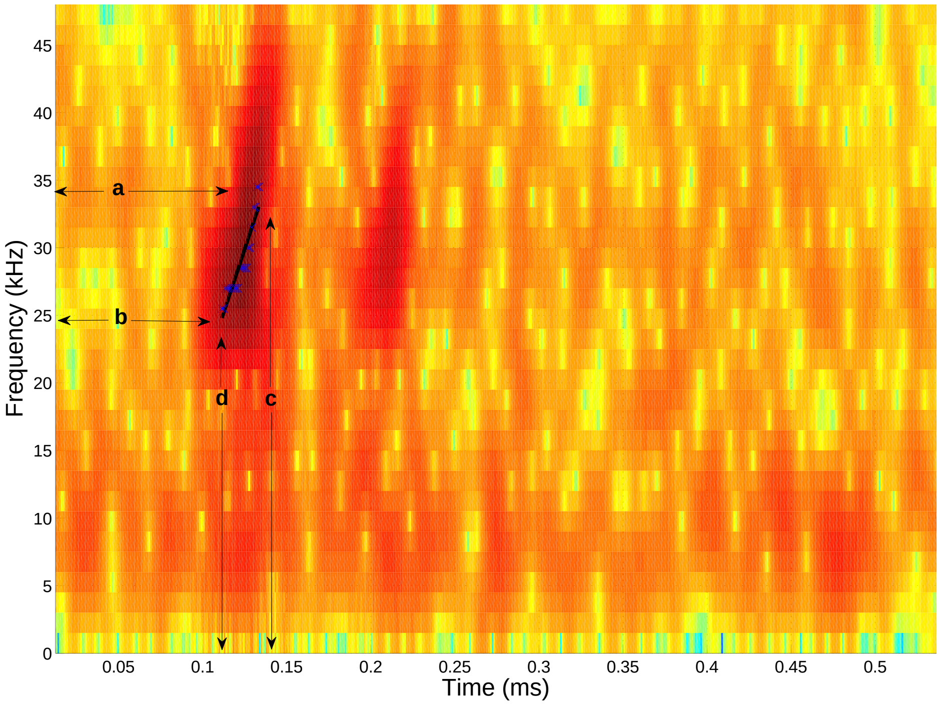

Figure 4.5. A spectrogram (NFFT 64, 99% overlap) showing peak frequencies in each time bin in blue crosses, and a black line of best fit through these frequencies. The difference in frequency (a-b) divided by the difference in time (c-d) gives the sweep rate in kHz/ms.

4.2.4 Clustering techniques

Where sightings of whales, and therefore recordings, consisted of more than one animal, there was no way of assigning clicks to individual whales. If there were reliable cues, one would nonetheless expect that multivariate plots of data from clicks produced by multiple animals would produce distinct clusters in click parameter space. Cluster analysis is a multivariate technique for identifying such groupings and has been used to separate individuals by their associations (Whitehead and Arnbom, 1987), and also by their acoustic attributes, as shown with killer whales, (Crance *et al.*, 2014). Therefore a hierarchical clustering technique was chosen to try and distinguish between different animals' clicks based on the parameters measured. Using all the data from the six parameters for each click, cluster analysis should be able to identify clicks that are similar, with the hypothesis that each cluster would represent an individual whale.

Hierarchical clustering was performed using the complete linkage method, which defines the distance between two clusters to be the maximum distance between any pair of points where one of the points belongs to each group. Therefore at each stage of the clustering process, the two nearest points or clusters (by complete linkage) are merged to become one cluster, and the process is repeated until the specified number of clusters is achieved. Complete linkage clustering generally produces more compact clusters than either single or average link clustering (Rokach and Maimon, 2005). Single linkage clustering can incorrectly join two clusters with a bridge because it identifies minimum differences between members of a cluster, and average-link clustering can produce the same error as well as causing elongated clusters to split (Guha *et al.*, 1998). For each dataset, the data were hierarchically clustered until the number of clusters was equal to the number of whales in the group.

To measure how well the clustering for each group of whales potentially mapped onto the individual identities of the clicking whales, click trains where only one animal was clicking were identified manually from the recordings and the percentage of these trains that crossed clusters was noted. If each cluster represented the clicks from an individual whale, then click trains containing a single animal’s clicks should only ever contain clicks from a single cluster. Only click trains with >5 clicks were used.

To identify click trains, the acoustic recordings were visually examined in Adobe Audition. An FFT length of 4096 samples was used with a 75% overlap and Hamming window. Only frequencies from 18 to 46 kHz were viewed to improve screen resolution at those frequencies. Click trains were identified as series of clicks with a pause before and after the group of clicks greater in duration than twice the regular ICI within the click train. The resultant click trains were assumed to contain only one animal’s clicks if the clicks had regular ICIs and any amplitude changes between clicks were gradual. The start time, duration, and number of clicks in the train were recorded.

Principal components analysis (PCA) was used to provide a visual representation of the clustering results. PCA (using standardised variables because of the different scales of measurement of the different click parameters) and cluster analysis were performed using the statistical software R (R Core Development Team 2010).

In four cases it was known which whale produced the recorded clicks. In these cases, animals were either sighted on their own (two occasions, different individuals), or instrumented with DTags and simultaneously recorded on the AUTEC hydrophones (two individuals). Analyses were carried out pairwise between these four whales, resulting in six pairs. For each pair, clustering was run until two clusters were obtained. The resulting clusters for each pair were compared to the known origin of the clicks. To calculate an error rate in terms of the percentage of incorrect click assignments, it was necessary to decide which of the output clusters would be labelled as being the ‘true’ cluster of each animal in the current pair. Since the error rate depended on this labelling, in each case the labels that gave the lowest percentage of incorrect whale click assignments were chosen, and this percentage recorded as the error rate. This approach was used to give the analysis the best chance of identifying any differences between the clicks in each pair, should they exist.

To understand how well the clustering of known whales performed relative to chance, a randomisation test was performed for each of these six pairs. The test randomly split the clicks in each pairwise comparison into two groups of the same size that the clustering algorithm had produced for that pair. This was done 10,000 times for each pair of animals and the lowest incorrect percentage of whale click assignments was recorded for each iteration. The median of these randomisation test error rates was recorded and compared to the error rates from the cluster analysis to see whether the clustering was separating clicks based on characteristics specific to the individual that made them.

4.3 Results

The total dataset for analysis contained recordings from ten groups of whales (Table 4.1). Three of the groups contained two age-classes, and two groups contained both sexes in the same age-class. There were four groups containing only a single animal, and two of these were from animals instrumented with DTags.

Table 4.1. Date, number of clicks, duration of recordings, number of hydrophones that recorded clicks over how many dives, and the group composition for all groups used in this analysis. (Groups 9 and 10 are the tagged animals; AF = adult female, SM = subadult male, C = calf, AM = adult male).

Group	Date	# Clicks	Total file length (min)	# Hyd	# Dives	Group Composition
1	01-Sep-07	1457	30	4	1	2AF
2	27-Sep-08	985	90	4	3*	AF & SM
3	22-May-08	639	30	1	1	2AF & SM
4	1-Oct-08	2259	37	5	1	AF & C
5	27-Apr-05	1228	60	4	1	AF & AM
6	26-Jul-12	73	10	1	1	2AF & AM
7	03-Sep-07	748	60	2	2	AF
8	08-Jul-12	705	36	2	1	AF
9	05-Sep-07	209	n/a	n/a	4	AM
10	05-Sep-07	89	n/a	n/a	4	AF

* there were 4 dives originally, see below

Five of the groups occurred at times when other beaked whales were detected on nearby surrounding hydrophones, within two hydrophones of the hydrophones being used in this analysis. However there was only one instance when there was another group of beaked whales detected on a hydrophone adjacent in the AUTEC array to a hydrophone whose recordings are used in this analysis (Appendix 4.1). That detection occurred during only one of the four dives for which the group of whales in group 2 was tracked (Figure A.4.1.1), therefore this dive was excluded from my analysis, but clicks from the remaining three dives during which there were no other adjacent detections were retained. Consequently, I am confident that the clicks analysed in this study were from the whales that were visually sighted and to whom sex and age-classes were assigned.

The ROC analysis resulted in a high number of false negatives (beaked whale clicks that the PAMGUARD detector did not detect but were identified by a human observer) in the 887 clicks analysed (10% of the total number of clicks). This was expected because the detector was set to detect clicks with more than 10 dB SNR, in a deliberate attempt to remove false positives, which were judged to be a bigger problem for this analysis than false negatives, since false positives may have resulted in the inclusion of non-biological sounds in the subsequent analysis. There was only one observed instance where PAMGUARD detected a transient that was not a beaked whale click (Table 4.2).

Table 4.2. ROC analysis results showing the PAMGUARD detector result versus the actual condition derived from visual inspection.

PAMGUARD	**Human observer**	
	Click	**No click**
Click	334	1
No click	552	-

The removal of negative sweep rates from the dataset resulted in removing 162 clicks (0.02% of the total), however initial clustering after these clicks had been removed still resulted in clusters that were biologically not meaningful, with group 5 for example being split into two clusters containing 5 and 1233 clicks respectively. It seems unlikely in a group of two adult whales that one whale would only produce detectable clicks five times. Investigation of the five clicks in the first cluster showed that each of these clicks had at least two parameters that were > 1.96 standard deviations (SD) away from the mean (Table 4.3), such that they could be considered outliers. Therefore this group (Appendix 4.5.2, Figure A.4.2.1) and the others were filtered to remove clicks whose parameters fell outside the 2.5% and 97.5% quantiles. Cluster analysis was then performed on the filtered dataset. This filtering resulted in removing a total of 1,610 clicks (19% of the total across all recordings), however it did result in clusters that contained reasonable numbers of clicks. Filtering was not carried out on the clicks from the whales instrumented with DTags (groups 9 and 10).

Table 4.3. Parameters for five clicks from group 5 separated into a cluster from a non-filtered set of clicks, showing SD's > 1.96 away from the mean, in bold outlined boxes.

Clicks from cluster 1	**-3 dB (kHz)**	**-10 dB (kHz)**	**Duration (μs)**	**Freq. (kHz)**	**Sweep Rate (kHz / ms)**	**Starting freq. (kHz)**
Mean for the group	1.63	12.80	273.89	28.15	43.91	26.44
SD for the group	1.39	4.35	38.67	3.63	7.88	3.15
Click # 27	0.19	4.85	118.78	28.80	64.09	27.75
# SD's from the mean	1.04	1.83	4.01	0.18	2.56	0.41
Click # 79	0.144	0.288	52.0322	35.568	149.143	30
# SD's from the mean	1.07	2.88	5.74	2.05	13.35	1.13
Click # 84	6.84	15.41	302.82	34.52	41.63	19.50
# SD's from the mean	3.75	0.60	0.75	1.76	0.29	2.20
Click # 1135	1.67	4.72	106.25	26.34	79.55	26.25
# SD's from the mean	0.03	1.86	4.34	0.50	4.52	0.06
Click # 1222	1.44	3.80	86.78	26.22	89.89	26.25
# SD's from the mean	0.14	2.07	4.84	0.53	5.83	0.06

Click trains crossed clusters for every group of whales in the filtered dataset where click trains from single animals could be identified (Table 4.4). Therefore observed clusters could not be representative of individual whales, since for this to be true, all the clicks from a click train with a single animal clicking would be in a single cluster. When there were three animals in a group (groups 3 and 6), all click trains were overlapping, therefore there was never a period in the recording when only one whale was vocalising, so it was not possible to separate out any click trains for these groups.

Table 4.4. Numbers of clicks in each cluster, the percentage of click trains that crossed clusters, the number of click trains used for analysis, and the total number of clicks used in the clustering (post-filtering), for each group analysed.

Group	**Cluster 1**	**Cluster 2**	**Cluster 3**	**% cross clusters**	**# trains**	**# clicks**
1 (AF & AF)	430	702	n/a	80	10	1132
2 (AF & SM)	264	539	n/a	70	13	803
3 (2AF & SM)	70	148	312	No single animal trains		530
4 (AF & C)	502	1360	n/a	33	24	1862
5 (no filter)	5	1223	n/a	0.08	12	1228
5 (AF & AM)	437	530	n/a	75	12	967
6 (2AF & AM)	9	16	28	No single animal trains		53

PCA on the click parameters for each of these six groups resulted in PCA scatterplots which all show overlap of the clusters (Figure 4.6), as expected from the click train analysis. The first two principal components explained between 57 and 66% of the data for the six groups, with sweep rate and the -10 dB bandwidth variables being dominant loadings for PC1 in five out of six of the groups (Appendix 4.5.3).

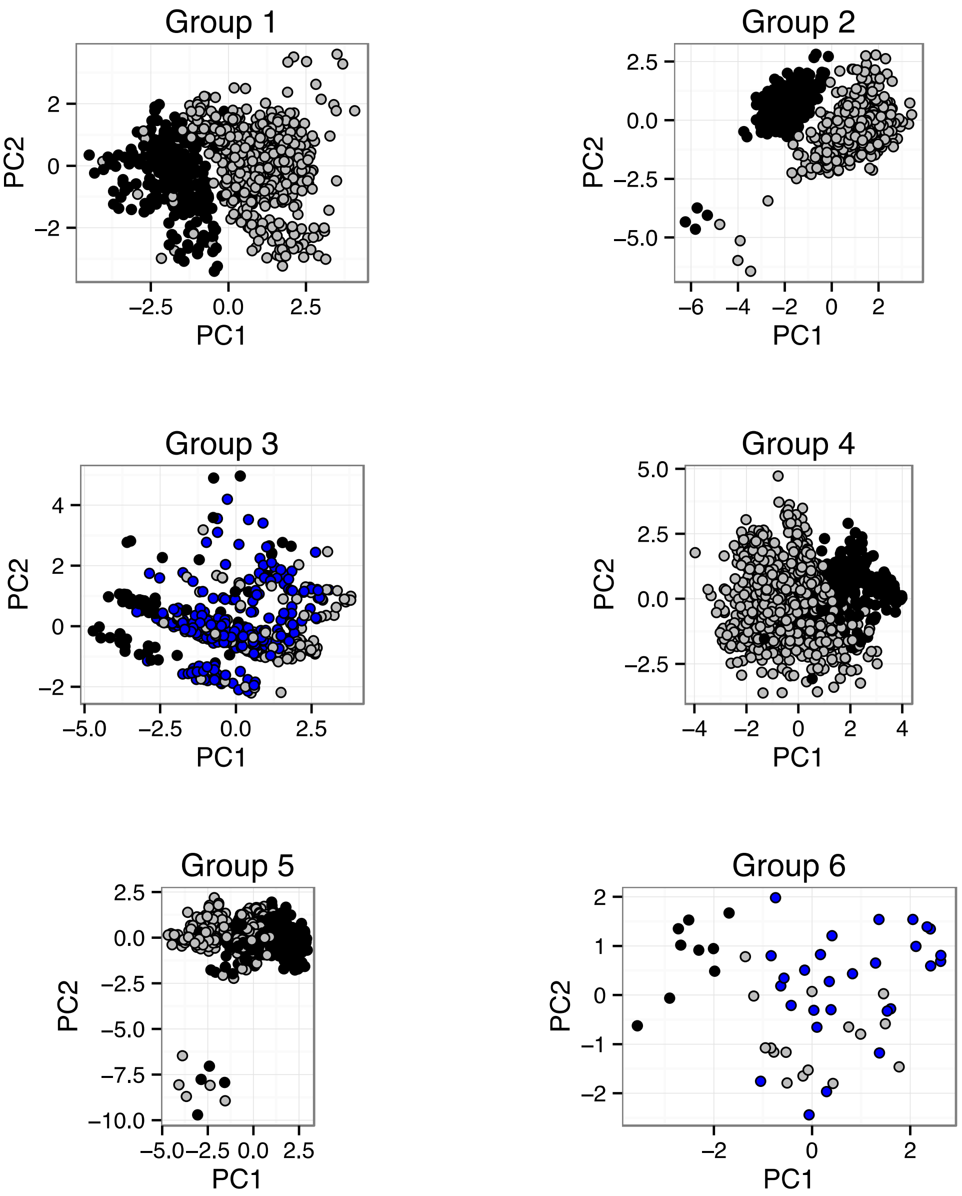

Figure 4.6. PCA of all six groups of whales showing clicks in the assigned clusters in different colours.

A possible exception to the general pattern of overlapping clusters is group 2 (containing an adult female and subadult male; Figure 4.6) where there does appear to be a separation of clusters with little overlap. To investigate this further, I produced an identical PCA scatterplot in which the clicks were coloured by which hydrophone they were recorded on (Figure 4.7).

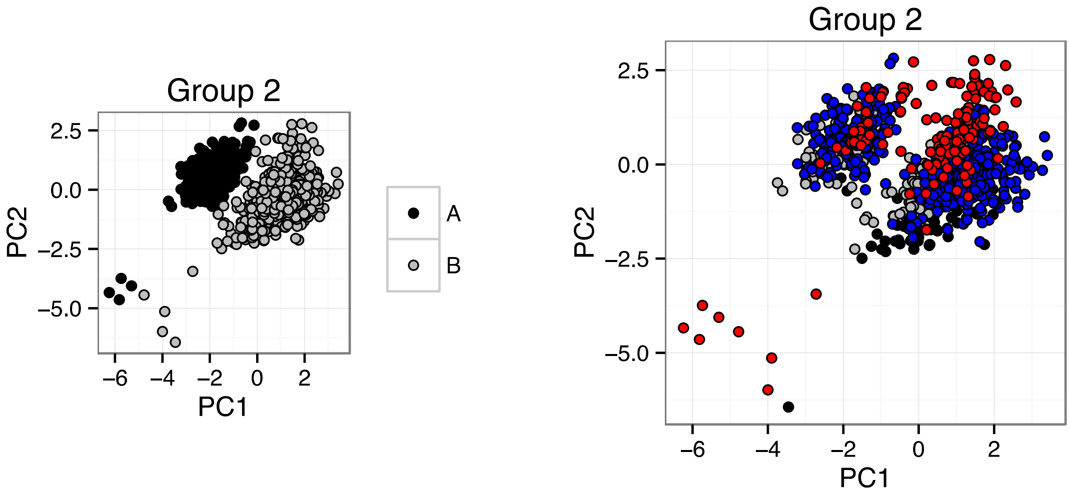

Figure 4.7. PCA of group 2, showing the clusters, A and B, in black and grey on the left, and coloured by each of the four receiving hydrophones on the right.

From Figure 4.7, one can see the separation of clicks is not due to the receiving hydrophone, therefore I plotted each of the six parameters for each cluster for this group to see how the two clusters were being separated (Figure 4.8).

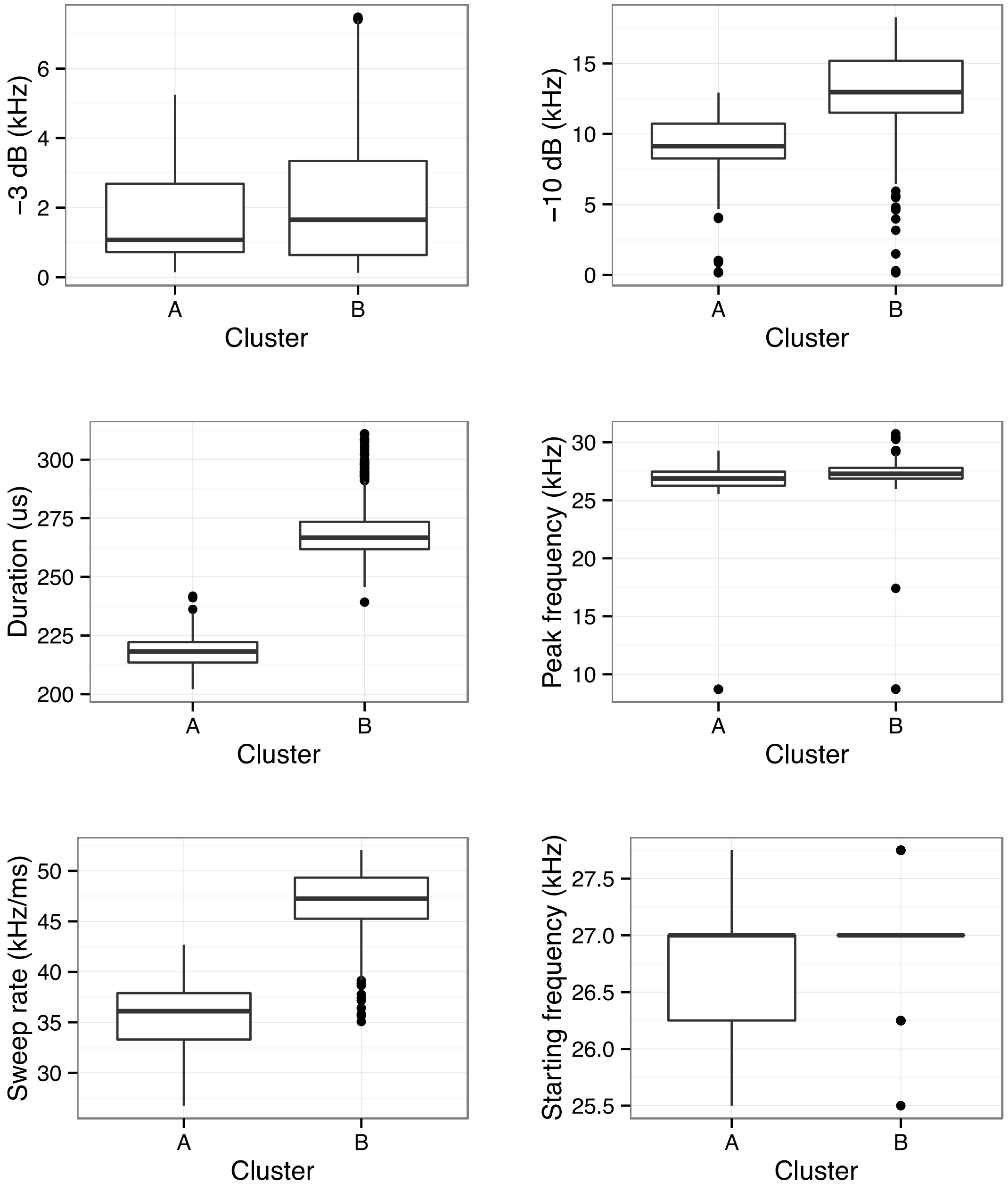

Figure 4.8. Boxplots for each parameter for group 2, separated by cluster.

The two parameters affecting the cluster differentiation are duration and sweep rate, as well as the -10 dB bandwidth parameter to some extent (Figure 4.8), which is representative of the dominant variables in the PC loadings (Appendix 4.5.3). Click duration is known to increase with off-axis clicks (Au, 1993), which would also influence and increase the -10 dB parameter. This group of whales (group 2) contained an adult female and a subadult male, therefore representing an interesting test case for a cue to differentiate sex and / or age-class. However the clusters cannot be representative of the individual whales as the click train analysis identified 70% of click trains crossing clusters where a single whale was clicking (Table 4.4). This suggests that the observed cluster separation is likely being caused by on versus off-axis clicks within the data.

The data from encounters of single animals where there was no ambiguity as to which animal produced the clicks (groups 7, 8, 9 and 10) were filtered as follows. The two untagged adult females that were in groups on their own, groups 7 and 8, were processed through the PAMGUARD beaked whale detector and then had all clicks outwith the 2.5% and 97.5% quantiles removed. The tagged adult male and adult female in groups 9 and 10 were filtered by the M3R group to only include assumed on-axis clicks at ranges less than 2500 m from the hydrophone (Shaffer *et al.*, 2013).

The results showed that for every pair of whales, the cluster analysis performed better than random, although only by a small amount in each case (Table 4.5). An example of the frequency distributions of the randomised error rates for the pair of whales from groups 8 and 10 are shown in Appendix A.4.4, Figure A.4.4.1. These results therefore show that hierarchical clustering techniques performed similarly to assigning clicks to individuals randomly without any data. Therefore the data from the six parameters for each click did not aid in correctly clustering clicks to the individual whale that produced them.

Table 4.5. Clustering error rates (Error) and the median of the 10,000 error rates from randomised partitions (Median).

	7 (AF)		**8 (AF)**		**9 (AM)**		**10 (AF)**	
	Error	Median	Error	Median	Error	Median	Error	Median
7								
8	46%	49%						
9	38%	44%	31%	44%				
10	23%	40%	25%	28%	39%	39%		

I provide plots for the six parameters for each pair of whales whose recordings underwent the same data processing in Appendix 4.5, groups 7 and 8, and groups 9 and 10. None of the parameters appear significantly different between each whale in either pair.

4.4 Discussion

This investigation into the presence of cues in Blainville’s beaked whale clicks did not reveal any differences in echolocation clicks between animals of different sex and / or age. Although the number of individuals was small in this study, if cues were present in their echolocation clicks, they should be inherent in each and every click, and therefore would be detected regardless of sample size. In recordings of groups with multiple animals, the analysis produced clusters that had no relationship with individual animals because click trains from single animals were found in all clusters; therefore the clusters could not represent single individuals. Hierarchical clustering of clicks from pairs of single animals produced clusters with error rates only slightly better than random assignments, showing that there was no structure in the data that could be used to distinguish individuals.

Although this study benefited from an extensive underwater acoustic array directing the field team to recently vocalising groups of beaked whales, these animals are still a difficult cetacean to detect visually, resulting in a small sample size. They have short surfacing intervals, are cryptic when at the surface, and are typically in small groups (Barlow, 1999; Chapter Two). In addition, the filtering criteria for data collected from groups that were sighted and photographed led to only ten groups of whales for analysis. Fortunately there was only one dive of one group of whales that had to be removed from our analysis due to another group of Blainville’s beaked whales being detected on nearby hydrophones on the AUTEC array.

Apart from beaked whales, there was little else to affect the quality of the recordings on the hydrophones. TOTO is a body of water surrounded by shallow bank on all sides except its’ northern opening, and so not used for shipping traffic.

It is therefore typically quiet, which is why many of the world’s navies use it as a testing facility. The vast majority of noise in TOTO comes from military sources, however marine mammal field efforts are usually not allowed to coincide with any navy activities that are producing sound, so it is unlikely that military sound would trigger a false positive, explaining the low number (n=1) of false positives identified by the ROC analysis.

The dataset of clicks, although containing only beaked whale clicks attributable to specific groups of whales, could not be separated to individual animals in any situation where there was more than one animal present. Unlike this study, previous studies looking at acoustic parameters to distinguish individuals and or age-class of an animal have been able to directly attribute vocalisations to individuals. For example, free-ranging ravens (*Corvus corax*) have been individually marked and then simultaneously videotaped during foraging sessions to identify vocalising individuals. This resulted in finding individual call characteristics in fundamental frequency and intensity-related measurements (Boeckle *et al.*, 2012). Similar studies have been conducted on many captive animals to look at how call parameters differ between individuals and or class, including giant pandas (*Ailuropoda melanoleuca*), whose sex, age and body size were acoustically distinguishable (Charlton *et al.*, 2009) and many bats (reviewed in Jones and Siemers, 2011). Unfortunately with beaked whales these approaches are extremely difficult. By using individual click trains to quality test the clusters produced from the analysis however, I believe that this problem was somewhat overcome. Yet the clusters appear to have been influenced by the receiving angle of a click, explaining why both clusters contained a single animal’s clicks in every case. The differences in source parameters of clicks of varying angles outweighed the possible differences in individual whales’ clicks for cluster analysis to detect in this case.

Most studies that have found cues in acoustic traits of animals have attributed at least part of the information content to a frequency parameter indicating sex in giant pandas (Charlton *et al.*, 2009), age in chacma baboons (*Papio ursinus*) (Ey *et al.*, 2007), reproductive status in African elephants (Leong *et al.*, 2003), and both age and sex in many bat species (Chen *et al.*, 2009; Guillén *et al.*, 2000; Jones, 1995; Neuweiler *et al.*, 1987; Siemers *et al.*, 2005; Suga *et al.*, 1987; Yoshino *et al.*, 2006). Unfortunately frequency content in beaked whale clicks is sensitive to the relative aspect of the click and therefore difficult to compare between individuals, as there is so much overlap in the frequency bandwidth across clicks of different axes. In addition, many of the above studies have recognised that frequency can be correlated with vocal tracts and therefore the size of the animal, which in many cases is different between males and females. Blainville's beaked whales however are not sexually dimorphic in size (Pitman, 2002). Therefore if frequency provides any cues in beaked whale clicks other than species identity (Gillespie *et al.*, 2009; Johnson *et al.*, 2004; Zimmer *et al.*, 2005), it may only show itself in combination with another parameter, possibly one that was not included in this analysis.

The parameters included in this analysis for cues were chosen because of previous literature relating to information content in bat echolocation and species-specific variation in beaked whales. A possible weakness of this study may therefore be the limited number of parameters that were used, as well as those parameters being susceptible to off-axis distortion, although it does not make sense for cues to only be available if the whale is directly facing the receiver. Some extra parameters would become available to measure if recordings were made at a higher sampling rate than those made on the AUTEC hydrophone array (96 kHz). For example, age related information in little brown bats (*Myotis lucifugus*) was found in the shape of the frequency modulation in their clicks, described as curvature, using recordings with a sample rate of 500 kHz (Kazial *et al.*, 2008). Curvature values can range from -1 to +1 and are measured between the start and end frequencies of a click, with a 0 indicating a straight line, negative values indicating a concave shape and positive values a convex shape in the click. When I tried to extract the curvature parameter for beaked whale clicks recorded with a sample rate of 96 kHz, depending on how the samples were distributed across the click, there was enough error during the smoothing process to give a negative result when the click shape was actually convex and should therefore have resulted in a positive curvature. The sweep rate parameter in this study may also have been affected by low sampling rate, as conspecific clicks recorded on a DTag on a Blainville's beaked whale in the Canary Islands resulted in a median sweep rate of 112 kHz / ms (Johnson *et al.*, 2006), approximately twice the mean sweep rate found here. Though perhaps this is not an appropriate comparison due to the differences in recording methods. Thus, recording at higher sampling rates would aid in increasing the amount of parameters that could be analysed for possible cues.

In addition to a limited number of parameters being analysed, there was a narrow representation of group composition in this analysis. For example there were two groups of whales containing a single adult female. If there was a cue for reproductive state of an individual, as shown in Barbary macaques (*Macaca sylvanus*) (Semple and McComb, 2000), this would not be apparent here, as both these females were without a calf, and therefore were in the same reproductive state. For the encounter that contained a female and calf, the adult female’s clicks could not be separated from the calf’s (see also Chapter Five), therefore it was not possible to compare the lactating female’s clicks to either of the single adult female’s clicks in search for a possible reproductive state cue. Attempts should be made to include recordings from females in differing reproductive states in future studies.

As with all apparently negative results, interpretation can be challenging since it is very difficult to say with certainty that every possible acoustic aspect of the clicks within which identity cues might lie has been tested. Therefore I would suggest that before drawing a final conclusion that Blainville’s beaked whales are not producing acoustic cues in their echolocation clicks, future studies may benefit from an increased number of individual whales of varying age and both sexes, as well as an increased sampling frequency allowing for the investigation of cues from more acoustic parameters, including more parameters invariant to axis distortion. However, in the case that there are not cues being produced, I would conclude that beaked whale clicks are providing no more information than the presence of that animal, and sometimes the presence of prey through buzzes. This is a particularly interesting outcome considering the evidence for the relationship between social associations and age, sex, and reproductive state shown in Chapter Two. If there is a requirement for information to aid in association choices (Chapter Two) and the few atypical sounds that have been discovered, although sex specific, are only detectable at close ranges (Chapter Three), the questions of how are Blainville’s beaked whales choosing which groups to avoid or approach and join remains outstanding.

Chapter Five

5 HOW OLD ARE BLAINVILLE'S BEAKED WHALES (*MESOPLODON DENSIROSTRIS*) WHEN THEY START CLICKING, AND DO CALF CLICKS DIFFER FROM THEIR MOTHER'S?

5.1 Introduction

The ontogeny of vocalisations in mammals can be difficult to study because young animals are often closely protected by one of their parents or closely associated adults, restricting any access for possible acoustic recordings. Therefore the literature thus far, especially for marine mammals, is scant. Most young mammals appear to produce vocalisations that are either innate (Simmons *et al.*, 2003), or learnt (Janik and Slater, 1997), although many behaviours have elements of both, and the timing of the first production of vocalisations varies and is likely affected by the infant's environment.

In most mammals, vocal development is innate and not influenced by external factors (Simmons *et al.*, 2003). For example, squirrel monkeys (*Simia sciureus*) were shown to produce genetically pre-determined vocalisations without exposure to conspecifics (Winter *et al.*, 1973). Newborn bats vocalise on the day they are born, and also produce innate vocalisations that are robust to external factors (Gould 1975). Gould demonstrated that infant bats that were isolated from adults, or exposed to adults whose vocal cords had been altered, produced the same vocalisations as those reared normally. Infant bat vocalisations tend to be lower in frequency than adult vocalisations for several species including big brown bats (*Eptesicus fuscus*) and little brown bats (*Myotis lucifugus*) (Masters *et al.*, 1995; Moss *et al.*, 1997). However within three weeks the pulses of infants cannot be distinguished from the adult bats (Woolf, 1974). Knowledge on neonate vocalizations in cetaceans is more limited. Currently only two recordings of neonate sperm whales (*Physeter macrocephalus*) have been made (Madsen *et al.*, 2003; Watkins *et al.* 1988), and in both cases their vocalisations were also lower in frequency when compared to adults, akin to the above mentioned studies in bats. Although these sperm whale recordings show an evident pattern, it should be noted that both came from stranded animals in poor health who ultimately died in captivity.

For most species, in contrast to some bats and sperm whales, call frequency generally decreases as body size increases (Matthews *et al.*, 1999; May-Collado *et al.*, 2007). An African elephant's (*Loxodonta africana*) age can be determined from the absolute frequency of its call (Stoeger *et al.*, 2014), with younger and therefore smaller animals producing higher frequencies than adults. Likewise, across beaked whale species, smaller species produce higher frequency signals. Although this has been suggested to not only be linked to body size, but to an adaptation for detecting smaller prey (Baumann-Pickering *et al.*, 2013).

However, not all species produce genetically pre-determined vocalisations. Both male and female juvenile greater horseshoe bats (*Rhinolophus ferrumeguinum*) produce echolocation pulses similar in frequency to their mothers (Jones and Ransome, 1993), showing evidence of vocal learning. A one year old killer whale (*Orcinus orca*) born in captivity produced the same stereotyped call favoured by her mother for the vast majority of all her calls (90%) (Bowles *et al.*, 1988). Bottlenose dolphins (*Tursiops truncatus*) produce signature whistles that are individually characteristic (Caldwell and Caldwell, 1965), and are learnt from the signature whistles of community members (Fripp *et al.*, 2005). Juvenile male dolphins are more likely to produce a signature whistle similar to their mothers, presumably to avoid inbreeding, whereas juvenile females that remain with their mothers for extended periods, produce signature whistles dissimilar to their mothers (Sayigh *et al.*, 1990).

Whether vocalisations are innate or learnt, many mammals are able to vocalise at birth. Beluga whales (*Delphinapterus leucas*) vocalise within an hour after being born (Vergara and Barrett-Lennard, 2008), and bottlenose dolphins produce whistles and burst pulse sounds just after birth (Killebrew *et al.*, 2001). The timing of production of infant's calls may be correlated with when they first begin separating from their mother. If a mother and her offspring are separated there is a need for some sort of communication mechanism in order to facilitate reunions as the calf is still in need of the mother's care. Bottlenose dolphins separate for short periods of time from their mothers early in their development (Mann and Smuts, 1998), suggesting some form of mother-offspring communication is needed to enable reuniting. It has been shown that an adult female bottlenose dolphin will only produce her signature whistle during the first 15 days following the birth of her calf (Amundin and Mello, 2001), consistent with active imprinting of a recognition signal. Similarly, subantarctic fur seals (*Arctocephalus tropicalis*) have been shown to recognise their mother's voice within five days of birth. This recognition is important because it facilitates their reunion after the mother has returned from a three week foraging trip at sea (Charrier *et al.*, 2001). Greater horseshoe bats leave their infants in the roost while they forage, and reunite by both infants and adults repeatedly producing variable high pitched signals until the signals precisely overlap (Matsumura, 1981). Finally, ewes (*Ovis aries*) and their lambs recognise each other's calls using a simple call that uses only the frequency domain, but is thought to work in conjunction with visual and olfactory cues (Searby and Jouventin, 2003). The need for mothers to reunite with their offspring after foraging, or after separations caused by offspring mobility, can therefore drive the ontogeny of the calf's vocalisations, and/or mother-offspring recognition. Where this need is absent, these features need not develop. For example, cliff nesting black-legged kittiwakes (*Rissa tridactyla*) do not show early mother-offspring recognition although they do separate (Storey *et al.*, 1992). Females from this species are able to reunite with their offspring after foraging trips due to a roosting environment from which the chicks cannot leave, so spatial recognition is used instead.

In female deep diving marine mammals, strategies for foraging while having a dependent calf seem to vary. For example, young sperm whales are left at the surface with babysitters (Whitehead, 1996) while mothers forage at depth. However, young Blainville's beaked whales (*Mesoplodon densirostris*) appear to dive for the same duration of time as their mother, diving and surfacing in synchrony, and have never been observed at the surface alone (pers. obs.). Therefore there may not be a mother-offspring recognition requirement for a newborn Blainville's beaked whale due to the constant proximity of mother and calf.

Currently there is no information published on the ontogeny of vocalisations in any beaked whale. As a first step it is useful to analyse the contents of just three recordings in which a mother and calf were known to be the only animals that could have been vocalising, to see what insight, if any, could be gained. The aim of this study is to identify when young Blainville's beaked whales are (first) recorded vocalising, and whether these vocalisations differ to those produced by their mothers.

5.2 Methods

Data collection for this analysis was conducted as described in Chapter Four. In this study, a calf was determined as still being in the same group with its mother. Calves separate from their mothers between the age of 3 and 4 years old (Claridge, 2013). For all the recordings used in this analysis, the M3R group provided information regarding all marine mammal detections from nearby hydrophones, which are those located within two hydrophones of the hydrophones being used in this analysis. Very limited data were collected on mother-calf pair encounters (N = 3, ranging from 11 - 45 minutes; Table 5.1).

Hierarchical clustering was not attempted in this analysis as results from Chapter Four failed to distinguish between individual vocalisations for the older calf included in this analysis (the second row in Table 5.1), and data were too few for the other mother-calf pairs. Therefore I investigated potential differences between mother and calf vocalisations using Principal Components Analysis (PCA) to provide a visual representation of the clicks detected by the PAMGUARD software (www.pamguard.org, Gillespie *et al.*, 2008). The variables used for the PCA analysis were the same as defined in Chapter Four (section 4.2.3. Click Measurements); the -3 dB and -10 dB bandwidths, duration, peak frequency, sweep rate, and the starting frequency of the click. In line with the methodology in Chapter Four, negative sweep rate clicks were removed from the dataset. PCA, using standardised variables to account for different measurement scales of click parameters, was performed using the statistical software R (R Core Development Team 2010).

To investigate how well the PAMGUARD detector performed, and as described in Chapter Four, a receiver operating characteristics (ROC) analysis was carried out comparing manually selected detections of beaked whale clicks by a human observer to the output of the PAMGUARD automatic detector, which had the same settings as described in Chapter Four. In the ROC analysis described here, ten percent of each acoustic file was analysed manually from the start of each file.

To identify if more than one animal was vocalising, which in these recording contexts would indicate the calf was vocalising, each acoustic file was visually inspected, examining waveform and spectrogram views in Adobe Audition CS6 (4096 point FFT with a 75% overlap and Hamming window). Times were noted for the start and end of periods of silence, periods when only one animal was clicking, and periods when there were overlapping click trains, indicating more than one animal was clicking. To enhance the detection of overlapping clicks, each file was amplified by 10 dB. Amplification was required because often one animal’s clicks had much less energy than the other. Overlapping clicks from two different animals are easy to identify visually, as the inter click intervals (ICIs) between each click are very irregular, and usually two types of clicks are visually distinguishable based on differences in amplitude. These differences arise because one animal is either closer to the hydrophone, has a different aspect, or is producing louder clicks. In contrast, single animal clicks tend to have regular ICIs and similar amplitude, or amplitude that changes gradually over a few clicks, indicating the animal is moving its head in a sweeping motion towards and away from the hydrophone that is recordings its clicks.

5.3 Results

The total of three mother-calf pairs were included in the analysis (Table 5.1).

Table 5.1. The dataset used for analysis, detailing three encounters with a mother-calf pair, the estimated age of the calf, the date of the encounter, the duration of the visual encounters and recordings, the number of clicks detected by the PAMGUARD detector, and the number of hydrophones that recorded vocalisations during each encounter.

Ref.	Age of calf	Date	Duration of visual encounter	Duration of recordings	# Clicks	# Hyd.
1	~ 1 week	1-Oct-2008	41 mins	45 mins	117	4
2	2 – 3 months	25-Jul-2012	62 mins	11 mins	61	2
3	18 months – 2 years	1-Oct-2008	28 mins	37 mins	2259	5

No other beaked whales were detected on nearby surrounding hydrophones during each of the recordings. Therefore I am confident that the clicks analysed in this chapter were from the mother-calf pairs that were visually sighted.

The ROC analysis resulted in a high number of false negatives (beaked whale clicks that the PAMGUARD detector did not detect but were identified by a human observer) (Table 5.2). This was expected and in accordance with the results from Chapter Four because the detector was set to detect clicks with more than 10 dB SNR, in a deliberate attempt to remove false positives. This setting would prevent detecting clicks with less than 10 dB SNR, for example distant clicks.

Table 5.2. ROC analysis results showing the PAMGUARD detector result versus the actual condition derived from human visual inspection.

PAMGUARD	**Human observer**					
	Dataset reference 1		**Dataset reference 2**		**Dataset reference 3**	
	Click	**No click**	**Click**	**No click**	**Click**	**No click**
Click	7	0	5	0	93	0
No click	117	-	220	-	205	-

The removal of negative sweep rate clicks for the PCA analysis resulted in removing a single click from the first dataset, six from the second, and none from the third. PCA on the click parameters for each of these three groups are shown in Figure 5.1. If the PCA had shown different clusters of clicks, then these could have corresponded to clicks from different individuals in each dataset, but the PCA showed no such visually distinct groups (Figure 5.1).

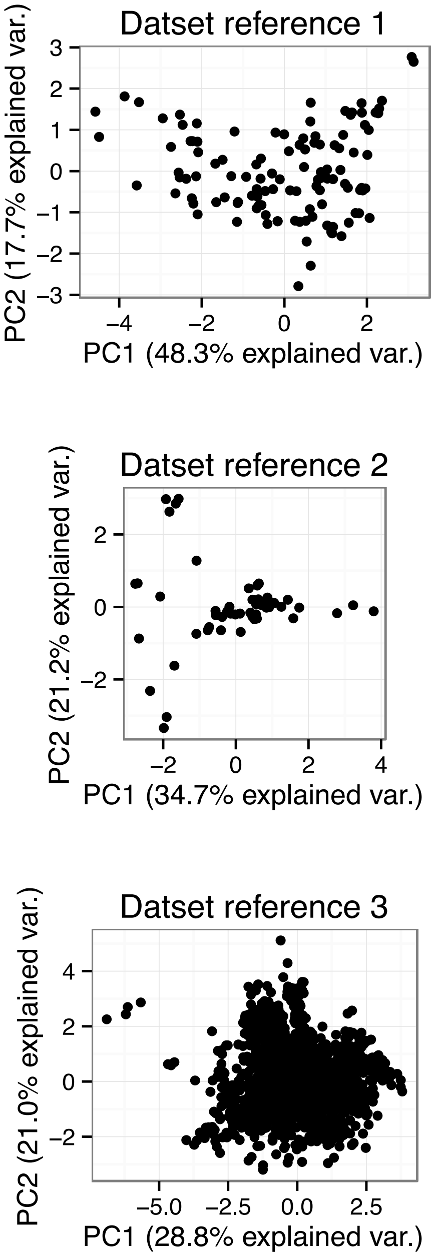

Figure 5.1. PCA scatterplots of click variables from the three mother-calf pairs.

The first two principal components explained between 50 and 66% of the variation for the three groups, with the -10 dB bandwidth variable being the dominant loading for PC1 in two of the datasets, and sweep rate in the other one (Table 5.3). Both these variables were also the dominant loadings for the PCA groups in Chapter Four (Figure 4.6).

Table 5.3. The loadings from PCA for three mother-calf pairs' click parameters, with the dominant variables shown in bold.

Group	PC	-3dB	-10dB	Duration	Peak frequency	Sweep rate	Starting frequency
1	1	-0.22	**0.55**	0.47	0.36	0.49	0.26
1	2	**-0.66**	-0.16	-0.06	0.48	-0.11	-0.54
2	1	0.50	**0.64**	0.02	0.21	0.47	-0.27
2	2	-0.07	-0.03	-0.34	**-0.69**	0.59	0.24
3	1	-0.25	0.43	0.41	0.46	**0.58**	0.20
3	2	**0.70**	0.53	0.10	-0.38	0.20	-0.18

The recordings from the encounter of a mother and her neonate (Reference 1, Table 5.1) never displayed more than one animal clicking at any time (Figure 5.2). On the contrary, the recordings from the encounter where the calf was around 3 months old (Reference 2, Table 5.1) contained some overlapping clicks, indicating that both animals were clicking at some points. The recordings from the encounter with the oldest calf (Reference 3, Table 1.5) contained the largest percentage of overlapping clicks (Figure 5.2).

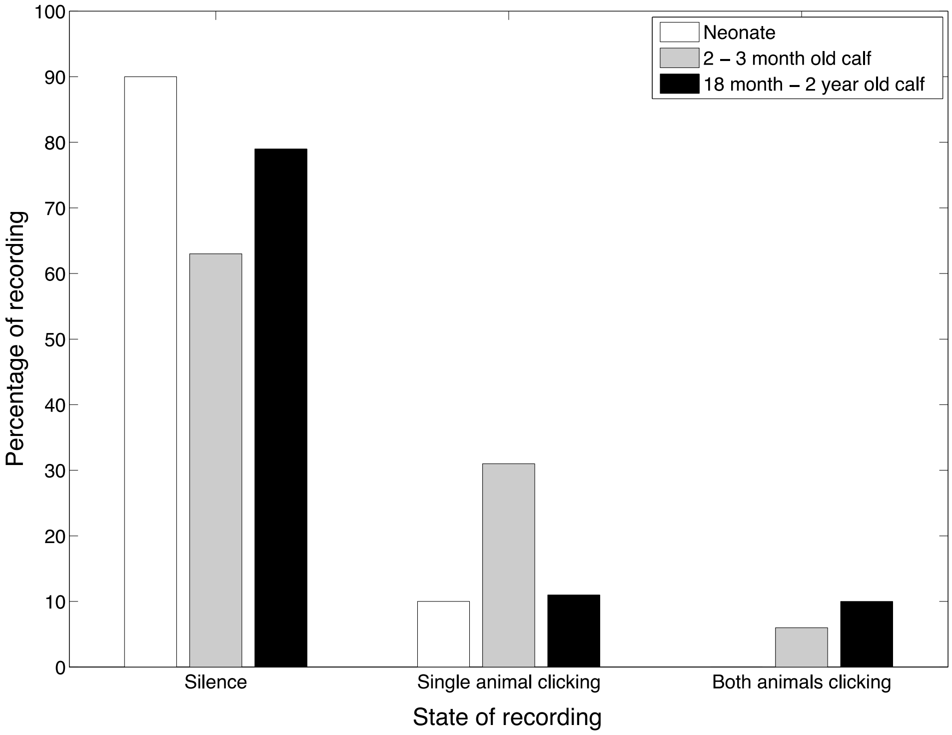

Figure 5.2. The difference in the contents of the recordings for the three mother-calf pairs, showing the percentage of the recording with no clicking, one animal clicking, or both animals clicking.

5.4 Discussion

The results of this study showed that for the one recording where a neonate (i.e. 1 week old) Blainville's beaked whale was present, only one animal appeared to be clicking, where as both mother and calf were clicking in the encounters with older calves (i.e. 3 months and older). This suggests that Blainville's beaked whales may not be vocalising as neonates, but are vocalising at least around three months of age.

Unlike sperm whale calves that are left at the surface with babysitters while their mothers go on foraging dives (Whitehead, 1996), Blainville's beaked whales remain in close proximity to their mothers, diving in synchrony with their mothers immediately after birth (pers. obs.). This is apparent at least while the animals are observable on the surface until they are approximately three years old and are weaned (Claridge, 2013). Blainville's beaked whale calves are proportionally larger at birth relative to their mothers than sperm whale calves (Huang *et al.*, 2011), which presumably helps make them more capable of diving with their mothers immediately after birth. Huang (2011) suggests that Blainville's beaked whales are capital breeders, enabling the birth of large calves. Therefore once a calf is born, the female may need to resume foraging activity quickly in order to meet her and her calf's metabolic requirements (i.e. through lactation). So it would be of benefit to mothers to have a large calf able to follow them on foraging dives immediately after birth and thus minimise the risk of predation associated with leaving the calf alone on the surface during such trips.

Although Blainville's beaked whale calves are known to dive for the same durations as their mothers (pers. obs.), it remains unknown whether they dive to the same depths. In other taxa with related dilemmas, calf behaviour can vary. In mountain goats (*Oreamnos americanus*) the energetic cost of following versus hiding was carried by the neonate, but following proved to be a relatively small cost (Carl and Robbins, 1988). In Blainville's beaked whales, the risk of predation for a calf left at a particular depth while the mother forages at a deeper depth may be greater than the energetic cost of the calf diving deeper, or than the mother foraging at shallower, less optimal depths until the calf can dive deeper. This would imply that if the neonate is not vocalising, that it recognises its mothers echolocation pulses in order to be able to reunite with her, even though as shown in Chapter Four, individual differences in vocalisations are subtle if any.

If Blainville's beaked whale calves dive to the same depths as their mothers and remain in echelon position with their mothers for the duration of a dive, this proximity may not require mother-offspring recognition or the need to vocalise immediately after birth. With this in mind, it has been shown that bottlenose dolphins decrease the proximity between mother and neonate from an infant to an echelon swimming position when the calf is between one and two months old (Mann, 1999), which is a similar timeframe to Blainville's beaked whales vocalising based on this analysis. It may well be then that the start of production of vocalisations in Blainville's beaked whales is linked to a change in swimming position analogous to dolphins. Although with such a small dataset and no knowledge of a beaked whale calf's swimming position at depth, this has to be considered speculative. Comparisons between these two species are also limited as bottlenose dolphin calves use tonal whistles to reunite with their mothers and not echolocation, while beaked whale calves have only been shown to produce echolocation pulses.

No differences were found using visual PCA scatterplots to distinguish between a mother and her calf's clicks. If Blainville's beaked whale vocalisations are innate, and the calves are born relatively large in size compared to their mother's size (Huang *et al.*, 2011), differences in frequency shown in sperm whales between infant and adult vocalisations may be less pronounced in beaked whales. Additionally, if Blainville's beaked whales are not vocalising immediately after birth, it may be that when they do begin to vocalise their anatomy is adequately developed to produce echolocation clicks that are similar to adults.

The age of producing efficient echolocation calls must be linked to the need to find and catch food. Most odontocetes nurse their young for at least a year (Whitehead and Mann, 2000), providing them time to develop their echolocation skills. Bottlenose dolphins take months to successfully capture their first fish, and years before they are nutritionally independent (Connor *et al.*, 2000), yet it is not clear whether this is due to developing echolocation or locomotion skills. It has been suggested that Atlantic spotted dolphins (*Stenella frontalis*) may be teaching foraging skills to their young through longer prey chase events and more body-orientating movements during foraging. Additionally, in some of these events the mother allows the still suckling calf to ingest the prey (Bender *et al.*, 2009). The same captive killer whale calf discussed in the introduction of this chapter was not producing echolocation clicks at two weeks of age, but when recorded again at eight months of age was producing clicks similar to adult killer whales (Bowles *et al.*, 1988). However, the ontogeny of vocalisations used for foraging in a captive marine mammal that has their prey provided may not be comparable to the ontogeny of the same vocalisations in free-swimming marine mammals.

Despite the limitations in this analysis (small sample size), the results suggest that Blainville's beaked whale calves are not necessarily vocalising immediately after birth, most likely because there is no requirement to do so if they are remaining with their mothers throughout their dives. When calves then begin to vocalise at least at 3 months old, any differences in their echolocation clicks due to their young age are subtle. I would also presume that it would take a beaked whale even longer to be able to master capturing prey than a dolphin due to the restricted acoustic only environment of the depth they are foraging. Presumably dolphins are learning foraging tactics from their mothers using visual observations as well as acoustic. In order to expand this dataset to include more mother-calf pairs, including calves of varying ages, I would recommend using the same recording method, i.e. a hydrophone range like that of AUTEC (as described in Chapter Four). This method provides two advantages; 1) confirmation, within reason, that the animals visually sighted were the ones recorded on the hydrophones, 2) avoidance of stress to a lactating female by attaching a digital acoustic recording tag (DTag), which would be the other method applicable to this question.

Chapter Six

6 DOUBLE CLICK PRODUCTION IN THREE SPECIES OF DEEP DIVING ODONTOCETES

6.1 Introduction

The extensive investigation into beaked whale vocalisations conducted thus far in this thesis alerted me to an apparent shorter inter click interval (ICI) between the first two clicks of a click train compared to the intervals in the subsequent train. Therefore I investigated this pattern in Blainville's beaked whales (*Mesoplodon densirostris*) and extended this study to include two other deep diving odontocetes, sperm whales (*Physeter macrocephalus*) and Cuvier's beaked whales (*Ziphius cavirostris*), for which I was able to use existing data.

6.1.1 Echolocation variation in cetaceans

Echolocation using click vocalisations is a critical part of odontocete sensory biology. The clicks themselves are not uniform across species, varying in duration, frequency content and temporal production pattern. For example, clicks produced by pygmy killer whales (*Feresa attenuata*) are extremely short (25 μs) with peak frequencies between 45 and 117 kHz (Madsen *et al.*, 2004); harbour porpoise (*Phocoena phocoena*) have a higher peak frequency ~ 130 kHz and longer duration ~ 100 μs (Dubrovskij *et al.*, 1971; Mohl and Andersen, 1973); false killer whales (*Pseudorca crassidens*) and Risso's dolphins (*Grampus griseus*) produce similar clicks in both duration, 30 and 40 μs respectively, and peak frequency, ~ 40 and 50 kHz respectively (Madsen, 2004). This variation between species is thought to be adapted to a specific class of target or prey species, but there is often variation within individuals that can depend on the task at hand.

Individuals vary their ICIs between the prey-search and prey-capture phase of foraging, producing buzzes during prey capture, and prey capture attempt events.

‘Buzz clicks’ in Blainville’s beaked whales occur as occasional brief bursts of clicks at the end of click trains produced at rates of *ca.* 250 clicks s^{-1}, with no obvious FM structure. These clicks have a short click duration of 100 μs, and a large bandwidth of 55 kHz at -10 dB (Johnson *et al.*, 2006). Sperm whales also transition into high repetition rate buzzes that are coincident with movements indicating prey capture attempts (Miller *et al.*, 2004). ICIs have also been shown to alter coincident with some behaviours, for example decreasing during aggressive behaviours in harbour porpoise and Hector’s dolphins (*Cephalorhynchus hectori*), when the animals produce even higher click repetition rates than during a buzz (Clausen *et al.*, 2010; Dawson, 1991), though it is unclear whether these clicks should be viewed purely as echolocation or considered a form of communication. Similarly, sperm whales use patterns of clicks deemed codas to communicate (Watkins and Schevill, 1977), and male sperm whales produce loud clicks sometimes called clangs (Gordon, 1987), with uncertain function - they may be an acoustic display in inter- and intrasexual interactions (Weilgart and Whitehead, 1988), and / or echolocation (Goold, 1999; Tyack and Clark, 2000).

6.1.2 Click production in odontocetes

Odontocetes produce echolocation clicks by pressurizing air in the nasal passages until the pressure is greater than the muscular tension of the phonic lips, causing the lips to briefly part allowing air to escape, generating a click (Cranford, 1998). Phonic lips are located just inside the blowhole, and act as a valve. It has also been noted that serous fluid is emitted between the phonic lips during bottlenose dolphin (*Tursiops truncatus*) click production (Cranford *et al.*, 2011), suggesting that having the surface of the lip coated in a fluid may be a requirement. In the common dolphin (*Delphinus delphis*), as clicks pass through the head they are reflected towards the melon by the animal’s skull and air sacs within it (Aroyan, 1992). The melon of a toothed whale is made up of lipids that conduct sound at differing velocities, with the lower sound velocity being at the core, where the click is then directed with increasing speed (Norris, 1974), resulting in a directional narrow beam click (Au, 1986; Au *et al.*, 2010).

The physiology of sound production presents special challenges for deep diving species, where sound production not only requires air, but also has to function in the high ambient pressure at depths of hundreds or thousands of metres. Beluga whales (*Delphinapterus leucas*) for example produce lower amplitude whistles at a depth of 300 m than at the surface (Ridgway *et al.*, 2001). Deep diving species who remain at depth for long periods of time have to recycle their air in order to continue producing echolocation clicks throughout the duration of their dive (Madsen *et al.*, 2005). This is possible because for each click that is generated, some air is passed into vestibular air sacs (Mackay and Liaw, 1981), and therefore retained by the whale and available for recycling.

6.1.3 Double click use in animals

As well as many bat species, there are two families of birds that use echolocation, both also nesting in caves. The Neotropical oilbird (*Steatornithidae*) and Paleotropical swiftlets (*Apodidae*) use echolocation primarily for navigation in the dark (Griffin and Thompson, 1982; Collins and Murphy, 1994). Most of the swiftlets produce their echolocation clicks in pairs (double clicks). They contract muscles to close the syrinx for around 20 ms with brief sounds being produced during both the closing and opening movements resulting in a double click (Suthers and Hector, 1982).

Double click production has also been noted in marine mammals. They were described as “doublets” in killer whale (*Orcinus orca*) vocal production as early as 1979 (Steiner *et al.*, 1979). The killer whale double clicks described were often the only clicks in a train and differed between each other in frequency “the first click was rich in low frequency energies, 200 to 900 Hz, while the second click consistently had additional higher frequencies to 7,000 Hz” (Steiner *et al.*, 1979). Hawaiian spinner dolphins (*Stenella longirostris*) produce double clicks that have a relatively narrowband frequency structure compared to their usual clicks (Lammers and Au, 2002). Double pulses have also been described for beluga whales (Turl and Penner, 1989) and were initially thought to be generated by the phonic lips acting concurrently (Lammers and Castellote, 2009). They are now however thought to be consistent with a single pulse being reflected within the head (Au *et al.*, 2012, see also Madsen *et al.*, 2013). Similar phenomena have been observed in Atlantic bottlenose dolphins with the first click of a double click produced by the phonic lips and the second resulting from reflection, giving the two clicks quite different centre frequencies (Au *et al.*, 2012). Finally, Cholewiak *et al.*, (2013), in describing Sowerby’s beaked whale (*Mesoplodon bidens*) echolocation clicks for the first time, refer to double clicks within click trains and suggest they may not be for foraging purposes.

Despite these numerous reports of double clicks, to my knowledge double clicks have not been systematically analysed across multiple odontocete species. Here I present a comparative analysis of double click vocalisations produced by Blainville’s beaked whales, Cuvier’s beaked whales and sperm whales. If double clicks are produced consistently across these species, it may indicate they are produced consistently across all deep diving species and therefore perhaps a result of pressure at depth. However if their production is not consistent across these species, there may be constraints that lead to double click production operating differently in the different species, or it might suggest double clicks could function as a form of communication.

6.2 Methods

6.2.1 Data collection

Recordings of sperm whales, Blainville’s and Cuvier’s beaked whales were obtained using suction cup acoustic DTags (Johnson and Tyack, 2003). Four Blainville’s beaked whales, three adult females and an adult male, were tagged in the Tongue of the Ocean off Andros Island in the Bahamas in 2006 and 2007. Three of the groups consisted of two adult females and an adult male (2007), and the other group of two mothers and their large juveniles (2006). These are the same whales and DTag data that were used for analysis in Chapter Three. Two Cuvier’s beaked whales, an unsexed subadult and probable adult female, were tagged in the Ligurian Sea, Italy in 2003, and an adult male and subadult male were tagged there in 2004 (Tyack *et al.*, 2006). Finally, an adult male sperm whale was tagged in the Ligurian Sea in 2002, and another adult male, two adult females and an individual that was either an adult female or a subadult male were tagged in the Gulf of Mexico between 2001 and 2003 (Miller, 2004). For all stereo tags, the channel with the best signal-to-noise ratio (SNR) was chosen for this analysis. (Data for this analysis was provided by Mark Johnson, Peter Tyack and Patrick Miller).

6.2.2 Data processing

Click trains, where a bout of clicks is separated by non-click periods at least double the ICI between regular clicks in the click train, were identified from spectrogram visualisations of the acoustic records in Adobe Audition CS6 (4096 point FFT with a 75% overlap and Hamming window), and saved to separate wav files, one file per click train. For each tag, click trains were searched for within the entire tag duration and all its acoustic records, therefore all phases of the animals' dives. The first dive post tagging in sperm whales is typically shorter than subsequent dives (Miller *et al.*, 2004), and as the tagging response may also involve vocalisation alterations, the first dive following a tag deployment for all species was not used in this analysis. Click trains are known to be from the tagged animals in all cases as the amplitude of the clicks was consistent throughout the duration of the tag, which would not be the case if the trains were from a conspecific. During the manual selection of click trains, the presence of a buzz before and or after the click train, and the time the click train commenced were noted.

Each click train wav file was then reviewed in Matlab R2014a (8.3.0.532), using the spectrogram function. Scripts were used to detect the first 25 clicks from each wav file using a band pass Hanning filter to concentrate on frequencies between 5 and 10 kHz, where DTag recorded clicks have a lot of energy (Burgess *et al.*, 1998; Goldbogen *et al.*, 2007; Insley *et al.*, 2008). Through trial and error, a limit was set for the minimum time between adjacent clicks to prevent loud echoes from being erroneously detected as separate clicks (75 ms for Blainville's beaked whales, and 110 ms for sperm whales and Cuvier's beaked whales). If the visual representation of the click train in Matlab did not correctly identify every click in the click train due to poor SNR, that entire click train was removed from the dataset. There were click trains removed for every animal at seemingly random intervals, therefore I do not believe the removal of click trains has created any bias in the remaining dataset used for this analysis. For sperm whales, because only click trains > 25 clicks were used in the analysis, codas made during the descent before regular clicking began were by default not included.

6.2.3 Statistical analysis

I quantified the presence of a double click by standardising the ICIs in each click train to the median ICI in the rest of the click train, thereby expressing each ICI as a proportion of the median ICI; this value for the first ICI thus gave a measure I termed "prop_ICI". Low values of this measure indicate the presence of double clicks, while values >1 imply a longer first interval than the median of the rest of the train. To quantify what might be driving the production of a double click, I used R software version 3.0.3 (R Development Core Team, 2012) for all statistical analysis. Generalized linear mixed and regular models ('glmer' function in R package lme4, Bates *et al.*, 2012) were fitted for each species with a normal (Gaussian) error structure, prop_ICI as the response variable, and a set of eight predictor variables. Each line of data represented a single click train and detailed the variables listed below, which were used as the predictors in the model(s).

1. [tag_id] This identifies the individual whale and was a random factor in mixed models to account for autocorrelation in click production within individuals.
2. [sex] Sex was split into three numeric variables; females -0.5, unknown sex 0, and males +0.5. This coding means that only animals of known sex can affect the coefficient estimation.
3. [age] Age was separated into subadults 'As', unknown age 'Av', and adults 'Az'.
4. [time_from_first_train] This is how far into the dive, in seconds, the animal was from the time of the first click train. This could indicate whether double click production is related to depletion of air reserves.
5. [depth] Depth in metres (as measured by the tag) at the time each click train started, to test whether double clicks are a feature of click production at depth.
6. [buzz_b4] If there was a buzz before the click train (Y/N factor), which may show some correlation between double click production and foraging attempts.
7. [buzz_after] If there was a buzz after the click train (Y/N factor).

8. [1st_train_of_dive] If this click train was the first click train of the dive (Y/N factor), although not all 'first trains' made it through the analysis, if there was poor SNR for example, they would have been removed from the dataset.

For each species, the Akaike Information Criterion (AIC) was used to select the best model (Burnham and Anderson, 2002), or which models to average, if more than one model was appropriate. In their review manuscript on the use of AIC in behavioural ecology, Symonds and Moussalli (2010) describe AIC as "a numerical value by which to rank competing models in terms of information loss in approximating the unknowable truth". This is fitting for modelling deep-diving odontocetes, who spend the majority of their time outwith our visual reach, although DTags are allowing a greater understanding of their behaviour during that time.

The 'dredge' function from the MuMIn package (Barton, 2014) was used to first identify the top models, which are those with the smallest AIC values. The actual AIC value is not important, but the difference between AIC values (ΔAIC) can indicate how much more supported one model is over another. ΔAIC from 0 to 2 indicates neither model can be preferred with certainty; ΔAIC from 4 to 7 shows some uncertainty and ΔAIC > 10 indicates considerable certainty in the preference of the model with the lower AIC value (Burnham and Anderson, 2002). Therefore for all models whose difference in AIC between it and the best model was < 3, model averaging was performed. Summed Akaike weights were used to estimate the relative importance of variables that were in a model (Burnham and Anderson, 2002), and I plotted those that tended towards 1.

6.3 Results

6.3.1 Overview of the dataset

From a total of 2773 click trains manually extracted, 1399 click trains from the 13 individual whales were used in the final analysis (Table 6.1). The excluded trains were either less than 25 clicks long, or had poor SNR resulting in the potential for missed click detections in a click train, which would strongly affect any ICI measurement.

Table 6.1. Dataset. (AF = adult female; AM = adult male; SM = subadult male; SU = subadult unknown; PF = probable female).

Species	Tag ID	Sex / Age-class	# Click trains
Blainville’s	Md06_296a	AF	118
Blainville’s	Md07_245a	AF	88
Blainville’s	Md07_248a	AF	185
Blainville’s	Md07_248b	AM	132
Total Blainville’s beaked whales			**523**
Cuvier’s	Zc04_160a	AM	15
Cuvier’s	Zc04_161a	SM	39
Cuvier’s	Zc04_179a	SU	73
Cuvier’s	Zc03_263a	PF	231
Total Cuvier’s beaked whales			**358**
Sperm whale	Sw03_156a	SM / AF	104
Sperm whale	Sw02_189b	AM	15
Sperm whale	Sw01_208b	AM	25
Sperm whale	Sw01_204	AF	113
Sperm whale	Sw02_254a	AF	261
Total Sperm whales			**518**

In an attempt to illustrate that double clicks differ from regular echolocation clicks in these species solely by their ICI, I calculated the duration of the first and second click in a double click and the remaining clicks in each click train (Figure 6.1). In order to be sure this was being done on click trains that began with a double click, I only used click trains where the first ICI was less than half the median ICI of the train (prop_ICI<0.5; Blainville’s beaked whales n = 325; Cuvier’s beaked whales n = 28; sperm whales n = 18). Duration was calculated using the same Matlab code used to calculate duration in Chapter Four, therefore calculating the time between the -10 dB points relative to the peak envelope of the waveform. However, this measurement is not especially reliable (Johnson *et al.*, 2006; Madsen *et al.*, 2002), as is the case for other measurements from high frequency vocalisations recorded on the tag (Johnson *et al.*, 2009), but could indicate large dissimilarities between clicks. It is worth noting that for the purpose of this study, measurement of the timing of click production is not compromised using DTags.

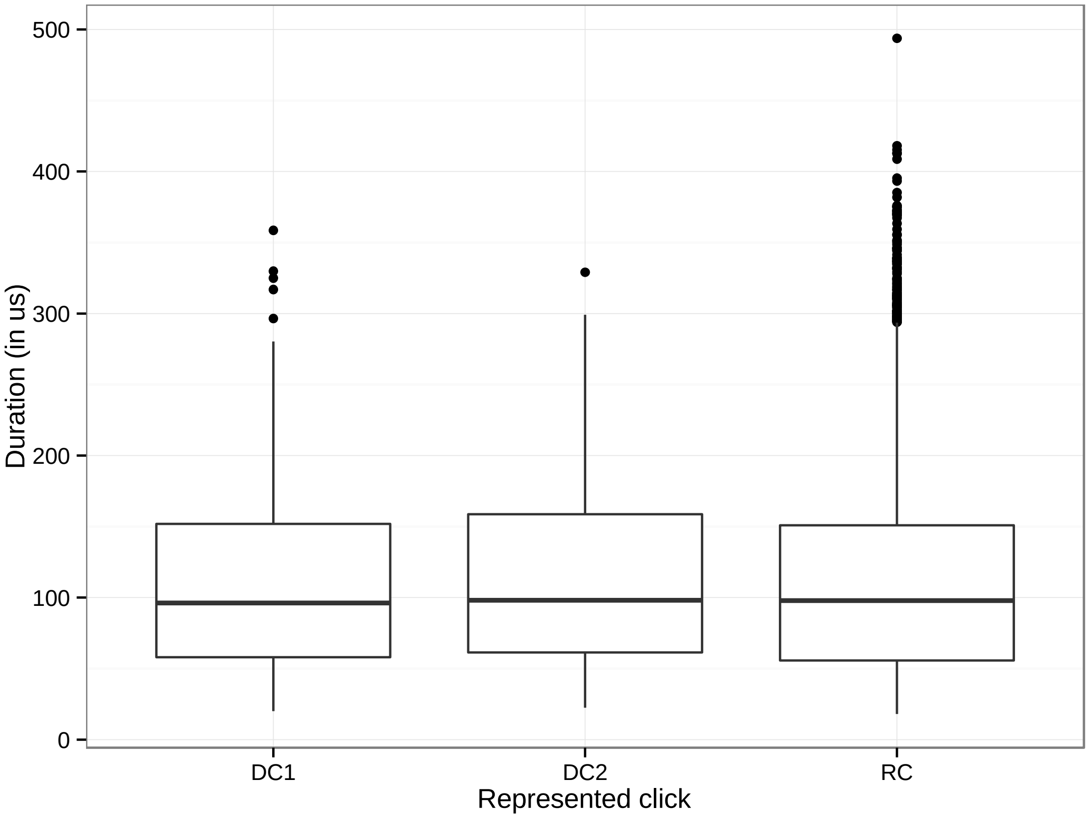

Figure 6.1. Boxplots of click duration (in μs) for the first and second click in a double click (DC1 and DC2), and all other regular clicks (RC) in all click trains with the proportion of the first ICI in a click train < 0.5 the median ICI for the entire train, for Blainville's beaked whales.

As an alternative method to show similarity across double and regular clicks, I plotted a waveform and Wigner plot from a double click and regular click from a DTag recording from a Blainville's beaked whale (Figure 6.2). This should be considered illustrative rather than systematic, but it was difficult to be more rigorous because the distortions introduced by tissue pathways when recording tagged animal clicks mean that many measures of frequency content are unreliable (Johnson *et al.*, 2009). Finally, because of the depths at which whales are producing double clicks (see below), not near the surface or the sea bed in most cases, I am certain the second click in a double click is not an environmental reflection. The ICIs of the double clicks analysed here are also too large to consider the second click being a reflection of the first click from within the head of the whale as shown in Belugas (Au *et al.*, 2012).

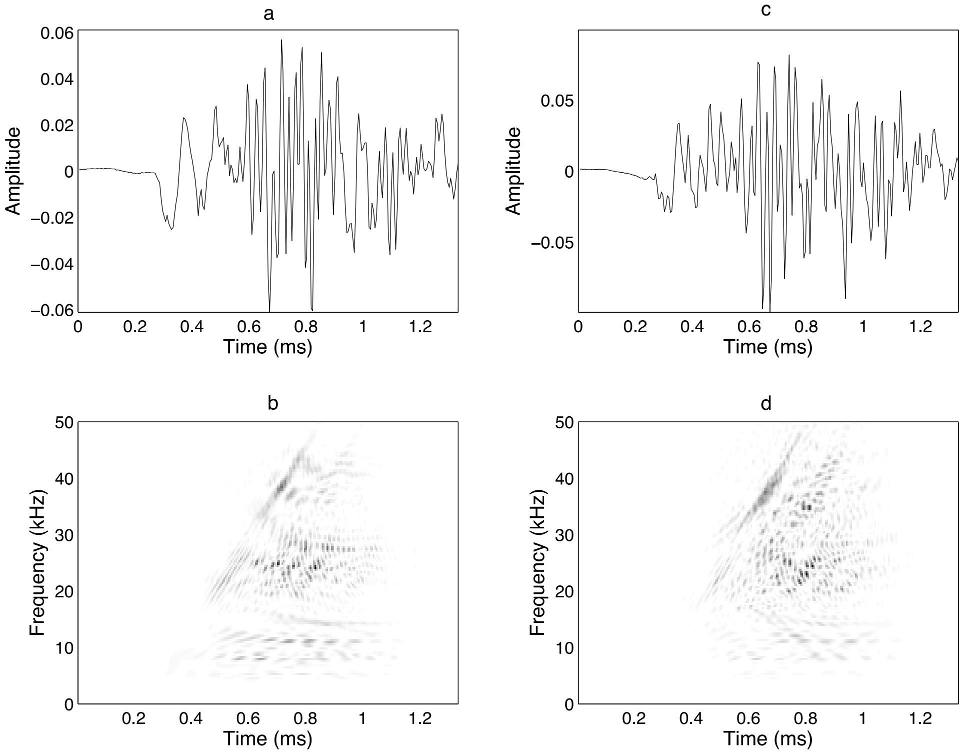

Figure 6.2. Waveforms and wigner plots for one click of a double click (a) and (b), and a regular click (c) and (d), from a DTag recording of a Blainville's beaked whale.

As an investigation into the response variable, prop_ICI, the proportion of the ICI of the first two clicks of a click train with respect to the median of all other ICIs in the click train, I plotted histograms for each species looking for bimodality (Figure 6.3). I highlighted proportions < 0.5 in a darker grey, as a possible indicator of double clicks, and some bimodality can be seen in the Blainville's beaked whales and sperm whales.

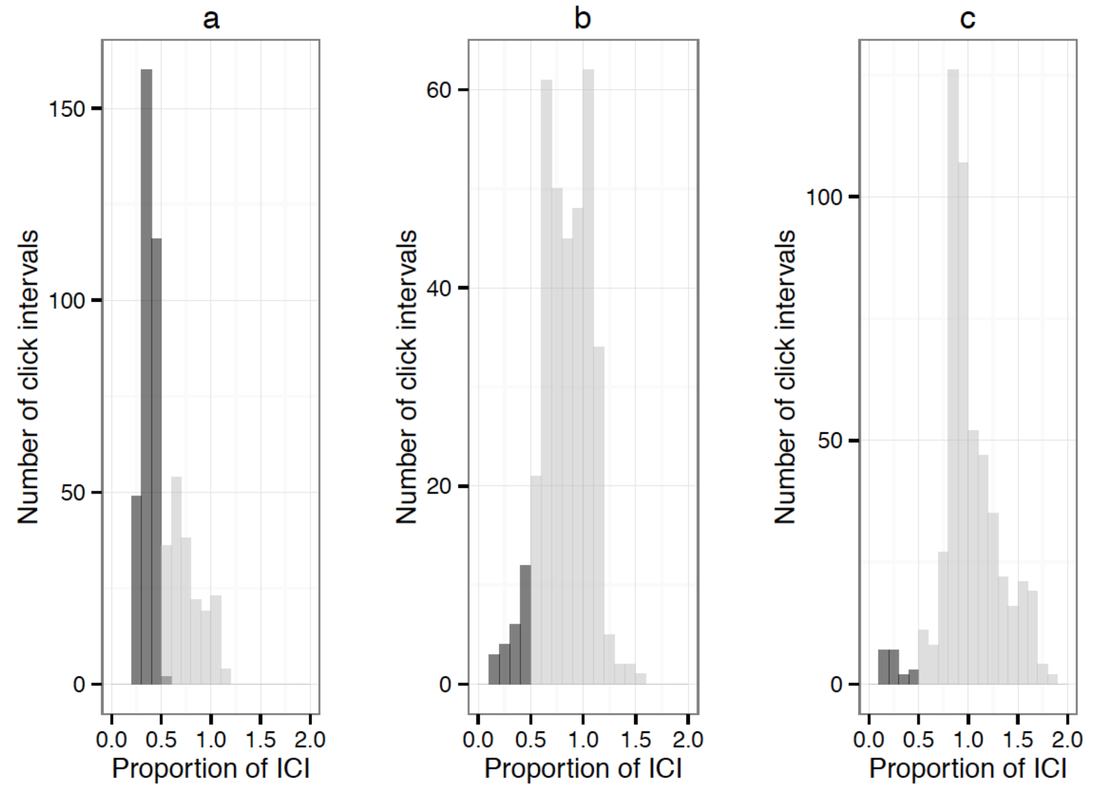

Figure 6.3. Plots for (a) Blainville's beaked whales, (b) Cuvier's beaked whales, and (c) sperm whales, showing the number of click intervals < 0.5 (in darker shading), and >= 0.5 of the proportion of the median ICI for the entire click train.

Finally, as part of an overall investigation into the data before looking at the species-specific model results, I plotted the amplitude of the first two clicks in a click train as a proportion of the median amplitude of all other clicks in the click train, against the proportion of ICI (Figure 6.4). This shows that for all species, the first clicks (those with a low proportional ICI), are relatively quiet compared to the rest of the train. The correlation coefficient of the median amplitude of the first two clicks in a train and the median amplitude of all other clicks in the click train is 0.9889, indicating a positive linear relationship.

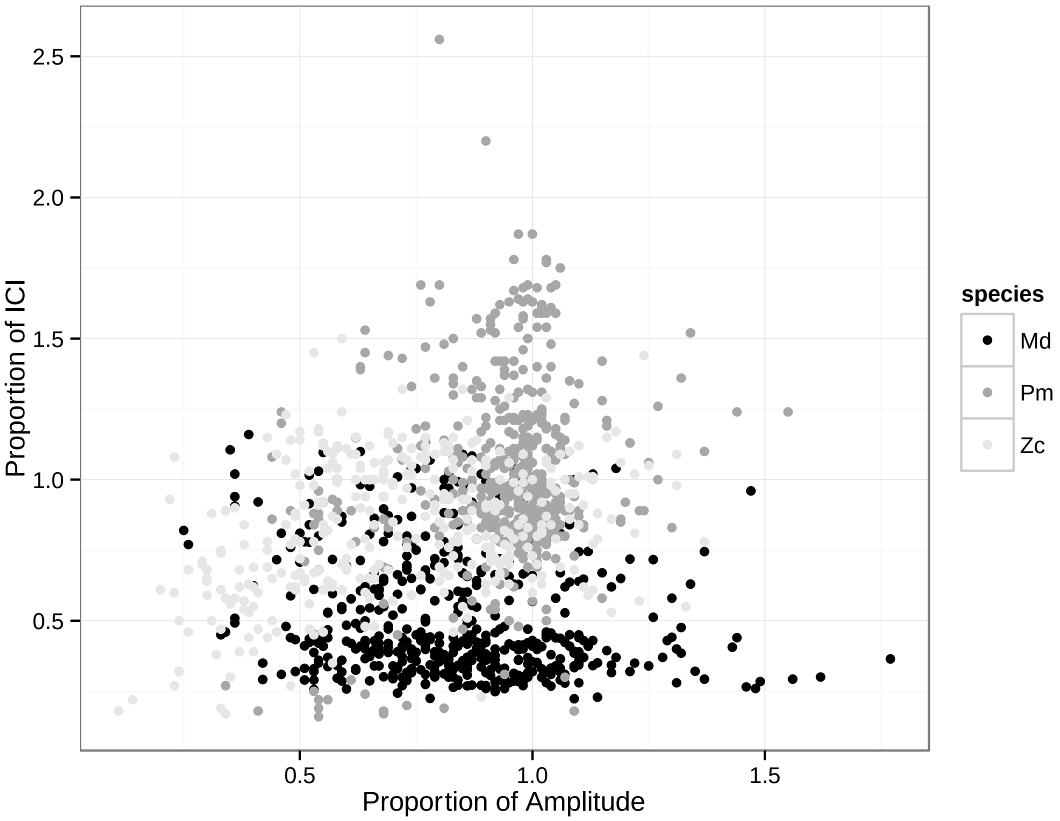

Figure 6.4. The amplitude of the first two clicks of each click train as a proportion of the amplitude of all clicks in the click train, plotted against the proportion of ICI of the first two clicks in the click train (Md = Blainville's beaked whales; Pm = sperm whales; Zc = Cuvier's beaked whales).

6.3.2 Double click use in Blainville's beaked whales

The tagged Blainville's beaked whales often produced two clicks at the start of a click train with a considerably shorter ICI than the median of the ICI for the entire click train (i.e. < 0.5 63% of the time; Figure 6.3. (a)), and then proceed to a regular ICI for the remainder of the click train immediately, with very little 'ramp-up' of ICI (Figure 6.5).

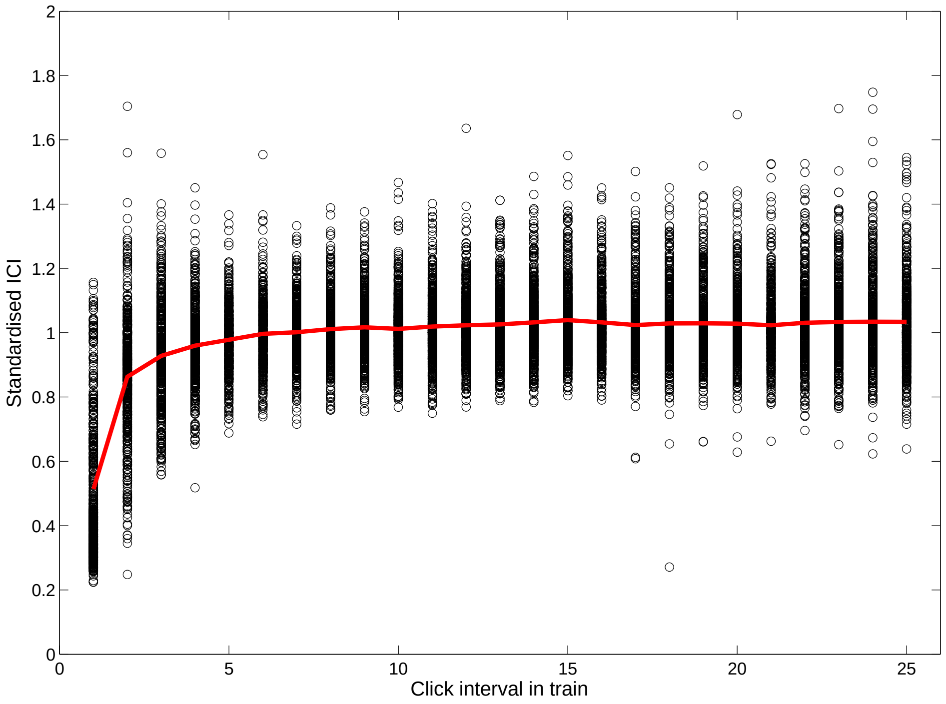

Figure 6.5. Click intervals standardised to the click train median ICI for all analysed Blainville's beaked whale click trains. The red line shows mean values for each click train interval.

The estimated random effects (produced by including the individual animal [tag_id] as a random effect in the model) showed significant overlap with each other (Appendix 6.1, Figure A.6.1.1). This indicates differences in model outputs were not due to different whales. Therefore I removed the random effect of individual whale and used a generalised linear model. The model included all parameters except age, as all Blainville's beaked whales in this study were adults. There were seven models with a ΔAIC less than 3 from the best model, indicating model selection uncertainty. Therefore results from these seven models were averaged (weighted by each model's Akaike weight), and the relative variable importances (shown as the summed Akaike weights in Table 6.2) suggest that the important variables were whether or not there was a buzz before a click train, the depth of the animal at the time of the production of a click train, and how long the animal was into the dive. The response variable was the proportion of ICI of the first two clicks, and the smaller this is, the higher the likelihood of a double click, therefore negative coefficient estimates, as seen for 'Buzz before' and 'Time from first train' in Table 6.2, mean that the factor is associated with double clicks. A typical dive has depth ranges from approximately 500 m to 1000 m during the clicking phase, so this effect size represents a 0.08 increase in the proportion of ICI of the first two clicks over the average depth range of a dive.

Table 6.2. Click train effects for Blainville's beaked whales. Summed Akaike weights ($\sum\omega_i$), model averaged estimates and their standard errors for click train variables from GLM analysis.

Variable	$\sum\omega_i$	Estimate	Std. Error
Buzz before	1.00	-0.3139	0.0162
Depth	1.00	1.609e-04	5.389e-05
Time from first train	1.00	-2.982e-05	1.224e-05
Buzz after	0.60	0.0025	0.0152
First train of dive	0.42	0.0801	0.0694
Sex	0.23	0.0039	0.0184

I have plotted the three variables whose summed Akaike weights added to 1, indicating they were present in all seven models that were averaged, and are therefore important predictors of double click production in Blainville's beaked whales. Buzzes occurred before Blainville's beaked whale click trains in this analysis 67% of the time, and 86% of those trains began with a standardised ICI < 0.5 (Figure 6.6).

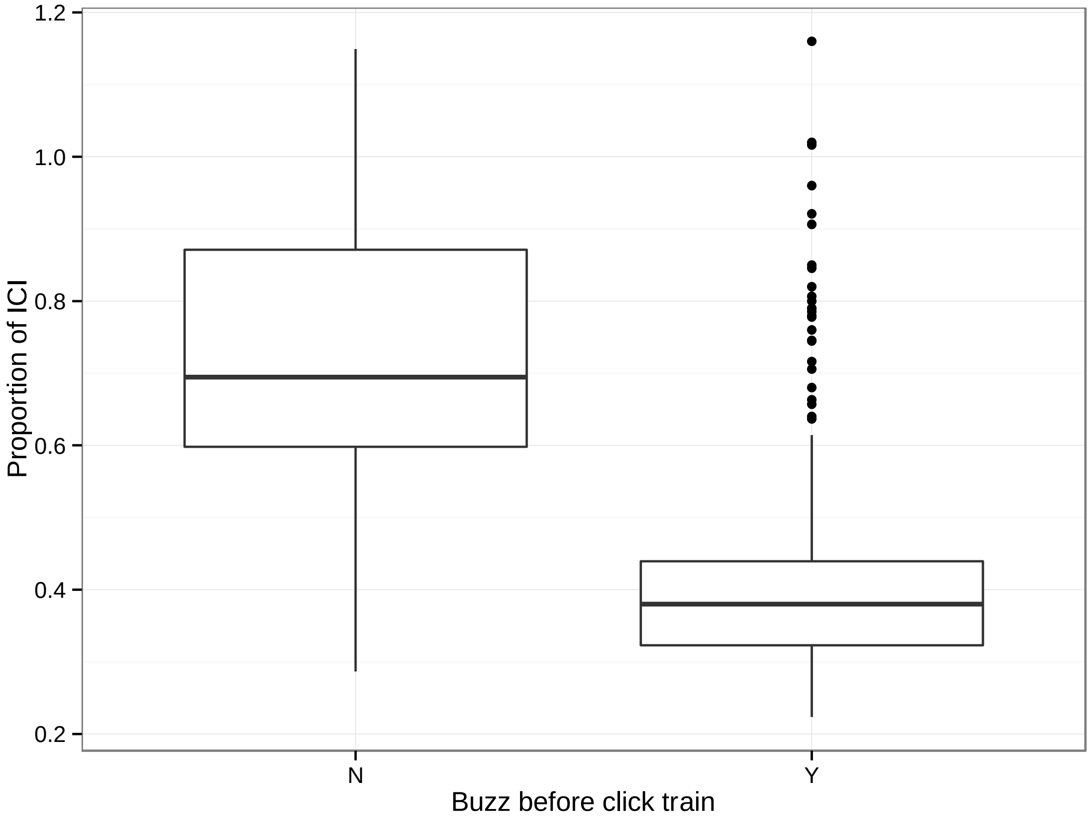

Figure 6.6. Distributions of the first ICI in a click train (expressed as a proportion of the median ICI for the entire train) for trains that were and were not preceded by a buzz.

Blainville's beaked whales produce the majority of their double clicks between depths of approximately 700 and 1050 m (Figure 6.7). These depths are coincident with where they would find prey, and therefore produce buzzes, already shown to be a variable of relative importance (Table 6.2).

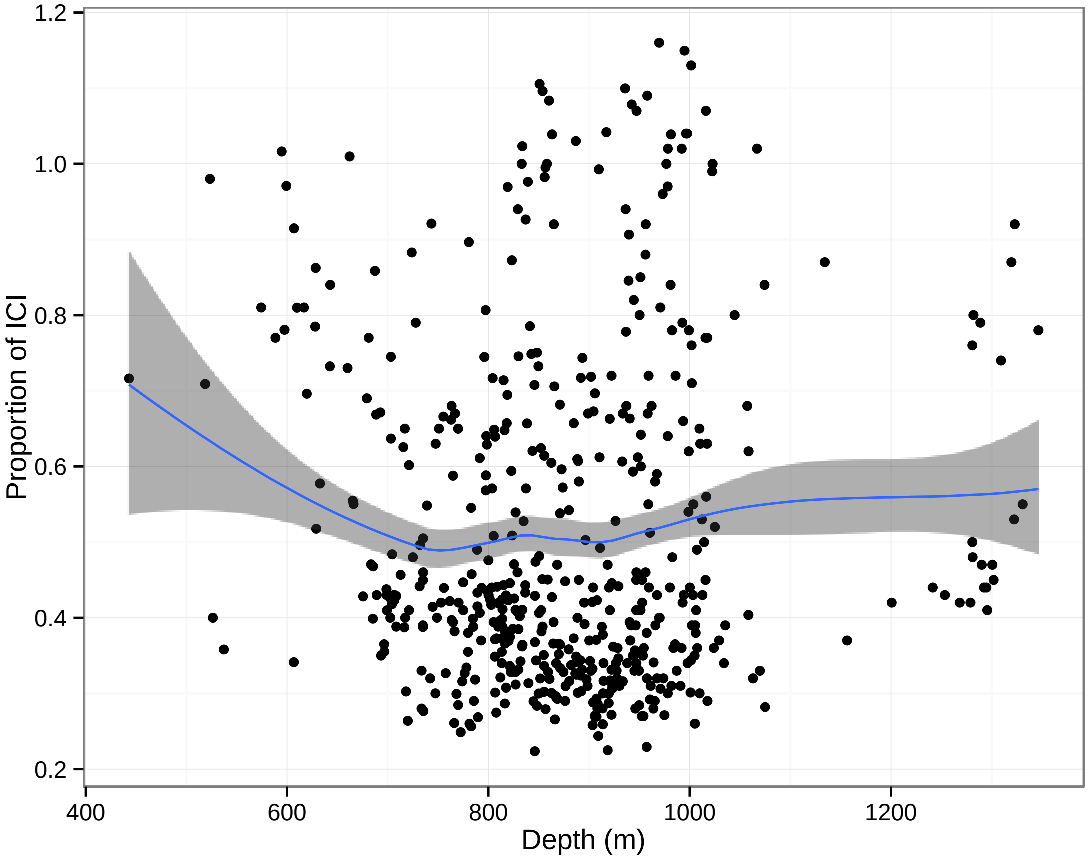

Figure 6.7. The depth of each click train, taken at the time of the first click of the click train, plotted against the first ICI in the click train (expressed as a proportion of the median ICI for the entire train). The blue line represents the fitted line from the best model.

There are more double clicks (shorter first ICIs in a click train) at the start of a Blainville’s beaked whale dive (Figure 6.8), however the double clicks are occurring throughout the dive.

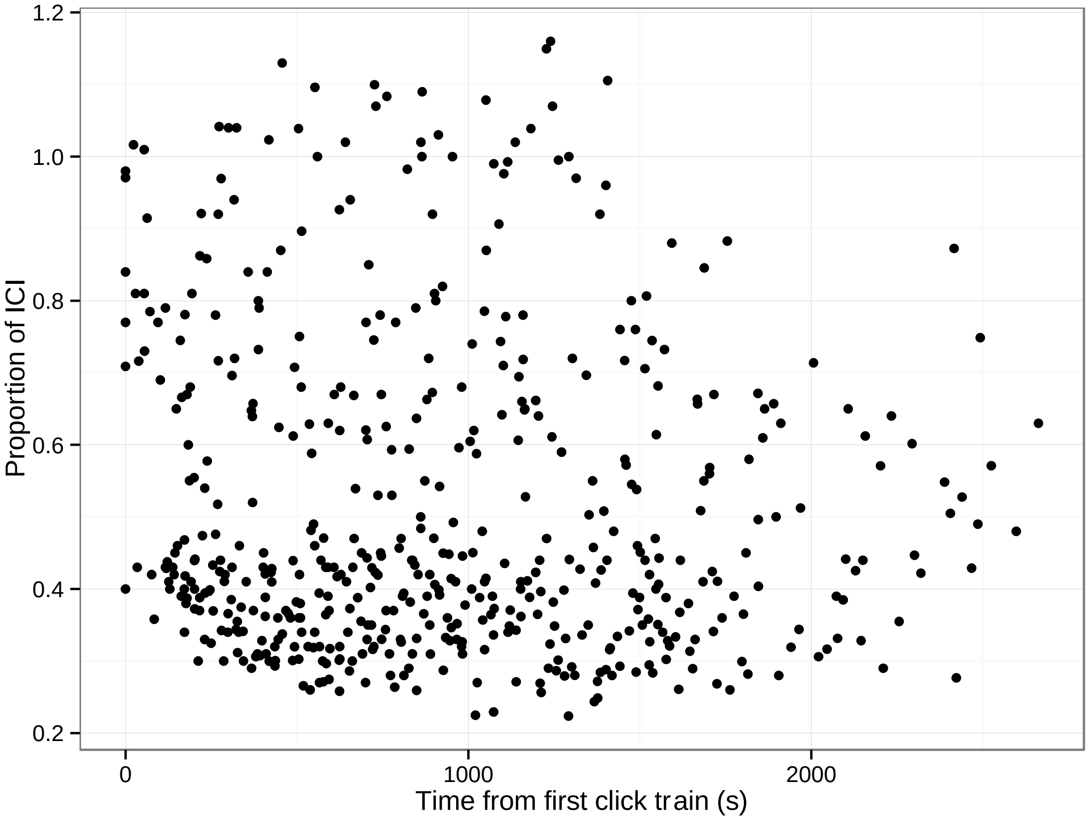

Figure 6.8. The time since the first click train (in seconds), plotted against the first ICI in the click train (expressed as a proportion of the median ICI for the entire train).

6.3.3 Double click use in Cuvier's beaked whales

The tagged Cuvier's beaked whales also produced first clicks in a click train with a smaller ICI than the median ICI of the remaining clicks in each train (Figure 6.9). The first clicks start, on average at 0.8 of the click train median ICI, and approach the median values over the next two or three intervals, so the distinctiveness of the double clicks are not as great as in the Blainville's beaked whales, whose ICIs became immediately regular after the first interval.

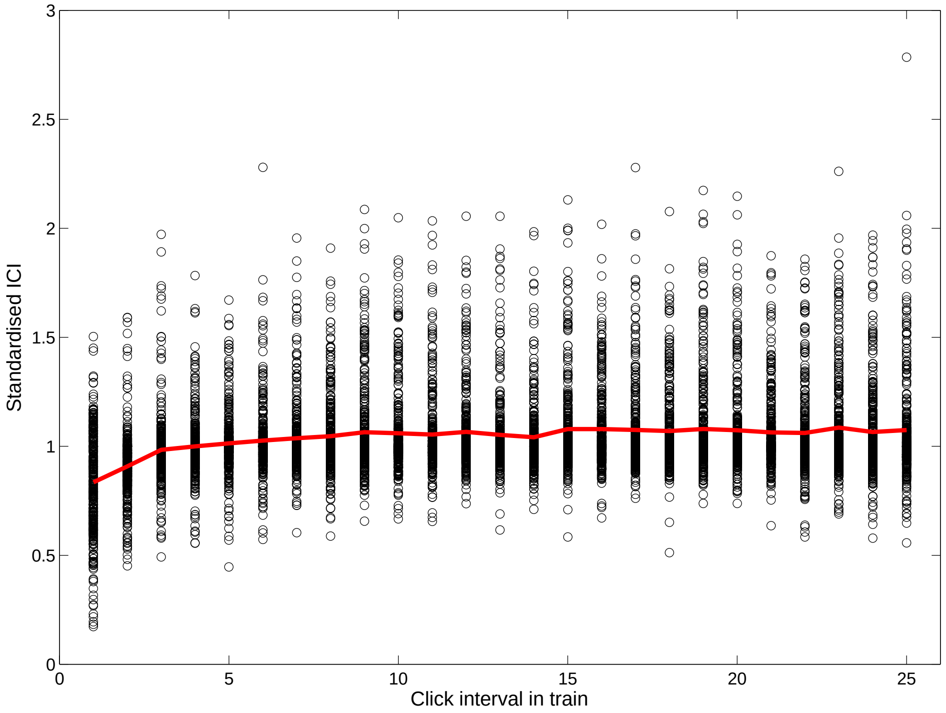

Figure 6.9. Click intervals standardised to the click train median ICI for all analysed Cuvier’s beaked whale click trains. The red line shows mean values for each click train interval.

The estimated random effects from the mixed effects model for Cuvier’s beaked whales with all predictor variables showed no overlap, and therefore substantial variability between individuals (Appendix 6.1, Figure A.6.1.2). This was confirmed by comparing the AIC of the original model (-229.5) with the AIC from a glm without the random effect but identical in all fixed effects (-216.1). Therefore in this case the random effect was retained in the model. There were eight models with a ΔAIC less than 3 from the best model, indicating considerable model uncertainty. These models were averaged, and the relative variable importances (shown as the summed Akaike weights in Table 6.3) suggest that important variables included all the important variables for Blainville’s beaked whales, as well as whether or not the click train was the first train of the dive.

Table 6.3. Click train effects for Cuvier's beaked whales. Summed Akaike weights ($\sum\omega_i$), model averaged estimates and their standard errors for click train variables from GLMM analysis.

Variable	$\sum\omega_i$	Estimate	Std. Error
Buzz before	1.00	0.0944	0.0195
Depth	1.00	5.249e-04	5.894e-05
First train of dive	1.00	0.2034	0.0749
Time from first train	1.00	3.677e-05	1.309e-05
Sex	0.61	-0.2554	0.1242
Buzz after	0.46	-0.0257	0.0192
Age	0.36	-0.1090	0.1239

Because the estimated random effects from individuals showed some differences, I plotted each individual's first click intervals (Figure 6.10). The mean distribution of standardised first ICIs was centred on 1 for both adults, implying little or no occurrence of double clicks at the start of their click trains. This was in contrast to the subadults whose click trains began with an ICI of approximately 0.6 of the median of the ICIs in the rest of the click train. The relative variable importances do not highlight age as an important factor, however the negative coefficient estimate indicates it is associated with double clicks (Table 6.3), although the standard errors are large, and Figure 6.10 shows that there is an apparent ontogenetic loss of the double click at the start of the train in Cuvier's beaked whales.

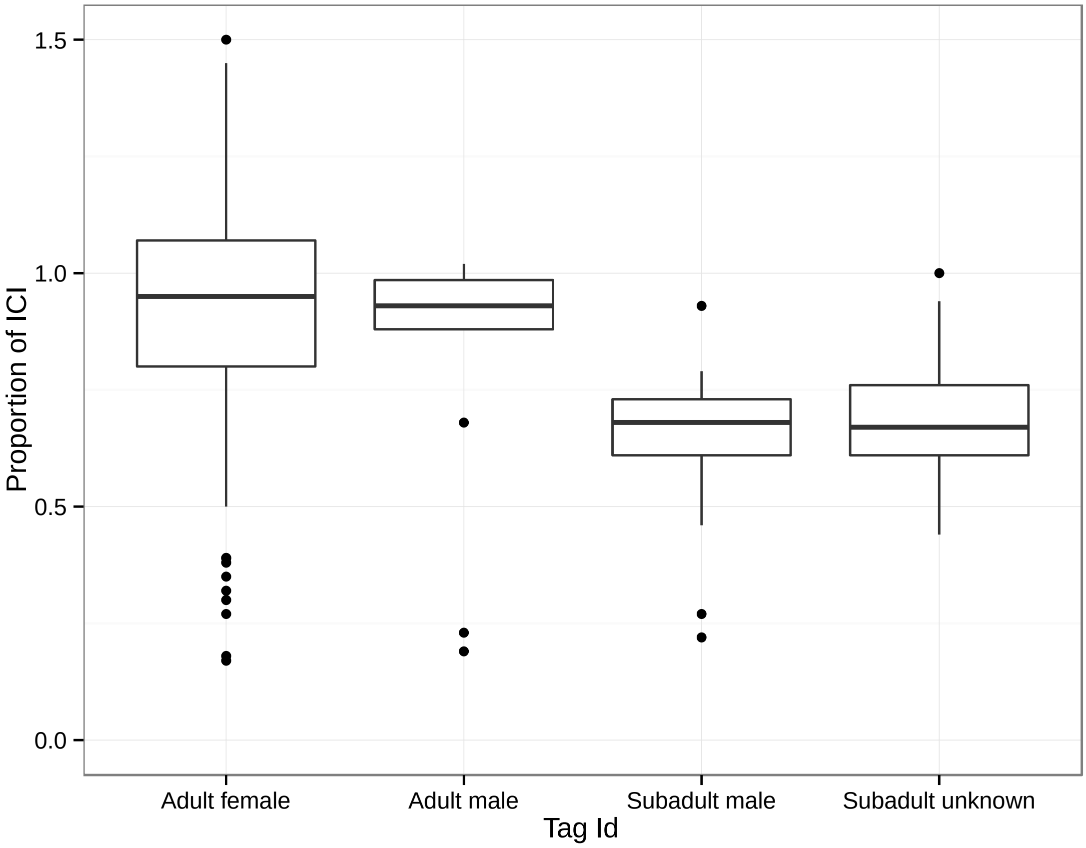

Figure 6.10. The proportion of the ICI of the first two clicks in all click trains for two adult and two subadult Cuvier's beaked whales.

I have plotted the four variables with high relative importance values (Table 6.3), from the averaged model results for Cuvier's beaked whales (Figure 6.11). There do not appear to be large differences whether there was or was not a buzz before a click train (a), or whether the click train was the first of the dive (b). The depth (c) and time into the dive (d) plots relative to the proportion of ICI of the first two clicks in a train show a cluster of clicks at depths > 1500 m, and corresponding longer times into the dive. These clusters are click trains from the single adult male, and so the model results might be sensitive to the presence of this particular individual and should thus be treated with caution.

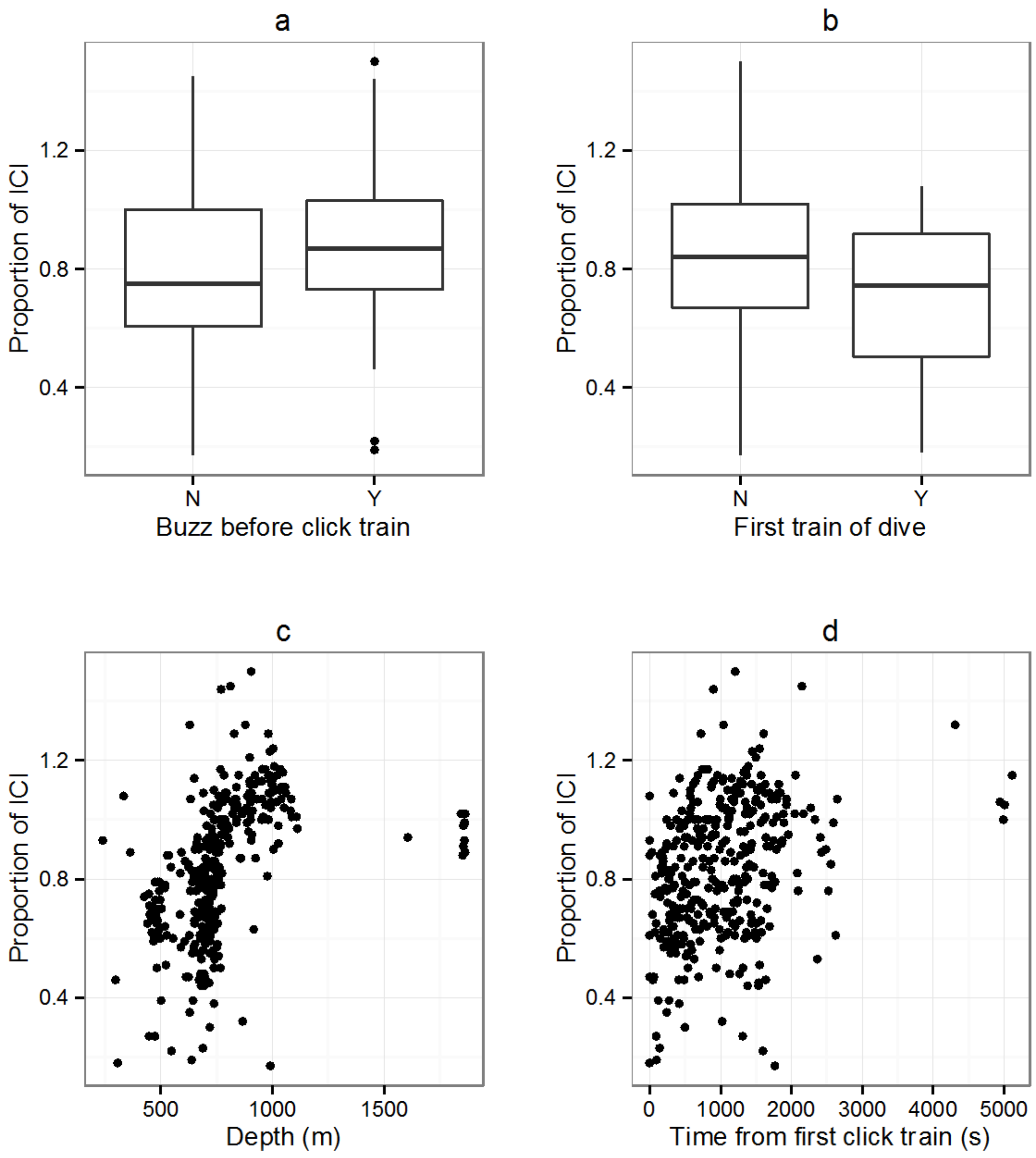

Figure 6.11. The four important variables as per the model averaging; whether or not there was a buzz before a click train (a), whether or not the click train was the first in the dive (b), the depth (c), and the time since the first click train (d), plotted against the proportion of the ICI of the first two clicks in all click trains for the four Cuvier's beaked whales.

6.3.4 Double click use in sperm whales

The mean of the first ICI across click trains for sperm whales does not indicate the production of double clicks, however there is a bimodal distribution in the prop_ICI value (also shown in Figure 6.3) with a sub-group of trains having a first interval whose standardised ICI is lower than 0.5 (Figure 6.12). This indicates that while sperm whales do produce double clicks, they only do so rarely.

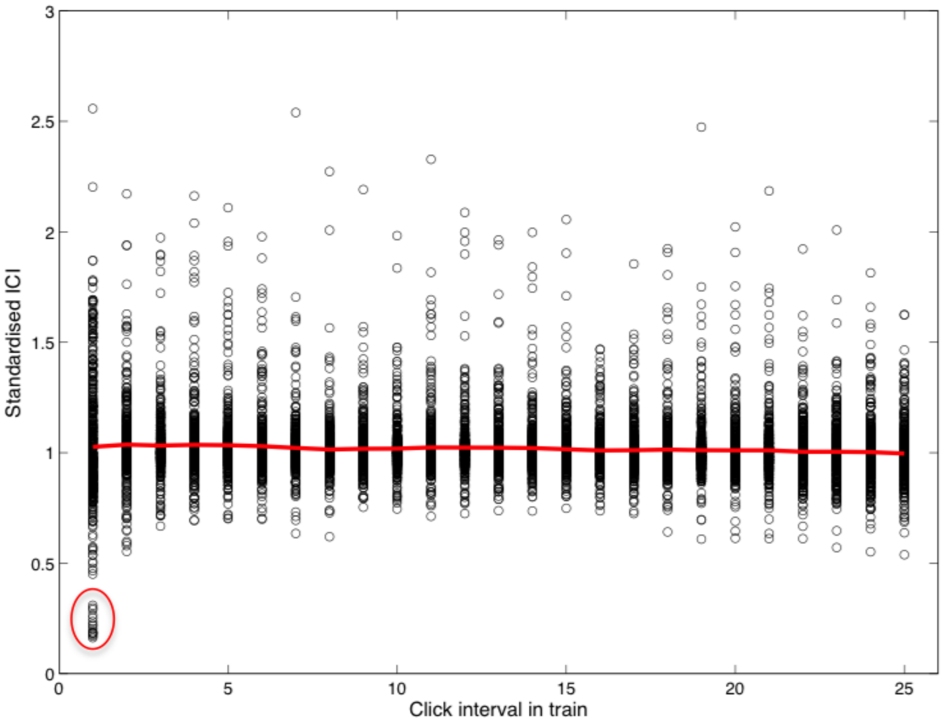

Figure 6.12. Click intervals standardised to the click train median ICI for all analysed sperm whale click trains. The red line shows mean values for each click train interval, and the clicks in the red circle indicate double clicks are occurring. Note the discontinuity in the distribution.

A mixed effects model for sperm whales resulted in the estimated random effects from the variable of individual animal showing some overlap and therefore some variability between individuals (Appendix 6.1, Figure A.6.1.3). Removing the random effect variable produced a slightly reduced AIC (99.85) than the full model (100.22), therefore the random effect was removed and a regular glm was fit to the data. As all animals were presumed to be adults, age was not included in the model (the animal whose tag was Sw03_156a, which was recorded in field notes as either a subadult male or adult female was presumed to be an adult female for this analysis). There were five models with a ΔAIC less than 3 from the best model that were averaged, resulting in four high relative variable importances (Table 6.4); the presence of a buzz after a click train, whether or not the click train was the first of that dive, the sex of the whale and the depth the click train was produced.

Table 6.4. Click train effects for sperm whales. Summed Akaike weights ($\sum\omega_i$), model averaged estimates and their standard errors for click train variables from GLM analysis.

Variable	$\sum\omega_i$	Estimate	Std. Error
Buzz after	1.00	0.1209	0.0241
First train of dive	1.00	-0.6565	0.0752
Sex	1.00	-0.2858	0.0418
Depth	0.90	1.169e-04	5.673e-05
Time from first train	0.36	-8.820e-06	7.941e-06
Buzz before	0.29	0.0191	0.0248

Although the random effect of individual animal was not included in this model, its estimated effects showed some overlap and therefore I plotted the proportional first ICIs for each individual (Figure 6.13). Adult male sperm whales appear to be producing more first clicks with smaller ICIs than adult female sperm whales. However, there are standardised ICIs that are outliers for each of the females that are all around 0.25. This is because both adult male tags only recorded data for the duration of one dive, and neither animal began any click train with an ICI < 0.5 of the median of the rest of the trains ICIs. In contrast, all three adult females produced double clicks at the start of their dives 100 percent of the time, where the first click train of a dive was included in the analysis. This result indicates that classifying Sw03_156a as an adult female was the correct choice, as the whale is producing double clicks in the same manner as the whales that are known to be adult females.

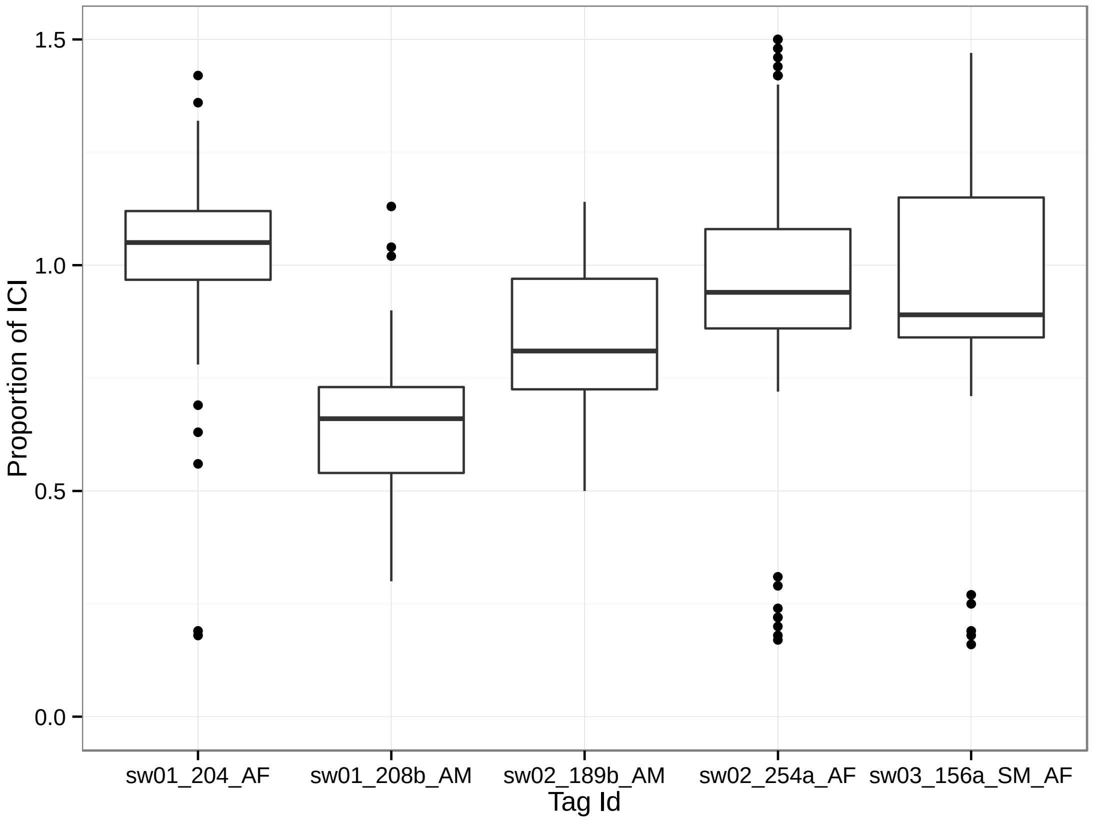

Figure 6.13. The standardised ICI of the first two clicks for the five sperm whales.

I have plotted the four variables with high relative importance values (Table 6.4), from the averaged model results for sperm whales (Figure 6.14). The strong result that sperm whales produce a double click on the first train of a dive corresponds to the result of producing a double click when a buzz has not been produced. This is because it is unlikely that the whale will have been able to detect and localise on prey (requiring a buzz) at the shallow depths where it produces the first click train of a dive. For this plot I indicated tag Sw03_156a as unknown sex, and its results mirror that of the adult female, confirming classifying this animal as an adult female for the model was a good choice.

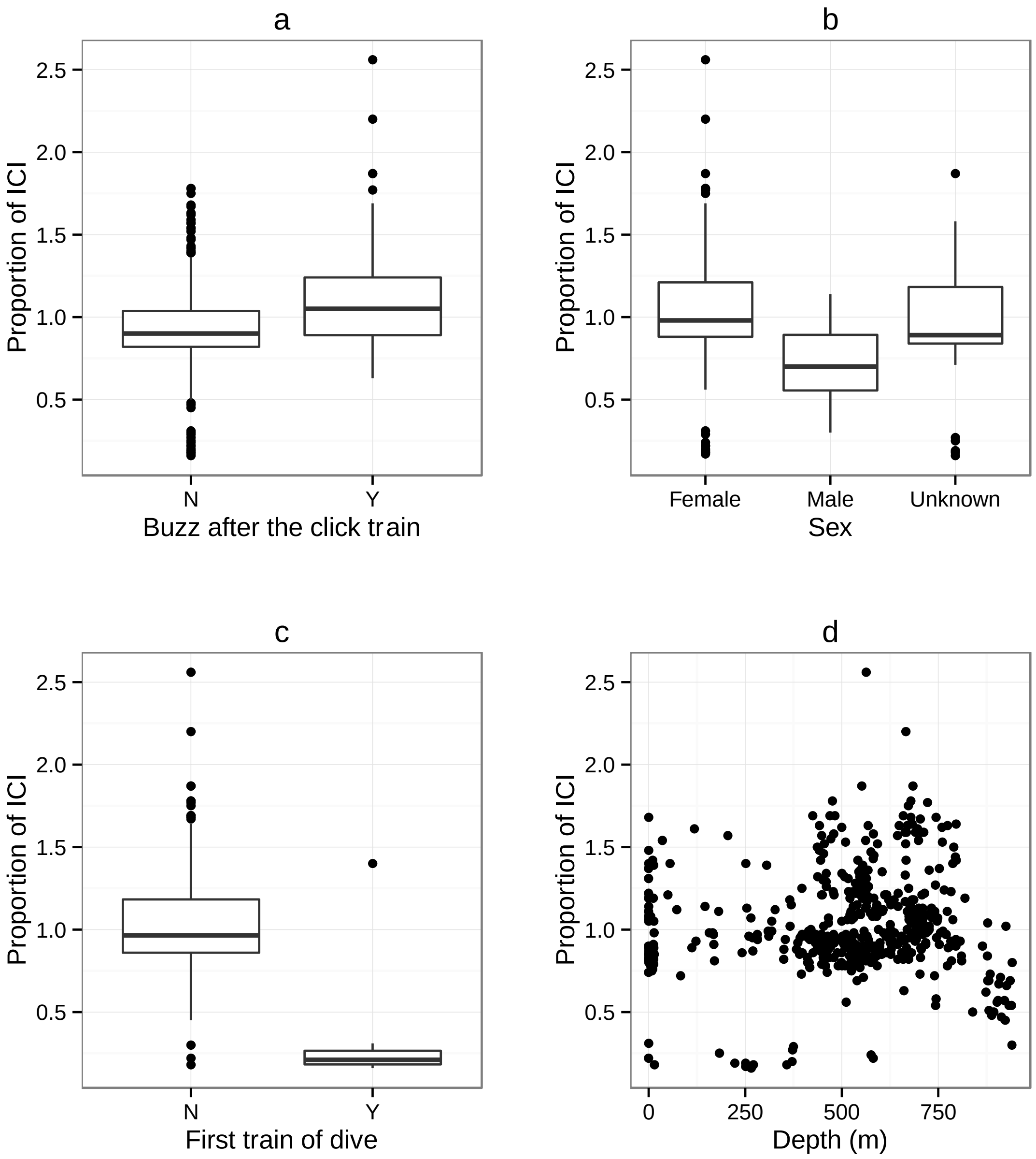

Figure 6.14. The four important variables as per the model averaging; whether or not there was a buzz after a click train (a), the sex of the animal producing the click train (b), whether or not it was the first click train of the dive (c), and the depth (d), plotted against the proportion of the ICI of the first two clicks in all click trains for sperm whales.

6.3.5 Comparative patterns of double click production

There were four variables that were relatively important for at least two of the species, so I have plotted those to compare across species. Blainville's beaked whales clearly produce more double clicks following a buzz than if a buzz was not produced. In contrast, the other two species' mean proportion of ICI (indicating a double click if it is small), does not appear to differ depending on the production of a buzz before a click train (Figure 6.15). However, there is a cluster of outliers with a small proportional ICI shown for sperm whales if there was not a buzz preceding a click train, supporting the results of sperm whales more likely to produce a double click if a buzz has not been produced (Figure 6.14).

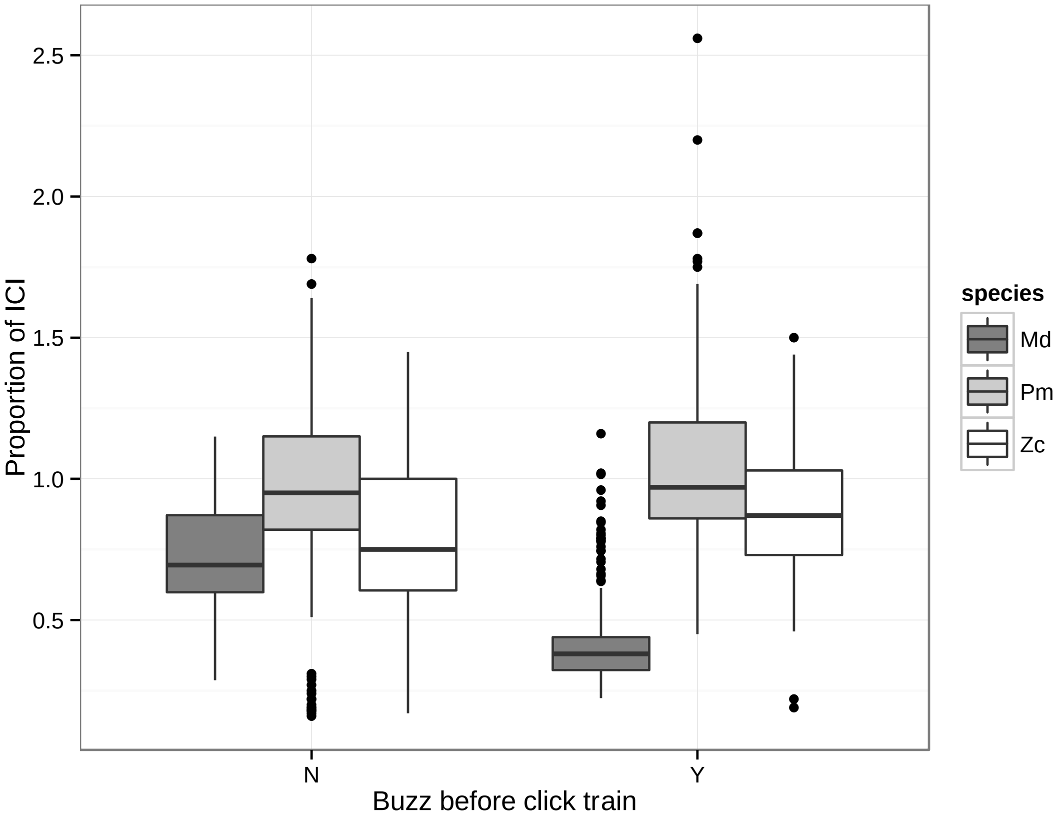

Figure 6.15. Distributions of the first ICI in a click rain (expressed as a proportion of the median ICI for the entire train) for trains that were and were not preceded by a buzz, for all three species (Md = Blainville's beaked whales; Pm = sperm whales; Zc = Cuvier's beaked whales).

At the time of the first train of a dive, it is unlikely there will have been a buzz produced, as the animal would just have begun its prey searching phase, and is likely to be at a depth less than 500 m, explaining the pattern evident for sperm whales and Cuvier's beaked whales who are more likely to produce a double click on the first click train of a dive (Figure 6.16), and at shallower depths (Figure 6.17). Cuvier's beaked whales produce double clicks between approximately 300 and 1000 m and, whereas Blainville's beaked whales are producing them deeper, more in coincident with their foraging depths, between approximately 700 and 1050 m, although Cuvier's beaked whales regularly dive to and forage at greater depths than Blainville's beaked whales (Schorr *et al.*, 2014).

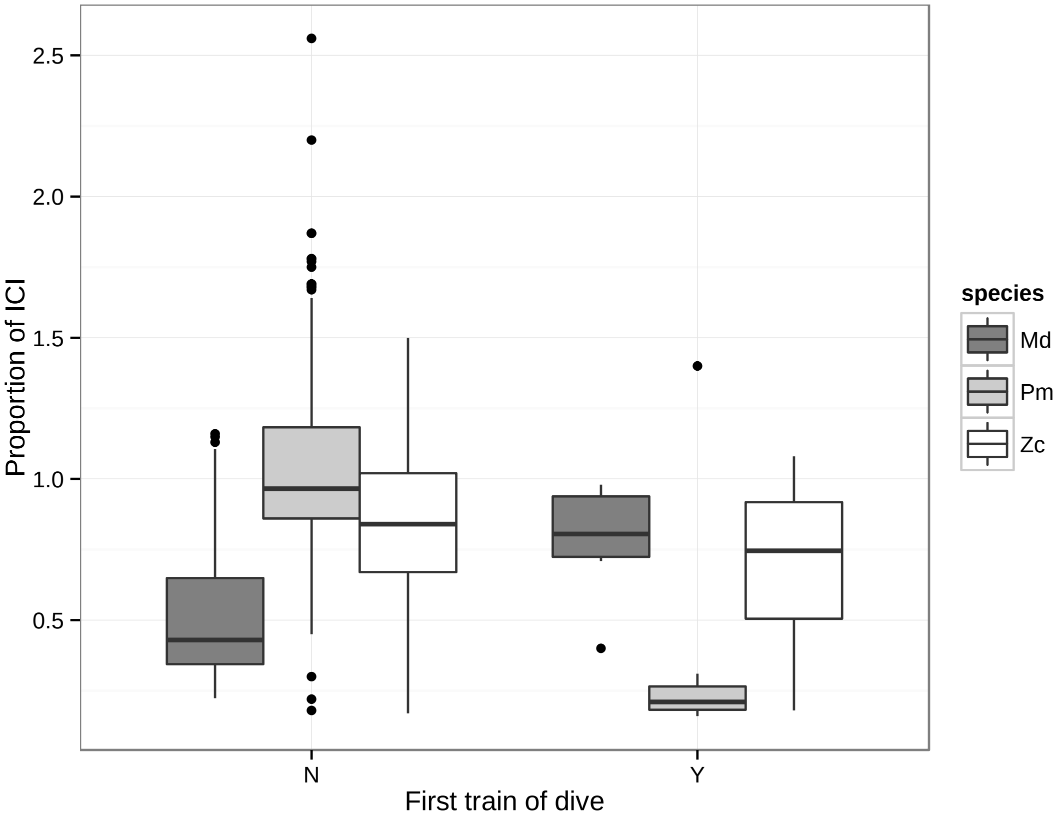

Figure 6.16. Distributions of the first ICI in a click train (expressed as a proportion of the median ICI for the entire train) for trains that were and were not the first click train of a dive, for all species (Md = Blainville's beaked whales; Pm = sperm whales; Zc = Cuvier's beaked whales).

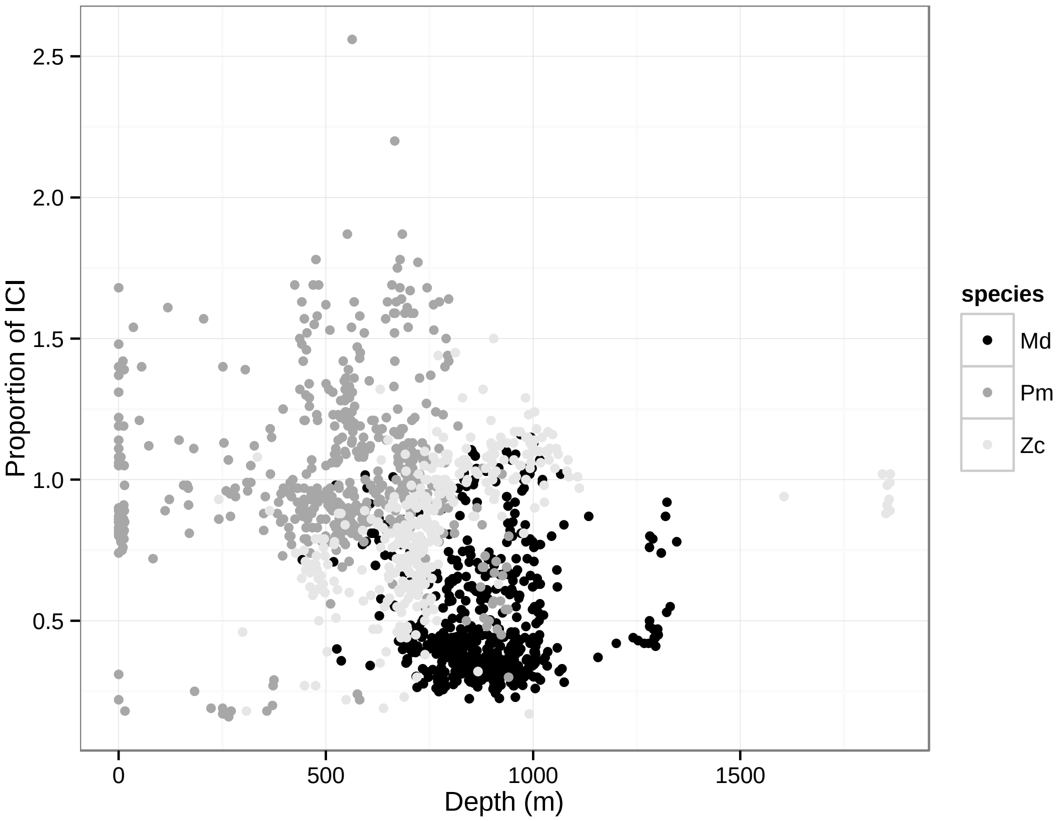

Figure 6.17. The depth of each click train, taken at the time of the first click of the click train, for all three species, plotted against the ICI of the first two clicks in the click train (expressed as a proportion of the median ICI for the entire train).

In line with the results so far, Blainville's beaked whales are producing double clicks throughout their dives, Cuvier's beaked whales produce more double clicks at the start of their dives, and sperm whales are producing them only at the beginning (Figure 6.18).

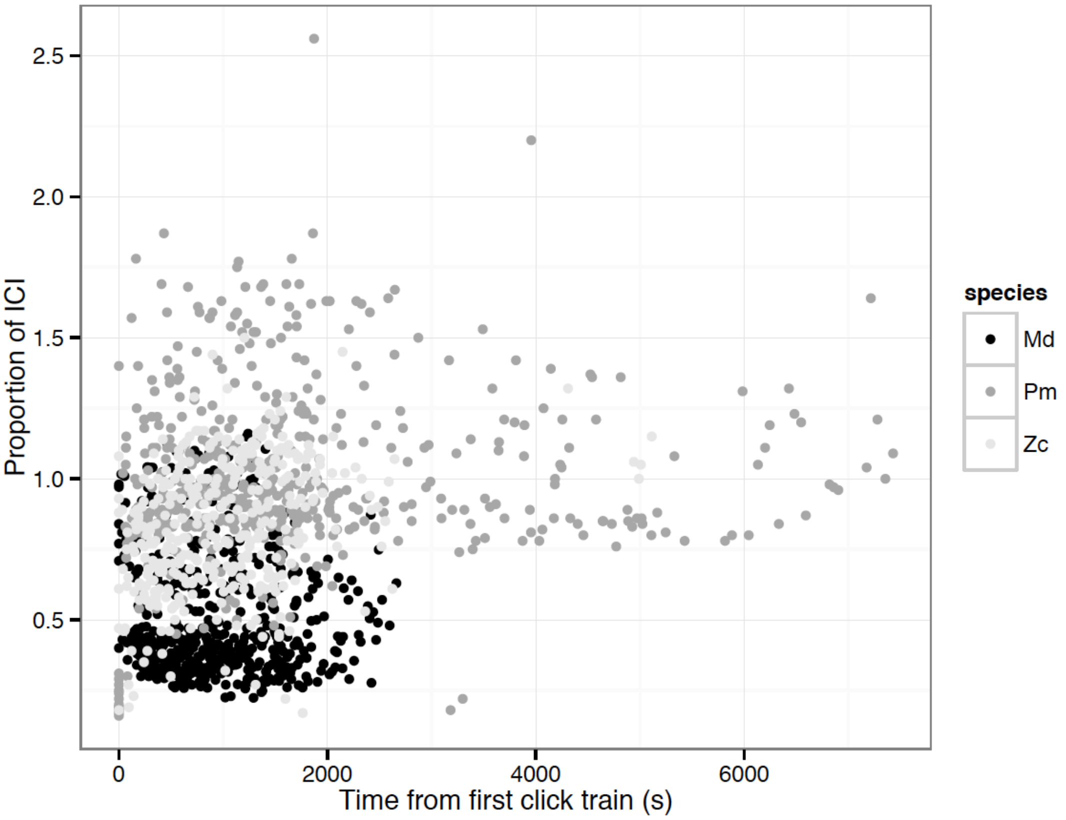

Figure 6.18. Distributions of the time since the first click train, plotted against the ICI of the first two clicks in a train (expressed as a proportion of the median ICI for the entire train), for all species (Md = Blainville's beaked whales; Pm = sperm whales; Zc = Cuvier's beaked whales).

6.4 Discussion

These results show notably strong but different patterns across the three species studied. Blainville's beaked whales produce more double clicks at the start of the majority of their click trains compared to the other species in all age and sex classes analysed. Comparatively only subadult Cuvier's beaked whales are producing double clicks, and only occasionally, whereas only sperm whale adult females produce double clicks, and only on the first train of every dive, but not otherwise. These patterns are intriguing, but in many ways this exploratory analysis raises more questions than it answers.

The single variable that was highlighted as having high relative importance in the models of all three species was depth. However the effect of this variable on the production of double clicks was not driving the production of double clicks across the species in the same way, i.e. with increased depth came increased production of double clicks. Blainville's beaked whales produce double clicks at depths where they are foraging, producing them on almost every click train following a buzz. Sperm whales in contrast only produce double clicks at shallow depths; they produce them on the first train of a dive. Finally Cuvier's beaked whales produce more double clicks during the first portion of their dives and therefore somewhat shallower depths than Blainville's beaked whales.

The differences in the amount of double clicks produced by the three species analysed in this chapter may be linked to evolution. It is thought that the difference between swiftlets that do and do not produce double clicks is possibly an evolved specialisation in orientation skills, with the single click species having evolved from the double click species to produce solely single clicks, potentially avoiding interference between the source and echoes (Price *et al.*, 2004). However, there may be a trade off in the production of single clicks being more energetically demanding, explaining why only two known species of swiftlets have evolved to single click echolocation (Price *et al.*, 2004).

If the production of single clicks is more demanding, this may explain why sperm whales, the species with the most derived sound production apparatus, produce so few double clicks, and subadult Cuvier's beaked whales overcome double click production ontogenetically, with Blainville's beaked whales being the least derived species in this scenario. Although there is the possibility that the clicks of young Cuvier's beaked whales, unlike young Blainville's beaked whales clicks (Chapter Five), are different from adult clicks, therefore explaining the difference in production across age class for this species although this is unlikely based on the findings of my study. However, as both clicks in the double clicks for all three species are noticeably lower in amplitude than their regular clicks (Figure 6.4), double clicks of odontocetes may not be linked to echolocation. In harbor porpoises, it has been suggested that clicks with short ICIs cannot be processed individually with their corresponding echoes (Wisniewska *et al.*, 2012). Therefore double clicks may be the function of a physiological requirement for deep diving odontocetes, which explains why they are being produced at the start of a click train.

It is possible that the first click in a dive may be significantly different due to the phonic lips having been parted for surface breathing. If the suggestion that phonic lips require a layer of fluid (Cranford *et al.*, 2011) stands, double clicks may be allowing these fluid levels on the lips to be re-established before reliable single clicking can commence. Moreover, the production of double clicks may be related to the adjustment of the spacing and tension of the phonic lips, coupled with re-pressuring the nasal passages after some pause, i.e. a surface interval or time between click trains.

Following this hypothesis, it would appear that Blainville's beaked whales need to fine-tune their phonic lips more often than the other two species, for example seemingly after each foraging capture attempt, i.e. after they produce a buzz. The lesser requirement in sperm whales and Cuvier's beaked whales to produce double clicks may be related to the differences in the clicks they are producing, although it must be said that the characteristics of Cuvier's beaked whale clicks are very similar to those of Blainville's beaked whale clicks. Blainville's beaked whale clicks have a click duration = 250 μs, an ICI = 200-400 ms, -10 dB bandwidth = 25-51 kHz (Johnson *et al.*, 2006) and a 3 dB beamwidth and directivity index of 13° and 23 dB respectively. Cuvier's beaked whale clicks have a click duration ~ 200 μs, and ICI ~ 400 ms, -10 dB bandwidth = 22 kHz, and a 3 dB beamwidth and directivity index of 12.6° and 24.3 dB respectively (Zimmer *et al.*, 2005). Therefore perhaps anatomy is the driver of the differences in double click production. In this scenario the bigger you are, the fewer double clicks you require to 'reset' your phonic lips. Interestingly, the Cuvier's beaked whales are taking a few intervals after producing a double click to achieve regular ICIs, which is in contrast to the Blainville's beaked whales and the sperm whales, who both appear to arrive at median train ICI immediately following the production of a double click.

The question remains are these double clicks communicative in nature? Although the production of double clicks within species is consistent, it is quite different between species. If double clicks are communicative, it could be in the form of cues. The cue for sperm whales is that there are females beginning a foraging dive and for Cuvier's beaked whales, subadults are in the first half of their foraging dive. The cue for Blainville's beaked whales however seems redundant, as there is a high correlation between the production of a double click and when a buzz has been produced, and therefore the cue is that there has been a prey capture attempt. However, this cue is more reliable from buzzes. Why would these cues have been selected for? Perhaps a more likely explanation is that they are not communicative, but an artifact of sub-optimal click production and will eventually be removed entirely from the repertoire of these whales, as is occurring in swiftlets. If this is the case, then further work on more species and differing sex and age-classes may highlight a possible window into the evolutionary history of odontocete echolocation.

Chapter Seven

7 GENERAL DISCUSSION

7.1 Summary of findings

As anthropogenic sound in the ocean increases, its effect on marine mammals must be understood to aid in mitigation and conservation management. Blainville's beaked whales (*Mesoplodon densirostris*) have been shown to be vulnerable to navy sonar (Cox *et al.*, 2006; Tyack *et al.*, 2011). Understanding their communication systems can provide insights as to how all noise pollution affects them, as well as deepening our understanding of the consequences of navy sonar on this species.

However, the underlying question driving this thesis is how the unusual social structure and unique ecological pressures of Blainville's beaked whales have driven the form of communication they employ. They live at physiological and ecological extremes, and provide another alternative social structure for deep-diving odontocetes. Gowans *et al.* (2001) showed that the social structure of northern bottlenose whales (*Hyperoodon ampullatus*) was unexpectedly different to that of sperm whales (*Physeter macrocephalus*), with features of sperm whale societies such as long-term bonds between females and caring for young while mothers forage at depth being absent. Similarly, my study did not show allocare, but did reveal female bonds. Unlike sperm whales, the bonds are not stable and it is not known if the females in the groups are related. Therefore, I have provided further evidence that social evolution in deep-diving cetaceans has led to very different societies despite shared ecological drivers. My findings provide clues into how the social structure of Blainville's beaked whales, shown here to be somewhere between the stable associations of sperm whales and the fission-fusion societies of dolphins and bottlenose whales, came to be.

7.1.1 How are social units formed and maintained?

Members of a group of Blainville's beaked whales remain within approximately ten body lengths of one another at all observed times. They surface and dive in synchrony, usually in the same spatial configuration, with the adult male at the back of the group (pers. obs.). Although they dive to great depths for long durations, they still spend enough time at or near the surface between foraging dives (64%, Arranz *et al.*, 2011) to provide opportunity to choose their associates using visual cues.

The core of Blainville's beaked whale groups is females in the same reproductive state (Chapter Two). These non-random associations may be an example of visually chosen companions, as a female with a calf will be able to see if another female is also with a calf while they are at or near the surface. However, there may also be acoustic cues to aid in finding these preferred associates, as seen in the female Barbary macaques (*Macaca sylvanus*) which produce calls that contain information on their reproductive state (Semple and McComb, 2000). Limited recordings from female Blainville's beaked whales in differing reproductive states did not allow for investigation into either an acoustic signal or cue.

In other group living species with a harem social structure, females choose a group by evaluating signals produced by the male in the group. For example, male great reed warblers (*Acrocephalus arundinaceus*) indicate both their harem size and their philopatry through their whistle (Węgrzyn *et al.*, 2010). Philopatry is preferred in great reed warbler females as an indicator of breeding ground familiarity. In the case of the beaked whales, a female could determine the harem size from the number of whales clicking, and a signal of natal philopatry may help a female avoid related males. I did not investigate for a cue of philopatry, however I did discover sexually distinctive sounds (Chapter Three) that males produce that may enable females in their evaluation of mate choice.

These sexually distinctive sounds have not been described before, and as potential communication sounds, it is worth noting the active space of these sounds is quite small. They have a maximum source level of 132 dB re 1μPa @ 1m, whereas Blainville's clicks are thought to have a source level between 200 – 210 dB (Tyack *et al.*, 2011) and can be detected for distances up to 6.5 km (Ward *et al.*, 2008). The sexually distinctive sounds produced by both males and females may be important cues for the more likely scenario of males choosing which group of females to join.

In Chapter Two, I have shown adult males will remain with the same group of reproductive females for up to a year. Harems are presumably formed if a male finds an unaccompanied group of females, or if he successfully ousts the existing harem male. Adult male Blainville’s beaked whales may engage in combat more often than other animals because of limited acoustic cues as indicators of individual fitness. In other species, such as red deer (*Cervus elaphus*), males use roars to evaluate one another’s fitness (Reby and McComb, 2003). Although this information may be in the newly described sexually distinctive sounds, recordings from a single adult male prevented finding connections between male competition and these vocalisations. In addition to possible acoustic cues, the accumulation of linear scars resulting from male-to-male combat provide strong visual cues. However, visual detection of these scars is limited to close ranges.

In the event the sexually distinctive signals do not contain fitness information, adult male Blainville’s beaked whales will have to get extremely close to each other to gather this information. Once a lone male has detected another group of whales through the echolocation clicks from the group, it may approach the group achieving a distance that the mid-frequency signals made by males found in this study can be detected. In addition, these signals are primarily made on the descent of the whale’s dives, therefore the lone male may need to wait for the group it has detected to go through another dive cycle, and therefore descent phase, to recognise the presence of a male in the group. Finally if a male is detected in the group, then the lone male challenger may move even closer to allow echoic imaging of the other male’s dense skull structure (Gol’din 2014) to ascertain the risk of combat.

Although association analyses did not show that males have preferred female associates, the question remains why a male would associate with a group of females if the females have calves and there is no immediate mating opportunity. One possible explanation is that the male is providing paternal care if he sired at least one of the calves. This begs the question of why the male would only remain and provide care for a year when calves do not separate from the mother for over 2 years? The other possible explanation is that the male is related to the mother, as shown in the example of known siblings associating in this study. In this case providing care for a year may represent a tradeoff between the male's direct reproductive success and that of his sisters. Genetic studies currently underway will show how individual Blainville's beaked whales within a group are related and whether or not paternal or sibling care exists in this species. Moreover, as more subadult males in this longitudinal dataset reach adulthood, social analysis will also provide more answers.

Due to the close proximity between group members, there may not be a requirement for group cohesion or maintenance cues for this species such as seen in female greater spear-nosed bats *(Phyllostomus hastatus)*. These bats live in un-related groups that provide co-operative pup care and defence, seemingly like our beaked whales, and produce a group specific 'screech' call that is thought to identify group mates (Boughman and Wilkinson, 1998). However, Blainville's beaked whales may be able to maintain group cohesion simply through their echolocation clicks. If a groups' echolocation clicks are also functioning as a group cohesion cue, this may be why Blainville's beaked whales click for part of the ascent of their dive once they have stopped producing buzzes (see Arranz *et al.*, 2011, Figure 3 (A)).

In summary, females may not need an acoustic cue to select their preferred associates, but there does appear to be a requirement for males to receive appropriate cues and / or signals. Males would seemingly benefit from relatedness cues from females, and fitness cues from males. It is possible that the sexually distinctive signals discovered in this study contain these required cues. To maintain group cohesion, it is likely that their echolocation clicks suffice.

7.1.2 Mother-calf communication: possible constraints and vulnerability

With respect to the calves in these groups, there do not appear to be mother-calf recognition signals (Chapter Five). I found that Blainville's beaked whale calves are producing echolocation clicks not significantly different to their mother's clicks by at least three months old. Mothers are not leaving their calves at the surface as seen with sperm whales, but the question is what is happening during the long foraging dives that calves are undertaking with their mothers?

One scenario is that the mother leaves her calf at a depth safe from predation, but not deep enough for the mother to forage. In this case, the calf may be producing communicative sounds similar to the sexually distinctive sounds (Chapter Three) to aid in reuniting with its mother. However these sounds do not travel great distances and are unlikely to be recorded on a hydrophone array such as the one at AUTEC, and therefore, were not detected in this study (Chapter Five). Alternatively, the calf may be able to recognise and track the mother's or the group's echolocation clicks, allowing it to reunite with the group once it has stopped detecting buzzes, but is still detecting clicks indicating the group has begun its ascent.

I hypothesise that the mother and calf remain together at all times during the dives, because the consequences of losing contact are so grave. Therefore, either the calf is diving to great depths for its age and size, or the mother is feeding at shallower depths temporarily. However, if a mother and calf are separated at depth for any reason, this could be fatal for the calf.

Blainville's beaked whales stop echolocating and move away from anthropogenic sounds such as navy sonar (Allen *et al.*, 2014; McCarthy *et al.*, 2011; Tyack *et al.*, 2011). In both scenarios described above, mother-calf pairs are extremely vulnerable to acoustic disturbance. Any event which causes a mother to cease echolocation will greatly reduce the chance of reuniting with her calf. This acoustic reliance makes mother-calf pairs a particularly vulnerable segment of the population and could lead to population consequences of disturbance as suggested by Claridge (2013).

In the case study of female-female associations, the longest associations found (lasting almost three years) were comprised of two females with calves. Notably three years is also the suggested time at which a Blainville's beaked whale weans her calf (Claridge, 2013). However, not all mother-calf pairs remained in the same group for three years and this may be because of differences in timing of birth and calf development. For example, if one of the calves begins to supplement its diet with prey, this would allow its mother to return to optimal foraging depths, if these have been compromised. This would affect group diving synchronicity with the other mother-calf pairs, so it would make sense to find another group with calves in the same developmental state. Photogrammetry studies (Durban and Parsons, 2006; Perryman and Lynn, 1993) to measure calves could test this hypothesis by comparing calf size intra and inter group. It is worth noting that any compromise taken on by mothers with young calves (shallower or shorter foraging dives), may also affect harem males, if the group remains together at depth. This may be another reason the male does not remain with a group until a calf is weaned.

7.1.3 Click patterns

I suggest that the double click patterns (Chapter Six) do not aid in forming or maintaining social groups, but instead are a physiological effect of initiating echolocation clicks. Double clicks may occur in different patterns in different species because of idiosyncrasies in the evolutionary histories of their sound production anatomy. In other odontocetes, click patterns have been linked to communication and different behaviours. The coda vocalisations made by sperm whales function as communication and are group specific (Watkins and Schevill, 1977; Weilgart and Whitehead, 1993). Harbour porpoises (*Phocoena phocoena*) and Hector’s dolphins (*Cephalorhynchus hectori*) use clicks with different repetition rates for different purposes. Increased repetition rates indicate aggressive behaviour, whereas slow repetition rates followed by a sudden increase were deduced to be contact calls in the porpoises between a mother and her calf (Clausen *et al.*, 2010; Dawson and Slooten, 1993). The unique click pattern that I found focused on the first two clicks of a click train having a shorter inter-click-interval under certain circumstances, and is very different to what has been previously described and explained behaviourally in porpoises and dolphins. The different production of double clicks across deep diving odontocete species may be providing an insight into the evolution of echolocation for cetaceans, with Blainville’s beaked whales being the least evolved of the three species studied here, because it has progressed least toward eliminating double click production.

The production of double clicks may nonetheless provide different cues in the different species. Perhaps most interesting is the cue in sperm whales that an adult female is commencing a foraging dive. Conceivably this is the cue that alerts other pod members to locate a calf left at the surface that needs babysitting. Sperm whale mother-calf pairs have been shown to possess different coda repertoires from the other members of their unit (Schulz *et al.*, 2010), therefore nearby whales would know that this female commencing a dive was a mother leaving a calf.

7.2 Limitations and future analysis

In addition to the novel findings described in this thesis, this work has also generated many new questions. With this new information in hand, direction can be given to future dedicated visual and acoustic studies that may be able to provide more answers. The choice to associate with females in the same reproductive state may have led to an acoustic cue that indicates the reproductive state of Blainville's beaked whales. Further studies should look at acoustic differences between females in different reproductive states, groups with and without calves. In addition, the surfacing times of groups with and without calves could be compared to provide more information on the costs mothers are experiencing, such as reduced foraging time. To overcome the restrictions of tagging mother-calf pairs, tags could be deployed on the adult male in a group of females and their calves. Tag data might provide insight into the depths mother-calf pairs are diving, whether calves are remaining with their mothers, and potentially if the calves are producing any communicative sounds.

Studying beaked whales is a particularly challenging undertaking. They dive to great depths for long periods of time and when they are at the surface are extremely difficult to see. Researchers face other challenges when studying beaked whale sounds. They only make sounds at depth, and only their on-axis sounds travel further than a few hundred metres. Their on-axis clicks have a narrow beam and the animals move their heads -10 / + 10 degrees whilst making echolocation clicks in search of prey, therefore constantly moving this beam. Consequently, stationary and towed hydrophones record only some sounds from beaked whales. In addition, on-animal tag recordings have been shown to be subject to distortion from the sound traveling through the animal's body.

However, developments of the signal processing of recordings from the AUTEC hydrophone array will soon be able to track individual clicking beaked whales on group deep dives. Therefore, in coordination with visual sighting data there will be an increased dataset and further opportunity to look for cues in beaked whale clicks. Although it won’t be known which whale the clicks came from, the clicks will be split into animal A and animal B. This will provide further opportunities to retrospectively look for age and / or sex differences in all groups, as well as between groups, and particularly between a mother and calf.

A potential limitation to this study is that the social structure analysis has been conducted on a different population of whales than the acoustic analysis, although the two populations are only 80 nautical miles apart. The acoustic analysis was all conducted on a population of whales resident to the AUTEC range. Some of the cues and signals expected due to the social structure of the population of whales residing in South Abaco may not be expected in the whales at the AUTEC range. The observed social structure from the AUTEC population of whales appears to be a similar harem structure to that of the South Abaco whales, with a single adult male and one or more adult females. I attempted to carry out a social structure analysis for the AUTEC population of whales as part of this study, however the number of re-sightings of whales was too low to achieve meaningful insight. Social analysis on the AUTEC population will become possible in the near future if mark-recapture studies are continued in that area.

Additionally, there may be differences between the acoustic repertoires between the two populations of whales. The animals in the South Abaco population are rarely exposed to military anthropogenic noise, whereas the animals that reside in the area of the AUTEC hydrophone array are frequently exposed to this disturbance, and adaptation of vocalisations to noise has been shown previously in other taxa. For example, echolocation clicks in captive Beluga whales (*Delphinapterus leucas*) shifted frequency and intensity when the animals were moved to a noisier environment (Au *et al.*, 1985). Though it is less clear whether physiological constraints would enable this sort of compensation by Blainville’s beaked whales, further studies on the sexually distinctive sounds from different populations could answer this question.

Because it is highly unlikely an underwater hydrophone array similar to AUTEC will ever be implemented in the South Abaco area, it makes more sense to conduct a social structure study on the AUTEC population of Blainville’s beaked whales to understand whether the signals and / or cues expected in the vocal repertoire of the South Abaco whales would also be expected in the AUTEC population of whales.

7.3 Conclusions

The results presented in this thesis provide support for the communication of sexual identity through Blainville’s beaked whales unique mid-frequency vocalisations. However, the study of beaked whale communication is still in its infancy, and will remain a difficult area of research due to the challenges that the behaviour of the animal presents. Presumably the limited production of sounds, other than their echolocation clicks, is related to predator avoidance as well as constraints that the physiological pressures of their diving behaviour present. This thesis has advanced our knowledge of the acoustic repertoire of this species, allowing future analysis to confirm hypotheses that are now based on some significant findings.

Beaked whales are a captivating family of whales to study. Having access to Blainville’s beaked whales as a study species is an opportunity that may also provide insights into the biology of the other beaked whale species, and in some cases help to uncover evolutionary history in odontocetes in general.

References

Abegglen, J. (1984). *On Socialization in Hamadryas Baboons*. Lewisburg: Bucknell University Press.

Aguilar de Soto, N., Madsen, P. T., Tyack, P., Arranz, P., Marrero, J., Fais, A., … Johnson, M. (2011). No shallow talk: Cryptic strategy in the vocal communication of Blainville’s beaked whales. *Marine Mammal Science, 28*(2), E75–E92.

Allen, A. N., Schanze, J. J., Solow, A. R., & Tyack, P. L. (2014). Analysis of a Blainville’s beaked whale's movement response to playback of killer whale vocalizations. *Marine Mammal Science, 30*(1), 154–168. doi:10.1111/mms.12028

Allen, J., Weinrich, M., Hoppitt, W., & Rendell, L. (2013). Network-based diffusion analysis reveals cultural transmission of lobtail feeding in humpback whales. *Science (New York, N.Y.), 340*(6131), 485–8. doi:10.1126/science.1231976

Amundin, M., & Mello, I. (2001). Whistle exchange between mother and neonate bottlenose dolphins (Tursiops truncatus). In *14th Biennial Conference on the Biology of Marine Mammals* (p. 6). Vancouver, Canada.

Antunes, R., Schulz, T., Gero, S., Whitehead, H., Gordon, J., & Rendell, L. (2011). Individually distinctive acoustic features in sperm whale codas. *Animal Behaviour*. doi:10.1016/j.anbehav.2010.12.019

Arnold, S. J. (1992). Constraints on Phenotypic Evolution. *American Naturalist, 140*(85-107).

Aroyan, J. L. (1992). Computer modeling of acoustic beam formation in Delphinus delphis. *The Journal of the Acoustical Society of America*, *92*(5), 2539. doi:10.1121/1.404424

Arranz, P., de Soto, N. A., Madsen, P. T., Brito, A., Bordes, F., & Johnson, M. P. (2011). Following a Foraging Fish-Finder: Diel Habitat Use of Blainville’s Beaked Whales Revealed by Echolocation. *PloS One*, *6*(12), e28353.

Au, W. W. L. (1986). Echolocation transmitting beam of the Atlantic bottlenose dolphin. *The Journal of the Acoustical Society of America, 80*(2), 688. doi:10.1121/1.394012

Au, W. W. L. (1993). *The Sonar of Dolphins.* Springer-Verlag, New York.

Au, W. W. L., Branstetter, B., Moore, P. W., & Finneran, J. J. (2012). Dolphin biosonar signals measured at extreme off-axis angles: insights to sound propagation in the head. *The Journal of the Acoustical Society of America*, *132*(2), 1199–206. doi:10.1121/1.4730901

Au, W. W. L., Carder, D. A., Penner, R. H., & Scronce, B. L. (1985). Demonstration of adaptation in beluga whale (D. leucas) echolocation signals. *Journal of the Acoustical Society of America*, *77*(2), 726–730.

Au, W. W. L., Houser, D. S., Finneran, J. J., Lee, W.-J., Talmadge, L. A., & Moore, P. W. (2010). The acoustic field on the forehead of echolocating Atlantic bottlenose dolphins (Tursiops truncatus). *The Journal of the Acoustical Society of America*, *128*(3), 1426–34. doi:10.1121/1.3372643

Baird, R. W. (2000). The killer whale: Foraging specializations and group hunting. In J. Mann, R. C. Connor, P. L. Tyack, & H. Whitehead (Eds.), *Cetacean Societies: Field Studies of Dolphins and Whales* (pp. 127–153). Chicago: University of Chicago Press.

Baird, R. W., Webster, D. L., Schorr, G. S., McSweeney, D. J., & Barlow, J. (2008). Diel variation in beaked whale diving behavior. *Marine Mammal Science*, *24*(3), 630–642.

Baird, R. W., & Whitehead, H. (2000). Social organization of mammal-eating killer whales: group stability and dispersal patterns. *Canadian Journal of Zoology*, *78*(12), 2096–2105. doi:10.1139/cjz-78-12-2096

Baker, C. S., & Herman, L. M. (1984). Seasonal contrasts in the behavior of the humpback whale. *Cetus*, *5*, 14–16.

Baker, M. (1982). *Genetic population structure and vocal dialects in Zonotrichia (Emberizidae)*. (D. E. Kroodsma & E. H. Miller, Eds.)*Acoustic communication in birds* (Acoustic C., pp. 209–232). London: Academic Press.

Balcomb, K. C., & Claridge, D. E. (2001). A mass stranding of cetaceans caused by naval sonar in the Bahamas. *Bahamas Journal of Science*, *5*, 2–12.

Barlow, J. (1999). Trackline detection probability for long-diving whales. In G. W. et al. Garner (Ed.), *Marine mammal survey and assessment methods* (pp. 209–221). Netherlands: Balkema Press.

Barrett-Lennard, L. G., Ford, J. K. B., & Heise, K. A. (1996). The mixed blessing of echolocation: differences in sonar use by fish-eating and mammal-eating killer whales. *Animal Behaviour*, *51*(3), 553–565. doi:10.1006/anbe.1996.0059

Bates, D., Martin, M., & Bolker, B. (2012). Journal of Statistical Software Fitting linear mixed-effects models using lme4. *Journal of Statistical Software*, II.

Baumann-Pickering, S., McDonald, M. a, Simonis, A. E., Solsona Berga, A., Merkens, K. P. B., Oleson, E. M., … Hildebrand, J. a. (2013). Species-specific beaked whale echolocation signals. *The Journal of the Acoustical Society of America*, *134*(3), 2293–301. doi:10.1121/1.4817832

Baumann-Pickering, S., Roch, M. a, Brownell, R. L., Simonis, A. E., McDonald, M. a, Solsona-Berga, A., … Hildebrand, J. a. (2014). Spatio-temporal patterns of beaked whale echolocation signals in the north pacific. *PloS One*, *9*(1), e86072. doi:10.1371/journal.pone.0086072

Baumann-Pickering, S., Simonis, A. E., Wiggins, S. M., Brownell, R. L., & Hildebrand, J. a. (2012). Aleutian Islands beaked whale echolocation signals. *Marine Mammal Science*, no–no. doi:10.1111/j.1748-7692.2011.00550.x

Baumann-Pickering, S., Wiggins, S. M., Roth, E. H., Roch, M. A., Schnitzler, H. U., & Hildebrand, J. A. (2010). Echolocation signals of a beaked whale at Palmyra Atoll. *The Journal of the Acoustical Society of America*, *127*, 3790.

Beckford, N. S., Schain, D., Roor, S. R., & Schanbacher, B. (1985). Androgen stimulation and laryngeal development. *Annals of Otology*, *94*, 634–640.

Bejder, L., Fletcher, D., & BrÄger, S. (1998). A method for testing association patterns of social animals. *Animal Behaviour*, *56*(3), 719–725. doi:10.1006/anbe.1998.0802

Bekoff, M. (1979). Scent marking by free-ranging domestic dogs. *Biology of Behaviour*, *4*, 123–139.

Bell, G. P. (1985). The sensory basis of prey location by the California leaf-nosed bat Macrotus californicus (Chiroptera: Phyllostomidae). *Behavioral Ecology and Sociobiology*, *16*(4), 343–347. doi:10.1007/BF00295547

Bender, C. E., Herzing, D. L., & Bjorklund, D. F. (2009). Evidence of teaching in atlantic spotted dolphins (Stenella frontalis) by mother dolphins foraging in the presence of their calves. *Animal Cognition*, *12*, 43–53. doi:10.1007/s10071-008-0169-9

Benjaminsen, T., & Christensen, I. (1979). The natural history of the bottlenose whale, Hyperoodon ampullatus. In H. E. Winn & B. L. Olla (Eds.), *Behaviour of marine animals* (pp. 143–164). New York: Plenum.

Bernard, H. J., & Hohn, A. A. (1989). Differences in Feeding Habits between Pregnant and Lactating Spotted Dolphins (Stenella attenuata). *Journal of Mammalogy*, *70*(1), 211–215.

Bertram, B. (1978). Living in groups: predators and prey. *Behavioural Ecology*. 64-96.

Best, P. B. (1979). Social organization in sperm whales. In H. E. Winn & B. L. Olla (Eds.), *Cetacea* (Behaviour ., pp. 227–290). New York: Plenum Press.

Bigg, M. A., Ellis, G. M., Ford, J. K. B., & Balcomb, K. C. (1987). *Killer Whales: a study of their identification, genealogy, and natural history in British Columbia and Washington State*. Nanaimo, B.C., Canada: Phantom Press.

Bigg, M. A., Olesiuk, P. F., Ellis, G. M., Ford, J. K. B., & Balcomb, K. C. (1990). Social organization and genealogy of resident killer whales (Orcinus orca) in the coastal waters of British Columbia and Washington State. *Report of the International Whaling Commission*, (12), 383–405.

Blainville, H. de. (1817). Page 178 in the article “dauphins” that comprises pp. 146-179. *Nouveau Dictionnaire d’Historie Naturelle, Appliquee Aux Arts a L'econimie Rurale et Domestique, a La Medicine, Etc., 9*(Deterville, Paris).

Blumstein, D. T., & Armitage, K. B. (1997). Does Sociality Drive the Evolution of Communicative Complexity ? A Comparative Test with Ground - Dwelling Sciurid Alarm Calls. *The American Naturalist, 150*(2), 179–200.

Boeckle, M., Szipl, G., & Bugnyar, T. (2012). Who wants food? Individual characteristics in raven yells. *Animal Behaviour*. doi:10.1016/j.anbehav.2012.08.011

Boughman, J. W. (2001). Divergent sexual selection enhances reproductive isolation in sticklebacks. *Nature, 411*(June), 944–948.

Boughman, J., & Wilkinson, G. (1998). Greater spear-nosed bats discriminate group mates by vocalizations. *Animal Behaviour, 55*(6), 1717–32. doi:10.1006/anbe.1997.0721

Bowles, A. E., Young, W. G., & Asper, E. D. (1988). Ontogeny of stereotyped calling of a killer whale calf, (*Orcinus orca*) during her first year. *Rit Fiskideildat, 11*, 225–250.

Bradbury, J., & Vehrencamp, S. (1998). *Principles of animal communication*. Sunderland, Mass.: Sinauer.

Bree, P. Van, & Kristensen, I. (1974). On the intriguing stranding of four Cuvier’s Beaked Whales, *Ziphius cavirostris* G. Cuvier, 1823, on the Lesser Antillean island of Bonaire. *Bijdragen Tot de Dierkunde, 44*(2), 235–238.

Brown, T., & Handford, P. (2003). Why birds sing at dawn: the role of consistent song transmission. *Ibis*, (145), 120–129.

Burgess, W. C., Tyack, P. L., Le Boeuf, B. J., & Costa, D. P. (1998). A programmable acoustic recording tag and first results from free-ranging northern elephant seals. *Deep Sea Research Part II: Topical Studies in Oceanography, 45*(7), 1327–1351. doi:10.1016/S0967-0645(98)00032-0

Burnham, K. P., & Anderson, D. R. (2002). *Model selection and multimodel inference: a pratical information-theoretic approach*. New York: Springer-Verlag, New York.

Caldwell, D. K., & Caldwell, M. C. (1971). *Sounds produced by two rare cetaceans stranded in Florida*. Biological Systems, inc., St Augustine, FLA.

Caldwell, M. C., & Caldwell, D. K. (1965). Individualized whistle contours in bottlenosed dolphins (Tursiops truncatus). *Nature, 207*, 434–435.

Carl, G. R., & Robbins, C. T. (1988). The energetic cost of predator avoidance in neonatal ungulates: hiding versus following. *Canadian Journal of Zoology*, *66*(1), 239–246. doi:10.1139/z88-034

Catchpole, C. K., & Slater, P. J. B. (1995). *Bird song: biological themes and variations. Cambridge University Press.* Cambridge University Press.

Charlton, B. D., Zhihe, Z., & Snyder, R. J. (2009). The information content of giant panda, *Ailuropoda melanoleuca*, bleats: acoustic cues to sex, age and size. *Animal Behaviour*, *78*(4), 893–898. doi:10.1016/j.anbehav.2009.06.029

Charrier, I., Mathevon, N., & Jouventin, P. (2001). Mother's voice recognition by seal pups. *Nature Communications*, 873–874.

Chen, S.-F., Jones, G., & Rossiter, S. J. (2009). Determinants of echolocation call frequency variation in the Formosan lesser horseshoe bat (*Rhinolophus monoceros*). *Proceedings. Biological Sciences / The Royal Society*, *276*(1674), 3901–9. doi:10.1098/rspb.2009.1185

Cholewiak, D., Baumann-Pickering, S., & Van Parijs, S. (2013). Description of sounds associated with Sowerby's beaked whales (Mesoplodon bidens) in the western North Atlantic Ocean. *The Journal of the Acoustical Society of America*, *134*(5), 3905. doi:10.1121/1.4823843

Clapham, M., Nevin, O. T., Ramsey, A. D., & Rosell, F. (2012). A Hypothetico-Deductive Approach to Assessing the Social Function of Chemical Signalling in a Non-Territorial Solitary Carnivore. *PloS One*, 7(4).

Clapham, P. J. (2000). The humpback whale. In J. Mann, R. Connor, P. Tyack, & H. Whitehead (Eds.), *Cetacean Societies: Field Studies of Dolphins and Whales* (pp. 173–196). Chicago: The University of Chicago.

Claridge, D. E. (2006). Distribution and habitat selection of beaked whales. *MSc Dissertation. University of Aberdeen. 119pp.*

Claridge, D. E. (2013). Population Ecology of Blainville's Beaked Whales (*Mesoplodon densirostris*). *PhD in Biology, University of St Andrews, Scotland*.

Clarke, M. R., Martins, H. R., & Pascoe, P. (1993). The diet of sperm whales (*Physeter macrocephalus* Linnaeus 1758) off the Azores. *Philosophical Transactions of the Royal Society of London. Series B, Biological Sciences, 339*(1287), 67–82. doi:10.1098/rstb.1993.0005

Clausen, K. T., Wahlberg, M., Beedholm, K., Deruiter, S., & Madsen, P. T. (2010). Click communication in harbour porpoises *Phocoena phocoena*. *Bioacoustics, 20*(1), 1–28. doi:10.1080/09524622.2011.9753630

Collins, C., & Murphy, R. (1994). Echolocation acuity of the Palawan swiftlet (*Aerodramus palawanensis*). *Avocetta*.

Connor, R. C., Heithaus, M. R., & Barre, L. M. (2001). Complex social structure, alliance stability and mating access in a bottlenose dolphin “super-alliance.” *Proceedings of the Royal Society of London, B - Biological Sciences*, *268*, 263–267.

Connor, R. C., Smolker, R. A., & Richards, A. F. (1992). Dolphin alliances and coalitions. In A. H. Harcourt & F. B. M. de Waal (Eds.), *Coalitions and alliances in humans and other animals.* Oxford: Oxford University Press.

Connor, R., Wells, R., Mann, J., & Read, A. (2000). The bottlenose dolphin: Social relationships in a fission-fusion society. In J. Mann, R. Connor, P. Tyack, & H. Whitehead (Eds.), *Cetacean Societies: Field Studies of Dolphins and Whales* (pp. 91–126). University of Chicago Press.

Conradt, L., & Roper, T. J. (2000). Activity synchrony and social cohesion: a fission-fusion model. *Proceedings. Biological Sciences / The Royal Society, 267*(1458), 2213–8. doi:10.1098/rspb.2000.1271

Corkeron, P. J., & Connor, R. S. (1999). Why do baleen whales migrate? *Marine Mammal Science*, *15*(4), 1228–1245.

Cox, T. M., Ragen, T. J., Read, A. J., Vos, E., Baird, R. W., Balcomb, K., Barlow, J., Caldwell, J., Cranford, T., & Crum, L. (2006). Understanding the impacts of anthropogenic sound on beaked whales. *Journal of Cetacean Research and Management*, *7*(3), 177–187.

Crance, J. L., Bowles, A. E., & Garver, A. (2014). Evidence for vocal learning in juvenile male killer whales, *Orcinus orca*, from an adventitious cross-socializing experiment. *The Journal of Experimental Biology, 217*(Pt 8), 1229–37. doi:10.1242/jeb.094300

Cranford, T. W. (1998). The anatomy of acoustic structures in teh spinner dolphin forehead as shown by x-ray computed tomography and computer graphics. In P. E. Nachtigall & P. W. B. Moore (Eds.), *Animal Sonar: Processes and performance* (pp. 67–77). New York: Plenum Press.

Cranford, T. W., Elsberry, W. R., Van Bonn, W. G., Jeffress, J. a., Chaplin, M. S., Blackwood, D. J., … Ridgway, S. H. (2011). Observation and analysis of sonar signal generation in the bottlenose dolphin (*Tursiops truncatus*): Evidence for two sonar sources. *Journal of Experimental Marine Biology and Ecology, 407*(1), 81–96. doi:10.1016/j.jembe.2011.07.010

Crook, J. H., Ellis, J. E., & Goss-Custard, J. D. (1976). Mammalian Social Systems: Structure and Function. *Animal Behaviour, 24*, 261–274.

D’Vincent, C., Nilson, R., & Hanna, R. (1985). Vocalization and coordinated feeding behavior of the humpback whale in southeastern Alaska. *Scientific Reports of the Whales Research Institute*, *36*, 41–47.

Dalebout, M. L., Baker, C. S., Cockroft, V. G., Mead, J. G., & Yamada, T. K. (2004). A comprehensive and validated molecular taxonomy of beaked whales, Family Ziphiidae. *Journal of Heredity*, *95*, 459–473.

Dalebout, M. L., Steel, D., & Baker, C. S. (2008). Phylogeny of the beaked whale genus *Mesoplodon* (Ziphiidae: Cetacea) revealed by nuclear introns: implications for the evolution of male tusks. *Systematic Biology*, *57*(6), 857.

Darwin, C. (1872). *The expression of the emotions in man and animals*. (J. Murray, Ed.) (reprinted .). London: University of Chicago Press.

Dawson, S., Barlow, J., & Ljungblad, D. (1998). Sounds recorded from Baird's beaked whale, Berardiu bairdii. *Marine Mammal Science*, *14*(2), 335–344.

Dawson, S. M. (1991). Clicks and communication: the behavioural and social contexts of Hector's dolphin vocalizations. *Ethology*, *88*(4), 265–276.

Dawson, S. M., & Slooten, E. (1993). Conservation of Hector's dolphins: the case and process which led to establishment of the Banks Peninsula Marine Mammal Sanctuary. *Aquatic Conservation: Marine and Freshwater Ecosystems*, *3*, 207–221.

De Waal, F. B. M. (1989). Food sharing and reciprocal obligations among chimpanzees. *Journal of Human Evolution*, *18*(5), 433–459. doi:10.1016/0047-2484(89)90074-2

Deecke, V. B., Barrett-Lennard, L. G., Spong, P., & Ford, J. K. B. (2010). The structure of stereotyped calls reflects kinship and social affiliation in resident killer whales (Orcinus orca). *Naturwissenschaften*, *97*(5), 513–518.

Deecke, V. B., Slater, P. J. B., & Ford, J. K. B. (2002). Selective habituation shapes acoustic predator recognition in harbour seals. *Nature*, *729*(2001), 2001–2003.

DeRuiter, S. L., Southall, B. L., Calambokidis, J., Zimmer, W. M. X., Sadykova, D., Falcone, E. A., … Tyack, P. L. (2013). First direct measurements of behavioural responses by Cuvier's beaked whales to mid-frequency active sonar. *Biology Letters*, *9*.

Dubrovskij, N. A., Krasnoff, P. S., & Titov, A. A. (1971). On the emission of echolocation signals by the Azov sea harbor porpoise. *Sov. Phys. Acoust.*, *16*, 444–447.

Dunbar, R. I. M. (1984). *Reproductive Decisions: An Economic Analysis of Gelada Baboon Reproductive Strategies*. Princeton: Princeton University Press.

Dunbar, R. I. M. (1989). Social systems as optimal strategy sets: the costs and benefits of sociality. *Comparative Socioecology*, 73–88.

Durban, J. W., & Parsons, K. M. (2006). Laser-Metrics of Free-Ranging Killer Whales. *Marine Mammal Science*, *22*(3), 735–743. doi:10.1111/j.1748-7692.2006.00068.x

Evans, D. L., & England, G. R. (2001). *Joint interim report Bahamas marine mammal stranding event of 14 - 16 March 2000. Unpublished report released by the U.S. Department of Commerce and the Secretary of the Navy* (p. vi + 59 pp.).

Ey, E., Hammerschmidt, K., Seyfarth, R. M., & Fischer, J. (2007). Age- and Sex-Related Variations in Clear Calls of *Papio ursinus*. *International Journal of Primatology*, *28*(4), 947–960. doi:10.1007/s10764-007-9139-3

Fernández, A., Edwards, J. F., Rodríguez, F., Espinosa de los Monteros, A., Herráez, P., Castro, P., Jaber, J. R., Martin, V., & Arbelo, M. (2005). “Gas and fat embolic syndrome” involving a mass stranding of beaked whales (family Ziphiidae) exposed to anthropogenic sonar signals. *Veterinary Pathology*, *42*, 446–457. doi:10.1354/vp.42-4-446

Fischhoff, I. R., Sundaresan, S. R., Cordingley, J., Larkin, H. M., Sellier, M.-J., & Rubenstein, D. I. (2007). Social relationships and reproductive state influence leadership roles in movements of plains zebra, Equus burchellii. *Animal Behaviour*, *73*(5), 825–831. doi:10.1016/j.anbehav.2006.10.012

Fitch, W. T., & Hauser, M. D. (1995). Vocal production in non-human primates: acoustics, physiology and functional constraints on “honest” advertising. *American Journal of Primatology*, *37*, 191–219.

Ford, J. K. B. (1991). Vocal traditions among resident killer whales (*Orcinus orca*) in coastal waters of British Columbia. *Canadian Journal of Zoology*, *69*(6), 1454–1483. doi:10.1139/z91-206

Frantzis, A. (1998). Does acoustic testing strand whales? *Nature*, *29*, 392.

Freeberg, T. M., Dunbar, R. I. M., & Ord, T. J. (2012). Social complexity as a proximate and ultimate factor in communicative complexity. *Philosophical Transactions of the Royal Society of London. Series B, Biological Sciences*, *367*(1597), 1785–801. doi:10.1098/rstb.2011.0213

Fripp, D., Owen, C., Quintana-Rizzo, E., Shapiro, A., Buckstaff, K., Jankowski, K., … Tyack, P. (2005). Bottlenose dolphin (*Tursiops truncatus*) calves appear to model their signature whistles on the signature whistles of community members. *Animal Cognition*, *8*(1), 17–26. doi:10.1007/s10071-004-0225-z

Gero, S., Engelhaupt, D., Rendell, L., & Whitehead, H. (2009). Who Cares? Between-group variation in alloparental caregiving in sperm whales. *Behavioral Ecology*, *20*(4), 838.

Gillespie, D., Dunn, C., Gordon, J., Claridge, D., Embling, C., & Boyd, I. (2009). Field recordings of Gervaisí beaked whales *Mesoplodon europaeus* from the Bahamas. *The Journal of the Acoustical Society of America*, *125*(5), 3428. doi:10.1121/1.3110832

Gillespie, D., Gordon, J., Mchugh, R., Mclaren, D., Mellinger, D., Red- mond, P., … Deng, X. Y. (2008). PAMGUARD: Semiautomated, open source software for real-time acoustic detection and localisation of cetaceans. *Proceedings of the Institute of Acoustics, 30*.

Ginsberg, J. R., & Young, T. P. (1992). Measuring association between individuals or groups in behavioural studies. *Animal Behaviour, 44*, 377–379.

Gol'din, P. (2014). "Antlers inside": are the skull structures of beaked whales (Cetacea : Ziphiidae) used for echoic imaging and visual display? *Biological Journal of the Linnean Society*.

Goldbogen, J., Pyenson, N., & Shadwick, R. (2007). Big gulps require high drag for fin whale lunge feeding. *Marine Ecology Progress Series*, *349*, 289–301. doi:10.3354/meps07066

Goold, J. C. (1999). Behavioural and acoustic observations of sperm whales in Scapa Flow, Orkney Islands. *Journal of the Marine Biological Association of the UK, 79*(3), 541–550.

Gordon, J. C. D. (1987). *Behaviour and ecology of sperm whales off Sri Lanka. Reports of the International Whaling Commission*. University of Cambridge.

Gordon, J. C. D. (1991). Evaluation of a method for determining the length of sperm whales (*Physeter macrocephalus*) from their vocalizations. *Journal of Zoology, 224*, 301–314.

Götz, T., Verfuss, U. K., & Schnitzler, H.-U. (2006). "Eavesdropping" in wild rough-toothed dolphins (*Steno bredanensis*)? *Biology Letters, 2*(1), 5–7. doi:10.1098/rsbl.2005.0407

Gould, E. (1975). Experimental studies of the ontogeny of ultrasonic vocalizations in bats. *Developmental Psychobiology, 8*(4), 333–46. doi:10.1002/dev.420080407

Gould, S. J., & Lewontin, R. C. (1979). The Spandrels of San Marco and the Panglossian Paradigm. *Proceedings of the Royal Society of London, B - Biological Sciences*, *205*, 581–598.

Gowans, S. (1999). *Social organization and population structure of northern bottlenose whales in the Gully*. Dalhousie University, Halifax, NS.

Gowans, S., & Rendell, L. (1999). Head-butting in northern bottlenose whales (*Hyperoodon ampullatus*): a possible function for big heads. *Marine Mammal Science, 15*(4), 1342–1350.

Gowans, S., Whitehead, H., & Hooker, S. K. (2001). Social organization in northern bottlenose whales, *Hyperoodon ampullatus*: not driven by deep-water foraging? *Animal Behaviour*, *62*(2), 369–377.

Gowans, S., Würsig, B., & Karczmarski, L. (2007). The social structure and strategies of delphinids: Predictions based on an ecological framework. *Advances in Marine Biology, 53*(07), 195–294. doi:10.1016/S0065-2881(07)53003-8

Griffin, D. R. (1958). *Listening in the Dark.* New York: Cornell University Press.

Griffin, D. R., & Thompson, D. (1982). Echolocation by cave swiftlets. *Behavioral Ecology and Sociobiology*, *10*(2), 119–123. doi:10.1007/BF00300171

Guha, S., Rastogi, R., & Shim, K. (1998). CURE: An efficient clustering algorithm for large databases. In *ACM SIGMOD International Conference on Management of Data* (pp. 73–84).

Hain, J. W., Carter, G. R., Kraus, S. D., Mayo, C. A., & Winn, H. E. (1982). Feeding behavior of the humpback whale Megaptera novaeangliae in the western North Atlantic. *Fishery Bulletin US, 80*, 259–268.

Harrington, F., & Asa, C. (2003). Wolf communication. In L. D. Mech & L. Boitani (Eds.), *Wolves: Bheaviour, Ecology, and Conservation* (pp. 66–103). Chicago: University of Chicago Press.

Heyning, J. E. (1984). Functional morphology involved in intraspecific fighting of the beaked whale, (*Mesoplodon carlhubbsi*). *Canadian Journal of Zoology*, *62,* 1645–1654.

Heyning, J. E. (1999). Whale origins-conquering the seas. *Science*, *283*, 943.

Hinde, R. A. (1976). Interactions , Relationships and Social Structure. *Royal Anthropological Institute of Great Britain and Ireland*, *11*(1), 1–17.

Hooker, S. K., & Baird, R. W. (1999). Deep diving behaviour of the northern bottlenose whale, *Hyperoodon ampullatus* (Cetacea: Ziphiidae). *Proceedings of the Royal Society of London. Series B: Biological Sciences*, *266*, 671–676.

Hooker, S. K., Iverson, S. J., Ostrom, P., & Smith, S. C. (2001). Diet of northern bottlenose whales inferred from fatty-acid and stable-isotope analyses of biopsy samples. *Canadian Journal of Zoology*, *79*(8), 1442–1454. doi:10.1139/cjz-79-8-1442

Huang, S. L., Chou, L. S., Shih, N. T., & Ni, I. (2011). Implication of life history strategies for prenatal investment in cetaceans. *Marine Mammal Science*, *27*(1), 182–194.

Insley, S., Robson, B., Yack, T., Ream, R., & Burgess, W. (2008). Acoustic determination of activity and flipper stroke rate in foraging northern fur seal females. *Endangered Species Research*, *4*(January), 147–155. doi:10.3354/esr00050

Janik, V. M. (2014). Cetacean vocal learning and communication. *Current Opinion in Neurobiology*, *28C*, 60–65. doi:10.1016/j.conb.2014.06.010

Janik, V. M., Sayigh, L. S., & Wells, R. S. (2006). Signature whistle shape conveys identity information to bottlenose dolphins. *PNAS*, *103*(21), 8293–8297.

Janik, V. M., & Slater, P. J. B. (1997). Vocal Learning in mammals. *Advances in the Study of Behaviour*, *26*, 59–99. doi:10.1016/S0065-3454(08)60377-0

Janik, V. M., & Slater, P. J. B. (1998). Context-specific use suggests that bottlenose dolphin signature whistles are cohesion calls. *Animal Behaviour, 56*, 829–838.

Jefferson, T., Stacey, P., & Baird, R. (1991). A review of Killer Whale interactions with other marine mammals: predation to co-existence. *Mammal Review*.

Jensen, F. H., Perez, J. M., Johnson, M., Soto, N. A., & Madsen, P. T. (2011). Calling under pressure: short-finned pilot whales make social calls during deep foraging dives. *Proceedings. Biological Sciences / The Royal Society*, *278*(1721), 3017–25. doi:10.1098/rspb.2010.2604

Jepson, P. D., Arbelo, M., Deaville, R., Patterson, I. A. P., Castro, P., Baker, J. R., … Fernández, A. (2003). Gas-bubble lesions in stranded cetaceans. *Nature, 425*, 575–576. doi:10.1038/425575a

Johnson, M., Hickmott, L. S., Aguilar Soto, N., & Madsen, P. T. (2008). Echolocation behaviour adapted to prey in foraging Blainville's beaked whale (Mesoplodon densirostris). *Proceedings of the Royal Society B: Biological Sciences*, *275*(1631), 133–139.

Johnson, M., Madsen, P. T., Zimmer, W. M. X., Aguilar Soto, N., & Tyack, P. L. (2006). Foraging Blainville's beaked whales (Mesoplodon densirostris) produce distinct click types matched to different phases of echolocation. *Journal of Experimental Biology*, *209*(24), 5038.

Johnson, M., Madsen, P. T., Zimmer, W. M. X., Aguilar Soto, N., Tyack, P. L., Soto, N. A. De, … Aguilar de Soto, N. (2006). Foraging Blainville's beaked whales (Mesoplodon densirostris) produce distinct click types matched to different phases of echolocation. *The Journal of Experimental Biology*, *209*(Pt 24), 4238. doi:10.1242/jeb.02596

Johnson, M., Madsen, P. T., Zimmer, W. M. X., De Soto, N. A., & Tyack, P. L. (2004). Beaked whales echolocate on prey. *Proceedings of the Royal Society of London. Series B: Biological Sciences*, *271*(6), S383–S386.

Johnson, M. P., Aguilar De Soto, N., & Madsen, P. T. (2009). Studying the behaviour and sensory ecology of marine mammals using acoustic recording tags: a review. *Marine Ecology Progress Series*, *395*, 55–73.

Johnson, M. P., & Tyack, P. L. (2003). A digital acoustic recording tag for measuring the response of wild marine mammals to sound. *IEEE Journal of Oceanic Engineering*, *28*(1), 3–12. doi:10.1109/JOE.2002.808212

Johnson, M., & Tyack, P. (2005). Measuring the behavior and response to sound of beaked whales using recording tags. *National Oceanographic Partnersip Program Report: Award Number: OCE-0427577*.

Jones, G. (1995). Variation in bat echolocation: implications for resource partitioning and communication. *Le Rhinolophe*, 11, 53-59.

Jones, G., Gordon, T., & Nightingale, J. (1992). Sex and age-differences in the encolocation calls of the lesser horseshoe bat, *Rhinolophus hipposideros*. *Mammalia*, *56*, 189–193.

Jones, G., & Ransome, R. D. (1993). Echolocation calls of bats are influenced by maternal effects and change over a lifetime. *Proceedings of the Royal Society B: Biological Sciences*, *252*, 125–28.

Jones, G., & Siemers, B. M. (2011). The communicative potential of bat echolocation pulses. *Journal of Comparative Physiology A: Neuroethology, Sensory, Neural, and Behavioral Physiology*, 1–11.

Jordan Price, J., P. Johnson, K., & H. Clayton, D. (2004). The evolution of echolocation in swiftlets. *Journal of Avian Biology*, *35*(2), 135–143. doi:10.1111/j.0908-8857.2004.03182.x

Juste, J. B. (2000). Variation in the frequency of the echolocation calls of Hipposideros ruber in the Gulf of Guinea: an exploration of the. *Journal of Evolutionary Biology*, 13(1) 70-80.

Kasuya, T., Brownell, R. L., & Balcomb, K. C. (1997). *Life history of Baird's beaked whales off the Pacific coast of Japan. Report of the International Whaling Commission* (pp. 47:969–79).

Kazial, K. A., Pacheco, S., & Zielinski, K. N. (2008). Information content of sonar calls of little brown bats (Myotis lucifugus): potential for communication. *Journal of Mammalogy*, *89*(1), 25–33.

Killebrew, D. A., Mercado, E., Herman, L. M., & Pack, A. A. (2001). Sound production of a neonate bottlenose dolphin. *Aquatic Mammals*, *27*(1), 34–44.

King, S. L., Sayigh, L. S., Wells, R. S., Fellner, W., & Janik, V. M. (2013). Vocal copying of individually distinctive signature whistles in bottlenose dolphins. *Proceedings. Biological Sciences / The Royal Society*, *280*(1757), 20130053. doi:10.1098/rspb.2013.0053

Krebs, J. R., & Dawkins, R. (1984). Animal signals: mind-reading and manipulation. In J. R. Krebs & N. B. Davies (Eds.), *Behavioural Ecology : An Evolutionary Approach* (2nd ed., pp. 380–402). Oxford: Blackwell.

Lamarck, J. B. (1809). *Philosophie Zoologique (Zoological Philosophie)* (English tr.). New York: NY: Hafner Publishing.

Lammers, M. O., & Au, W. W. L. (2002). Narrowband *Phocoena-* like clicks produced by a delphinid species. *The Journal of the Acoustical Society of America*, *112*(5), 2334.

Lammers, M. O., & Castellote, M. (2009). The beluga whale produces two pulses to form its sonar signal. *Biology Letters*, *5*(3), 297–301. doi:10.1098/rsbl.2008.0782

Leal, M. (1999). Honest signalling during prey-predator interactions in the lizard *Anolis cristatellus*. *Animal Behaviour*, *58*(3), 521–526. doi:10.1006/anbe.1999.1181

Leong, K. ., Ortolani, A., Graham, L. ., & Savage, A. (2003). The use of low-frequency vocalizations in African elephant (*Loxodonta africana*) reproductive strategies. *Hormones and Behavior*, *43*(4), 433–443. doi:10.1016/S0018-506X(03)00025-4

Lincoln, A. G. (1994). Teeth, horns and antlers: the weapons of sex. In V. R. Short & E. S. Balaban (Eds.), *The Differences between the Sexes* (pp. 131–158). Cambridge: Cambridge University Press.

Lorenz, K. (1954). *Man meets dog*. London: Methuen.

Mackay, R. S., & Liaw, H. M. (1981). Dolphin Vocalization Mechanisms. *Science*, *212*, 676–678.

MacLeod, C. D. (2006). How big is a beaked whale? A review of body size and sexual dimorphism in the family Ziphiidae. *Journal of Cetacean Research and Management*, *7*, 301–308.

MacLeod, C. D., Santos, M. B., & Pierce, G. J. (2003). A review of data on diets of beaked whales: Evidence of niche separation and geographic segregation between three genera. *Journal of the Marine Biological Association of the UK*, *83*, 651–655.

Madsen, P. T. (2004). Echolocation clicks of two free-ranging, oceanic delphinids with different food preferences: false killer whales *Pseudorca crassidens* and Risso's dolphins *Grampus griseus*. *Journal of Experimental Biology*, *207*(11), 1811–1823. doi:10.1242/jeb.00966

Madsen, P. T. (2012). Sperm whale coda communication studied with multiple acoustic tags. *The Journal of the Acoustical Society of America*, *131*(4), 3522–3522. doi:10.1121/1.4709325

Madsen, P. T., Carder, D. a., Au, W. W. L., Nachtigall, P. E., Møhl, B., & Ridgway, S. H. (2003). Sound production in neonate sperm whales (L). *The Journal of the Acoustical Society of America*, *113*(6), 2988. doi:10.1121/1.1572137

Madsen, P. T., Johnson, M., Aguilar DeSoto, N., Zimmer, W. M. X., & Tyack, P. (2005). Biosonar performance of foraging beaked whales, *Mesoplodon densirostris*. *Journal of Experimental Biology*, *208*, 181–194.

Madsen, P. T., Kerr, I., & Payne, R. (2004). Source parameter estimates of echolocation clicks from wild pygmy killer whales (*Feresa attenuata*)(L). *The Journal of the Acoustical Society of America*, *116*, 1909.

Madsen, P. T., Lammers, M., Wisniewska, D., & Beedholm, K. (2013). Nasal sound production in echolocating delphinids (*Tursiops truncatus* and *Pseudorca crassidens*) is dynamic, but unilateral: clicking on the right side and whistling on the left side. *The Journal of Experimental Biology*, *216*(Pt 21), 4091–102. doi:10.1242/jeb.091306

Madsen, P. T., Payne, R., Kristiansen, N. U., Wahlberg, M., Kerr, I., & Møhl, B. (2002). Sperm whale sound production studied with ultrasound time/depth-recording tags. *Journal of Experimental Biology*, *205*, 1899–1906.

Madsen, P. T., & Wahlberg, M. (2007). Recording and quantification of ultrasonic echolocation clicks from free-ranging toothed whales. *Deep Sea Research Part I: Oceanographic Research Papers*, *54*(8), 1421–1444.

Madsen, P., Wahlberg, M., & Møhl, B. (2002). Male sperm whale (*Physeter macrocephalus*) acoustics in a high-latitude habitat: implications for echolocation and communication. *Behavioral Ecology and Sociobiology*, *53*(1), 31–41. doi:10.1007/s00265-002-0548-1

Mann, J. B. (1999, June 1). Behavioural Development in Wild Bottlenose Dolphin Newborns (*Tursiops sp.*). *Behaviour*, 136(5) 529-566.

Mann, J., & Smuts, B. B. (1998). Natal attraction: allomaternal care and mother-infant separations in wild bottlenose dolphins. *Animal Behaviour*, *55*(5), 1097–1113. doi:10.1006/anbe.1997.0637

Marler, P. (1961). The logical analysis of animal communication. *The Journal of Theoretical Biology*, *1*, 295–317.

Masters, W. M., Raver, K. A. S., & Kazial, K. A. (1995). Sonar signals of big brown bats, Eptesicus fuscus, contain information about individual identity, age and family affiliation. *Animal Behaviour*, *50*(5), 1243–1260.

Matsumura, S. (1981). Mother-infant communication in a horseshoe bat (*Rhinolophus ferrumequinum nippon*): vocal communication in three-week-old infants. *Journal of Mammalogy*, *62*(1), 20–28.

Matthews, J. N., Rendell, L. E., Gordon, J. C. D., & MacDonald, D. W. (1999). A Review of Frequency and Time Parameters of Cetacean Tonal Calls. *Bioacoustics*, *10*(1), 47–71. doi:10.1080/09524622.1999.9753418

May-Collado, L. J., Agnarsson, I., & Wartzok, D. (2007). Reexamining the Relationship Between Body Size and Tonal Signals Frequency in Whales: a Comparative Approach Using a Novel Phylogeny. *Marine Mammal Science*, *23*(3), 524–552. doi:10.1111/j.1748-7692.2007.02250.x

McCann, C. (1963). Occurrence of Blainville’s beaked-whale *Mesoplodon densirostris* (Blainville) in the Indian Ocean. *Journal of the Bombay Natural History J Society*, *60*(3), 727–731.

McCann, C. (1974). Body scarring on cetacea-odontocetes. *Sci. Rep. Whales Res. Inst., Tokyo*, *26*, 145–55.

McCarthy, E., Moretti, D., Thomas, L., DiMarzio, N., Morrissey, R., Jarvis, S., … Dilley, A. (2011). Changes in spatial and temporal distribution and vocal behavior of Blainville’s beaked whales (*Mesoplodon densirostris*) during multiship exercises with mid-frequency sonar. *Marine Mammal Science*, *27*(3), E206–E226. doi:10.1111/j.1748-7692.2010.00457.x

McCracken, G. F., & Bradbury, J. W. (1977). Paternity and genetic heterogeneity in the polygynous bat, *Phyllostomus hastatus*. *Science, 198*, 303–306.

McGregor, P. K., & Peake, T. M. (2000). Communication networks: social environments for receiving and signalling behaviour. *Acta Ethol.*, *2*, 71–81.

McSweeney, D. J., Baird, R. W., & Mahaffy, S. D. (2007). Site Fidelity, Associations, and Movements of Cuvier’s (*Ziphius Cavirostris*) and Blainville's (*Mesoplodon Densirostris*) Beaked Whales Off the Island of Hawai'i. *Marine Mammal Science*, *23*(3), 666–687. doi:10.1111/j.1748-7692.2007.00135.x

Mead, J. G., Walker, W. A., & Houck, W. J. (1982). Biological observations on *Mesoplodon carlhubbsi* (Cetacea: Ziphiidae). *Smithsonian Contribution to Zoology*, *344*, 1–25.

Miller, L. a., & Surlykke, A. (2001). How Some Insects Detect and Avoid Being Eaten by Bats: Tactics and Countertactics of Prey and Predator. *BioScience*, *51*(7), 570–581. doi:10.1641/0006-3568(2001)051[0570:HSIDAA]2.0.CO;2

Miller, P. J. O. (2004). Swimming gaits, passive drag and buoyancy of diving sperm whales *Physeter macrocephalus*. *Journal of Experimental Biology*, *207*(11), 1953–1967. doi:10.1242/jeb.00993

Miller, P. J. O., Johnson, M. P., & Tyack, P. L. (2004). Sperm whale behaviour indicates the use of echolocation click buzzes creaks in prey capture. *Proceedings of the Royal Society of London. Series B: Biological Sciences*, *271*(1554), 2239.

Mohl, B., & Andersen, S. (1973). Echolocation: high-frequency component in the click of the Harbor Porpoise. *J. Acoust. Soc. Am*, *54*, 1368–1372.

Mohl, B., Surlykke, A., & Miller, L. A. (1990). High Intensity Narwhal Click. In J. Thomas & R. Kastelein (Eds.), *Sensory Abilities of Cetaceans* (pp. 295–304). New York: Plenum Press.

Möller, L. M., & Harcourt, R. G. (2008). Shared Reproductive State Enhances Female Associations in Dolphins. *Research Letters in Ecology*, *2008*, 1–5. doi:10.1155/2008/498390

Moretti, D., Dimarzio, N., Morrissey, R., Ward, J., & Jarvis, S. (2006). Estimating the density of Blainville’s beaked whale *(Mesoplodon densirostris)* in the Tongue of the Ocean (TOTO) using passive acoustics. IEEE, 1-5.

Morisaka, T., & Connor, R. C. (2007). Predation by killer whales (*Orcinus orca*) and the evolution of whistle loss and narrow-band high frequency clicks in odontocetes. *Journal of Evolutionary Biology*, *20*(4), 1439–58. doi:10.1111/j.1420-9101.2007.01336.x

Moss, C. F., Redish, D., Gounden, C., & Kunz, T. H. (1997). Ontogeny of vocal signals in the little brown bat, *Myotis lucifugus*. *Animal Behaviour*, *54*(1), 131–141. doi:10.1006/anbe.1996.0410

Musolf, K., Hoffmann, F., & Penn, D. J. (2010). Ultrasonic courtship vocalizations in wild house mice, *Mus musculus*. *Animal Behaviour*, *79*, 757–764.

Neuweiler, G., Metzner, W., Heilmann, U., Rubsamen, R., Eckrich, M., & Costa, H. H. (1987). Foraging behaviour and echolocation in the rufous horseshoe bat (Rhinolophus rouxi) of Sri Lanka. *Behavioral Ecology and Sociobiology*, *20*(1), 53–67.

New, L. F., Moretti, D. J., Hooker, S. K., Costa, D. P., & Simmons, S. E. (2013). Using energetic models to investigate the survival and reproduction of beaked whales (family Ziphiidae). *PloS One*, *8*(7), e68725. doi:10.1371/journal.pone.0068725

Norris, K. S. (1974). Sound transmission in the porpoise head. *The Journal of the Acoustical Society of America*, *56*(2), 659. doi:10.1121/1.1903305

Norris, K. S., & Harvey, G. W. (1972). Theory for the Function of the Spermaceti Organ of the Sperm Whale (*Physeter catodon* L.). *In NASA Special Publication 262, Animal Orientation and Navigation., ed. S. R.* , 397–417.

Owren, M. J., Rendall, D., & Ryan, M. J. (2010). Redefining animal signaling: influence versus information in communication. *Biology & Philosophy*, *25*(5), 755–780. doi:10.1007/s10539-010-9224-4

Paradis, E., Claude, J., & Strimmer, K. (2004). APE: analyses of phylogenetics and evolution in R language. *Bioinformatics*, *20*, 289–290.

Parks, S. E., Clark, C. W., & Tyack, P. L. (2007). Short- and long-term changes in right whale calling behavior: the potential effects of noise on acoustic communication. *The Journal of the Acoustical Society of America*, *122*(6), 3725–31. doi:10.1121/1.2799904

Payne, R., & Webb, D. (1971). Orientation by means of long range acoustic signaling in baleen whales. *Annals of the New York Academy of Sciences*, *188*(1 Orientation), 110–141. doi:10.1111/j.1749-6632.1971.tb13093.x

Peake, T. M. (2005). Eavesdropping in communication networks. In P. K. McGregor (Ed.), *Animal Communication Networks* (pp. 13–37). Cambridge: Cambridge University Press.

Perry, A., Baker, C. S., & Herman, L. M. (1990). Population characteristics of individually identified humpback whales in the central and eastern North Pacific:

A summary and critique. *Report of the International Whaling Commission*, *12*, 307–17.

Perryman, W. L., & Lynn, M. S. (1993). Identification of geographic forms of common dolphin (Delphinus delphis) from aerial photogrammetry. *Marine Mammal Science*, *9*(2), 119–137. doi:10.1111/j.1748-7692.1993.tb00438.x

Pitman, R. L. (2002). Mesoplodont whales. In W. F. Perrin, B. Wursig, & G. Thewissen (Eds.), *Encyclopedia of marine mammals* (pp. 738–742). San Diego: Academic Press.

Pruett-Jones, S., & Pruett-Jones, M. (1994). Sexual competition and courtship disruptions. Why do male bowerbirds destroy each other's bowers? *Animal Behaviour*, *47*, 602–607.

Rankin, S., & Barlow, J. (2007). Sounds recorded in the presence of Blainville's beaked whales, Mesoplodon densirostris, near Hawaiíi. *The Journal of the Acoustical Society of America*, *122*, 42.

Rasmussen, L., Schmidt, M., Henneous, R., Groves, D., & Daves, G. (1982). Asian bull elephants: Flehmen-like responses to extractable components in female elephant estrous urine. *Science*, *217*(4555), 159–162. doi:10.1126/science.7089549

Reby, D., & McComb, K. (2003). Anatomical constraints generate honesty: acoustic cues to age and weight in the roars of red deer stags. *Animal Behaviour*, *65*(3), 519–530. doi:10.1006/anbe.2003.2078

Rendall, D., & Owren, M. (2013). Communication without meaning or information: abandoning language-based and informational constructs in animal communication theory. In U. Stegmann (Ed.), *Animal Communication Theory: Information and Influence* (pp. 151–182). Cambridge: Cambridge University Press.

Rendall, D., Owren, M. J., & Rodman, P. S. (1998). The role of vocal tract filtering in identity cueing in rhesus monkey (Macaca mulatta) vocalisations. *Journal of Acoustical Society of America*, *103*, 602–614.

Rhinelander, M. Q., & Dawson, S. M. (2004). Measuring sperm whales from their clicks: Stability of interpulse intervals and validation that they indicate whale length. *The Journal of the Acoustical Society of America*, *115*, 1826.

Rice, D. W. (1989). Sperm whale. *Physeter macrocephalus* Linnaeus, 1758. In S. H. Ridgway & R. Harrison (Eds.), *Handbook of marine animals* (4th ed., pp. 177–233). London: Academic Press.

Richard, K. R., Dillon, M. C., Whitehead, H., & Wright, J. M. (1996). Patterns of kinship in groups of free-living sperm whales (*Physeter macrocephalus*) revealed by multiple molecular genetic analyses. *Proceedings of the National Academy of Sciences*, *93*(August), 8792–8795.

Ridgway, S. H., Carder, D. A., Kamolnick, T., Smith, R. R., Schlundt, C. E., & Elsberry, W. R. (2001). Hearing and whistling in the deep sea : depth influences whistle spectra but does not attenuate hearing by white whales (*Delphinapterus leucas*). *Journal of Experimental Biology, 204,* 3829–3841.

Ritter, F., & Brederlau, B. (1999). Behavioural observations of dense beaked whales (*Mesoplodon densirostris*) off La Gomera, Canary Islands (1995-1997). *Aquatic Mammals*, *25*(2), 55–61.

Rokach, L., & Maimon, O. (2005). Clustering Methods, Data Mining and Knowledge Discovery Handbook (pp. 321–352). Springer.

Ross, G. J. B. (1984). The smaller cetaceans of the south east coast of southern Africa. *Ann. Cape. Prov. Mus. (Nat. Hist.), 15,* 173–410.

Sailer, L. D., Gaulin, S. J. C., Sailer, L., D., & Gaulin, S., J., C. (1984). Proximity, Sociality, and Observation: The Definition of Social Groups. *American Anthropological Association*, *86*(1), 91–98.

Sayigh, L. S., Tyack, P. L., Wells, R. S., & Scott, M. D. (1990). Signature whistles of free-ranging bottlenose dolphins *Tursiops truncatus*: stability and mother-offspring comparisons. *Behavioral Ecology and Sociobiology*, *26*, 247–260.

Sayigh, L. S., Tyack, P. L., Wells, R. S., Solow, A. R., & Scott, M. D. (1999). Individual recognition in wild bottlenose dolphins : a field test using playback experiments. *Animal Behaviour*, *57*, 41–50.

Schaefer, H. M., & Ruxton, G. D. (2011). *Plant-Animal Communication*. Oxford: Oxford University Press.

Schaller, G. B. (1972). *The Serengeti Lion: a study of predator-prey relations* (p. 480). Chicago: University of Chicago Press.

Schorr, G. S., Falcone, E. a., Moretti, D. J., & Andrews, R. D. (2014). First Long-Term Behavioral Records from Cuvier’s Beaked Whales (*Ziphius cavirostris*) Reveal Record-Breaking Dives. *PLoS ONE*, *9*(3), e92633. doi:10.1371/journal.pone.0092633

Schulz, T. M., Whitehead, H., Gero, S., & Rendell, L. (2010). Individual vocal production in a sperm whale (*Physeter macrocephalus*) social unit. *Marine Mammal Science, 27*(1), 149–166.

Searby, A., & Jouventin, P. (2003). Mother-lamb acoustic recognition in sheep: a frequency coding. *Proceedings. Biological Sciences / The Royal Society, 270*(1526), 1765–71. doi:10.1098/rspb.2003.2442

Seeley, T. D. (1989). The honey bee colony as a superorganism. *American Scientist*, *77*, 546–553.

Semple, S., & McComb, K. (2000). Perception of female reproductive state from vocal cues in a mammal species. *Proceedings. Biological Sciences / The Royal Society*, *267*(1444), 707–12. doi:10.1098/rspb.2000.1060

Seyfarth, R. M., & Cheney, D. L. (1984). The natural vocalizations of non-human primates. *Trends in Neurosciences*, *7*(3), 66–73. doi:10.1016/S0166-2236(84)80159-9

Seyfarth, R. M., Cheney, D. L., Bergman, T., Fischer, J., Zuberbuhler, K., & Hammerschmidt, K. (2010). The Central Importance of Information in Studies of Animal Communication. *Animal Behaviour*, *80*(1), 3–8.

Seyfarth, R. M., Cheney, D. L., & Marler, P. (1980). Monkey Responses to Three Differnet Alarm Calls: Evidence of Predator Classification and Semantic Communication. *Science*, *210*(4471), 801–803.

Shaffer Ward, J., Moretti, D., & Jarvis, S. (2013). Effective beam pattern of the Blainville's beaked whale (*Mesoplodon densirostris*) and implications for passive acoustic monitoring. *J. Acoust. Soc. Am*, *133*(3).

Shallenberger, E. W. (1981). The status of Hawaiian cetaceans. *Final Report to U. S. Marine Mammal Commission.*, *MMC-77/23*, 79.

Siemers, B. M., Beedholm, K., Dietz, C., Dietz, I., & Ivanova, T. (2005). Is species identity, sex, age or individual quality conveyed by echolocation call frequency in European horseshoe bats? *Acta Chiropterologica*, *7*(2), 259–274. doi:10.3161/1733-5329(2005)7[259:ISISAO]2.0.CO;2

Simmonds, M. P., & Lopez-Juraco, L. F. (1991). Whales and the military. *Nature*, 351–448. doi:10.1038/351448a0

Simmons, A. M., Popper, A. N., & Fay, R. R. (2003). *Acoustic Communication*. New York: Springer.

Smolker, R. A., Richards, A. F., Connor, R. C., & Pepper, J. W. (1992). Sex differences in patterns of association among Indian Ocean bottlenose dolphins. *Behaviour*, *123*(1), 38–69.

Soldevilla, M. S., Henderson, E. E., Campbell, G. S., Wiggins, S. M., Hildebrand, J. A., & Roch, M. A. (2008). Classification of Rissos and Pacific white-sided dolphins using spectral properties of echolocation clicks. *The Journal of the Acoustical Society of America*, *124*, 609.

Steiner, W. W., Hain, J. H., Winn, H. E., Perkins, P. J., Journal, S., & Nov, N. (1979). American Society of Mammalogists Vocalizations and Feeding Behavior of the Killer Whale (*Orcinus orca*), *60*(4), 823–827.

Stoeger, A. S., Zeppelzauer, M., & Baotic, A. (2014). Age-group estimation in free-ranging African elephants based on acoustic cues of low-frequency rumbles. *Bioacoustics*, *23*(3), 231–246. doi:10.1080/09524622.2014.888375

Storey, A. E., Anderson, R. E., Porter, J. M., & MacCharles, A. M. (1992). Absence of Parent-Young Recognition in Kittiwakes: A Re-Examination. *Behaviour*, *120*, 3–4.

Suga, N., Niwa, H., Taniguchi, I., & Margoliash, D. (1987). The personalized auditory cortex of the mustached bat: adaptation for echolocation. *J Neurophysiol*, *58*(4), 643–654.

Sutherland, W. J. (1998). The importance of behavioural studies in conservation biology. *Animal Behaviour, 56*, 801–809.

Suthers, R. A., & Hector, D. H. (1982). Mechanism for the production of echolocating clicks by the grey swiftlet, *Collocalia spodiopygia*. *Journal of Comparative Physiology A: Neuroethology, Sensory, Neural, and Behavioral Physiology*, *148*(4), 457–470.

Swartz, S. (1986). Gray whale migratory, social and breeding behaviour. *Rep. int. Whal. Comm.*, 207–29.

Symonds, M. R. E., & Moussalli, A. (2010). A brief guide to model selection, multimodel inference and model averaging in behavioural ecology using Akaike's information criterion. *Behavioral Ecology and Sociobiology*, *65*(1), 13–21. doi:10.1007/s00265-010-1037-6

Team, R. D. C. (2012). R: A language and environment for statsitical computing. *Vienna: R Foundation for Statistical Computing.*

Tinbergen, N. (1952). "Derived" Activities; Their Causation, Biological Significance, Origin, and Emancipation During Evolution. *The Quarterly Review of Biology*, *27*(1), 1. doi:10.1086/398642

Tomilin, A. G. (1967). Mammals of the U.S.S.R. and adjacent countries. In V. G. Heptner (Ed.), *Cetacea* (Vol. 9.). Moscow: Nauk. S.S.S.R. (English translation, Israel Program for Scientific Translations, Ltd., Jerusalem).

Turl, C. W., & Penner, R. H. (1989). Differences in echolocation click patterns of the beluga (*Delphinapterus leucas*) and the bottlenose dolphin (*Tursiops truncatus*). *JASA* 86(2): 497–502.

Tyack, P. (1981). Interactions between singing Hawaiian humpback whales and conspecifics nearby. *Behavioral Ecology and Sociobiology*, *8*(2), 105–116. doi:10.1007/BF00300822

Tyack, P., & Clark, C. W. (2000). Communication and acoustic behaviour of whales and dolphins. In W. W. L. Au, A. N. Popper, & R. R. Fay (Eds.), *Hearing in whales and dolphins. Handbook on Auditory Research* (pp. 156–224). New York: Springer.

Tyack, P., Johnson, M., & Soto, N. (2006). Extreme diving of beaked whales. *Journal of Experimental Biology*, *209*(21), 4238–4253.

Tyack, P. L., Johnson, M., Soto, N., Madsen, P. T., Zimmer, W. M. X., & Aguilar Soto, N. (2006). Extreme diving of beaked whales. *Journal of Experimental Biology, 209*(21), 4238–4253.

Tyack, P. L., Zimmer, W. M. X., Moretti, D., Southall, B. L., Claridge, D. E., Durban, J. W., Clark, C., D'Amico, A., DiMarzio, N., Jarvis, S., McCarthy, E., Morrissey, R., Ward, J. & Boyd, I. L. (2011). Beaked Whales Respond to Simulated and Actual Navy Sonar. *PloS One, 6*(3). doi:doi:10.1371/journal.pone.0017009

Tyack, P. L. & Sayigh, L. S. (1997). Vocal learning in cetaceans. *In: Social Influences on Vocal Development (Ed. by C. T. Snowdon & M. Hausberger),* 08–233.

Vergara, V., & Barrett-Lennard, L. G. (2008). Vocal Development in a Beluga Calf (*Delphinapterus leucas*). *Aquatic Mammals, 34*(1), 123–143. doi:10.1578/AM.34.1.2008.123

Walker, W. A., & Hanson, M. B. (1999). Biological observations on Stejneger's beaked whale, *Mesoplodon stejnegeri*, from strandings on Adak Island, Alaska. *Marine Mammal Science*, *15*(4), 1314–1329.

Ward, J., Jarvis, S., Moretti, D., Morrissey, R., Dimarzio, N., Johnson, M., Tyack, P., Thomas, L. & Marques, T. (2011). Beaked whale (*Mesoplodon densirostris*) passive acoustic detection in increasing ambient noise. *The Journal of the Acoustical Society of America, 129*(2), 662.

Ward, J., Morrissey, R., Moretti, D., DiMarzio, N., Jarvis, S., Johnson, M., Tyack, P. & White, C. (2008). Passive Acoustic Detection and Localization of *Mesoplodon densirostris* (Blainville's Beaked Whale) Vocalization Using Distributed Bottom-Mounted Hydrophones in Conjunction With a Digital Tag (DTAG) Recording. *RI, NAVAL UNDERSEA WARFARE CENTER DIV NEWPORT.*

Watkins, W. A., Daher, M. A., DiMarzio, N. A., Samuels, A., Wartzok, D., Fristrup, K. M., … Maiefski, R. (2002). Sperm whale dives tracked by radio tag telemetry. *Marine Mammal Science*, *18*(1), 42–54.

Watkins, W. A., Moore, K. E., Clark, C. W., & Dahlheim, M. E. (1988). The sounds of sperm whale calves. In P. E. Nachtigall & P. W. B. Moore (Eds.), *Animal sonar* (pp. 99–107). New York: Plenum Press.

Watkins, W. A., & Schevill, W. E. (1977). Sperm whale codas. *The Journal of the Acoustical Society of America, 62*, 1485.

Węgrzyn, E., Leniowski, K., & Osiejuk, T. S. (2010). Whistle duration and consistency reflect philopatry and harem size in great reed warblers. *Animal Behaviour*, *79*(6), 1363–1372. doi:10.1016/j.anbehav.2010.03.012

Weilgart, L. S., & Whitehead, H. (1988). Distinctive vocalizations from mature male sperm whales (Physeter macrocephalus). *Canadian Journal of Zoology*, *66*, 1931–1937.

Weilgart, L., & Whitehead, H. (1993). Coda vocalizations in sperm whales (Physeter macrocephalus) off the Galapagos Islands. *Canadian Journal of Zoology, 71*, 744–752.

Wells, R. S. (1991). *The role of long-term study in understanding the social structure of a bottlenose dolphin community*. (K. Pryor & K. S. Norris, Eds.) (Dolphin So., pp. 199–225). Berkeley: University of California Press.

Wells, R. S., Scott, M. D., & Irvine, A. B. (1987). The social structure of free-ranging bottlenose dolphins. In H. H. Genoways (Ed.), *Current Mammalogy* (Vol. 1, pp. 247–305). New York: Plenum Press.

Whitehead, H. (1995). Investigating structure and temporal scale in social organizations using identified individuals. *Behavioral Ecology, 6*(2), 199–208. doi:10.1093/beheco/6.2.199

Whitehead, H. (1996). Babysitting, dive synchrony, and indications of alloparental care in sperm whales. *Behavioral Ecology and Sociobiology, 38*(4), 237–244.

Whitehead, H. (2003). *Sperm Whales: Social Evolution in the Ocean*. Chicago: University of Chicago Press.

Whitehead, H. (2007). Selection of Models of Lagged Identification Rates and Lagged Association Rates Using AIC and QAIC. *Communications in Statistics - Simulation and Computation*, *36*(6), 1233–1246. doi:10.1080/03610910701569531

Whitehead, H. (2008). *Analyzing Animal Societies: Quantitative Methods for Vertebrate Social Analysis (Google eBook)* (p. 320). University of Chicago Press.

Whitehead, H. (2009). SOCPROG programs: analysing animal social structures. *Behavioral Ecology and Sociobiology*, *63*(5), 765–778. doi:10.1007/s00265-008-0697-y

Whitehead, H., & Arnbom, T. (1987). Social organization of sperm whales off the Galapagos Islands, February-April 1985. *Canadian Journal of Zoology, 65*(4), 913–919.

Whitehead, H., Bejder, L., & Andrea Ottensmeyer, C. (2005). Testing association patterns: issues arising and extensions. *Animal Behaviour*, *69*(5), e1. doi:10.1016/j.anbehav.2004.11.004

Whitehead, H., & Dufault, S. (1999). Techniques for analyzing vertebrate social structure using identified individuals: review and recommendations. *Advances in the Study of Behaviour*, *28*, 33–74.

Whitehead, H., & Mann, J. (2000). Female reproductive strategies of cetaceans. In J. Mann, R. Connor, O. L. Tyack, & H. Whitehead (Eds.), *Cetacean Societies: Field Studies of Dolphins and Whales*. Chicago: University of Chicago Press.

Whitehead, H., & Waters, S. (1990). Social organisation and population structure of sperm whales off the Galapagos Islands, Ecuador (1985 and 1987). *Reports of the International Whaling Commission (Special Issue), 12*, 249–257.

Whitehead, H., & Weilgart, L. (2000). The sperm whale: Social females and roving males. In J. Mann, R. C. Connor, P. L. Tyack, & H. Whitehead (Eds.), *Cetacean Societies: Field Studies of Dolphins and Whales* (pp. 154–172). Chicago: University of Chicago Press.

Whitten, A. (1982). The ecology of singing in kloss gibbons (*Hylobates klosii*) on Siberut island. *Indonesia. Int J Primatol, 3*, 33–51.

Wilson, E. O. (1975). *Sociobiology*. Boston: Belknap Press of the Harvard University Press.

Wilson, E. O. (1992). *The diversity of life*. Cambridge, Massachusetts: Belknap Press of Harvard University.

Winter, P., Handley, P., & Schott, D. (1973). Ontogeny of squirrel monkey calls under normal conditions and under acoustic isolation. *Behaviour*, *47*, 230–239.

Wisniewska, D. M., Johnson, M., Beedholm, K., Wahlberg, M., & Madsen, P. T. (2012). Acoustic gaze adjustments during active target selection in echolocating porpoises. *Journal of Experimental Biology*, *215*(24), 4358–4373. doi:10.1242/jeb.074013

Woolf, N. (1974). *The ontogeny of bat sonar sounds: with special emphasis on sensory deprivation*. John Hopkins University, Baltimore.

Wrangham, R. W., & Rubenstein, D. I. (1986). Social evolution in birds and mammals. In D. I. Rubenstein & R. W. Wrangham (Eds.), *Ecological aspects of social evolution.* Princeton: Princeton University Press.

Xitco, M. J., & Roitblat, H. L. (1996). Object recognition through eavesdropping : Passive echolocation in bottlenose dolphins. *Animal Learning & Behavior*, *24*(4), 355–365.

Yoshino, H., Matsumura, S., Kinjo, K., Tamura, H., Ota, H., & Izawa, M. (2006). Geographical Variation in Echolocation Call and Body Size of the Okinawan Least Horseshoe Bat, *Rhinolophus pumilus* (Mammalia: Rhinolophidae), on Okinawa-jima Island, Ryukyu Archipelago, Japan. *Zoological Science*, *23*(8), 661–667. doi:10.2108/zsj.23.661

Zimmer, W. M. X., Johnson, M. P., Madsen, P. T., & Tyack, P. L. (2005). Echolocation clicks of free-ranging Cuvier's beaked whales (*Ziphius cavirostris*). *The Journal of the Acoustical Society of America*, *117*, 3919.

Zotti, A., Poggi, R., & Cozzi, B. (2009). Exceptional bone density DXA values of the rostrum of a deep-diving marine mammal: a new technical insight in the adaptation of bone to aquatic life. *Skeletal Radiology*, *38*(12), 1123–5. doi:10.1007/s00256-009-0647-4

Appendix 3.1. Detections on AUTEC Hydrophones

For the following nine figures showing beaked whale and delphinid detections on the AUTEC range, red diamonds represent hydrophones with beaked whale detections, and black circles represent nearby hydrophones. Solid circles represent hydrophones with delphinid detections, and solid diamonds represent hydrophones with both beaked whale and delphinid detections.

Data was provided for hydrophones within an approximate six nautical mile range (three hydrophone radius) of the tagged beaked whales' group detections. These figures show any detections within this range. Where there are no hydrophones shown surrounding those hydrophones with beaked whale detections, i.e. red diamonds, there were either no hydrophones as it was the edge of the range, or there were no delphinid detections on surrounding hydrophones.

All four of the male dives are shown including a dive with no delphinid detections, (Figure A.3.1.2), as well as all of the five female dives, from three of the tagged females, during which there were delphinid detections.

Please note the AUTEC hydrophones are spaced approximately two nautical miles apart, except some portions of the range where their spacing is less, e.g. Figure A.3.1.5, but the latitude and longitudes cannot be shown in public literature.

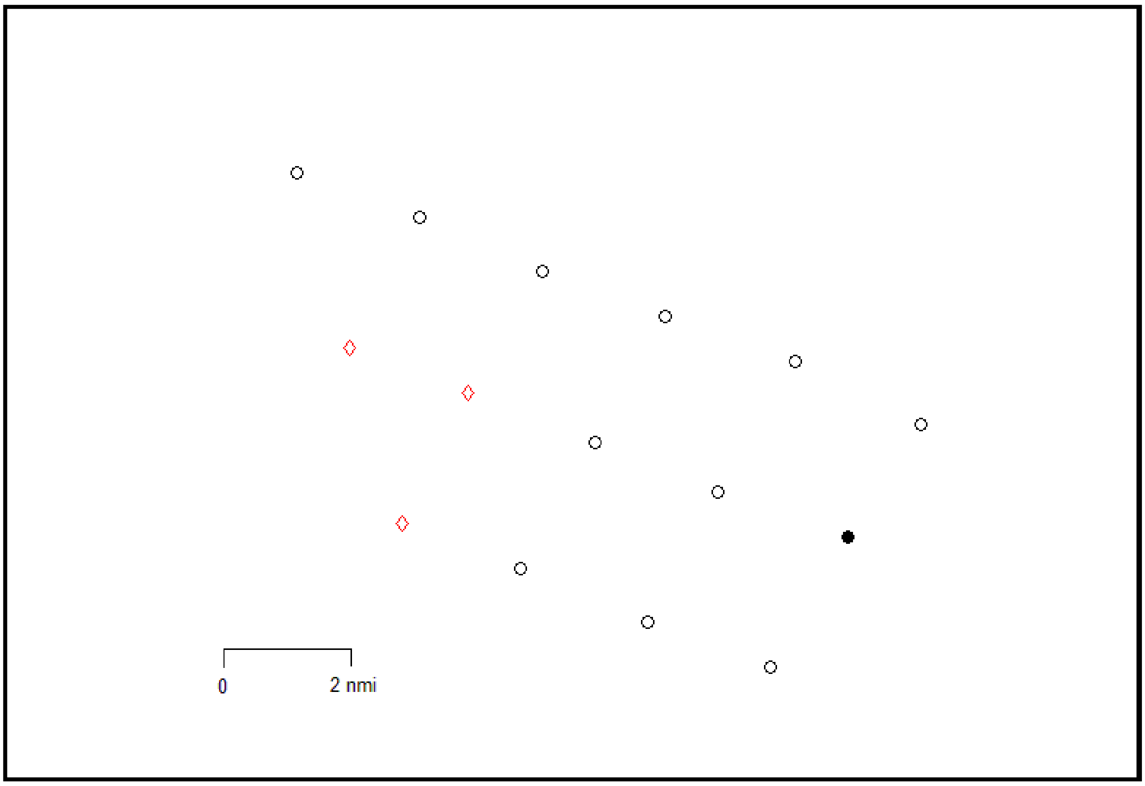

Figure A.3.1.1. Male dive 1

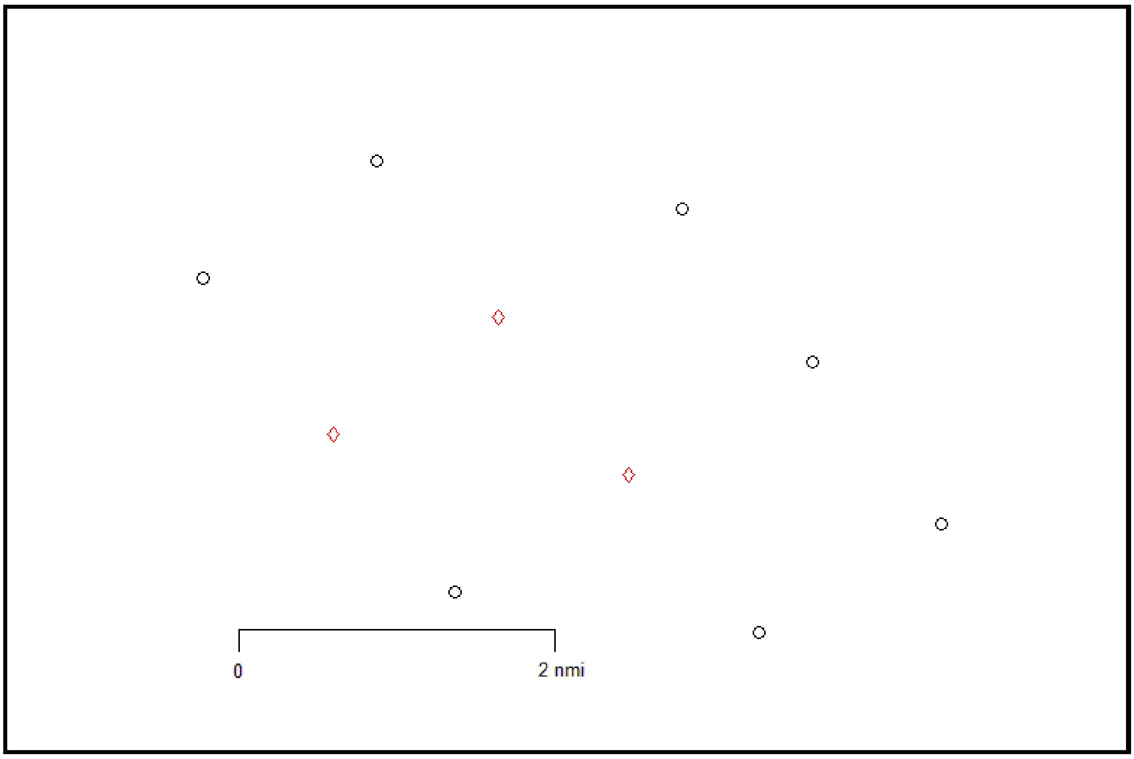

Figure A.3.1.2. Male dive 2

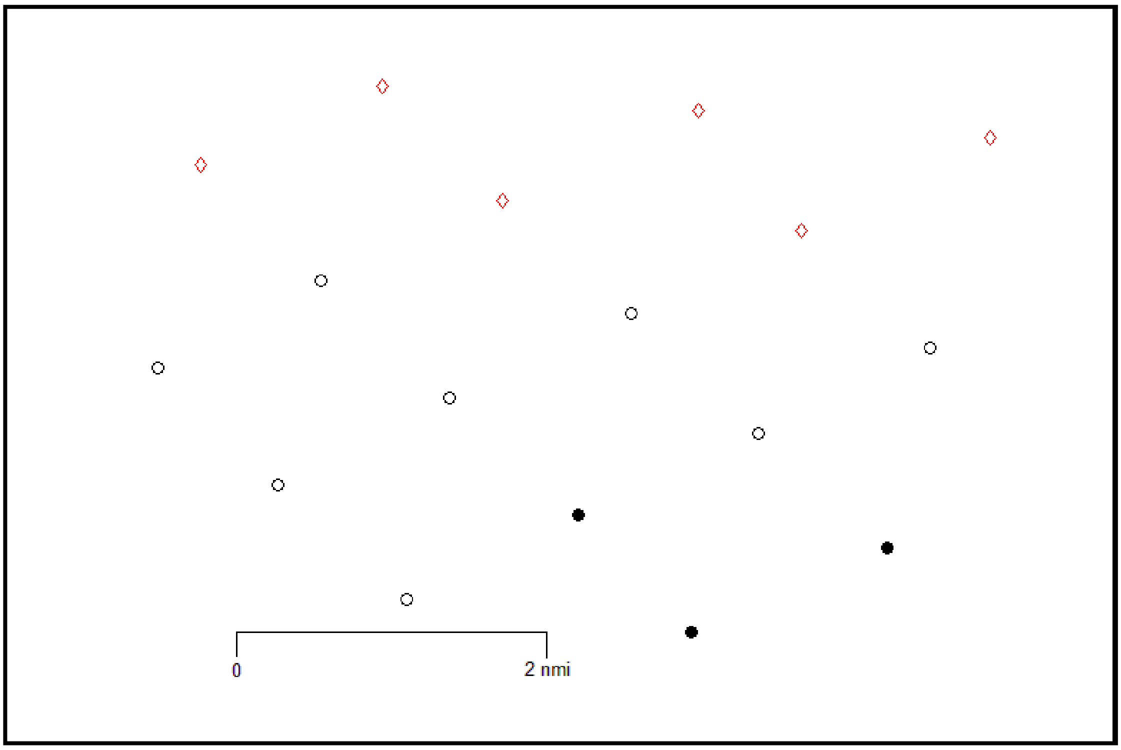

Figure A.3.1.3. Male dive 3

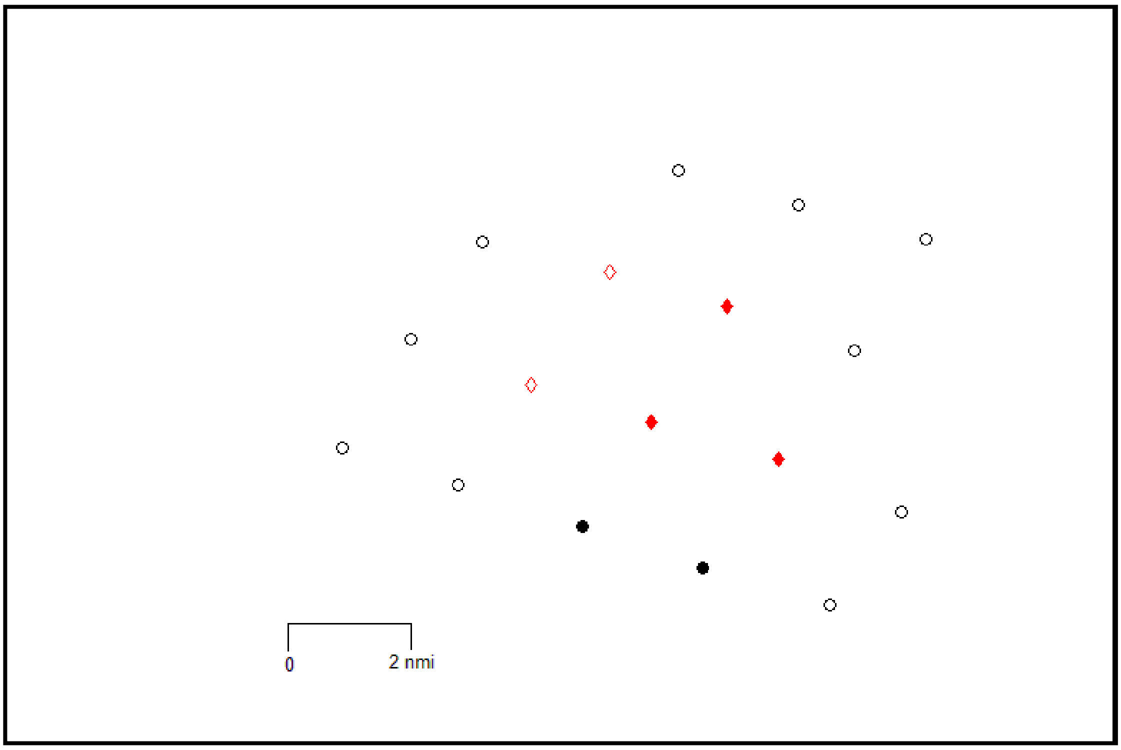

Figure A.3.1.4. Male dive 4

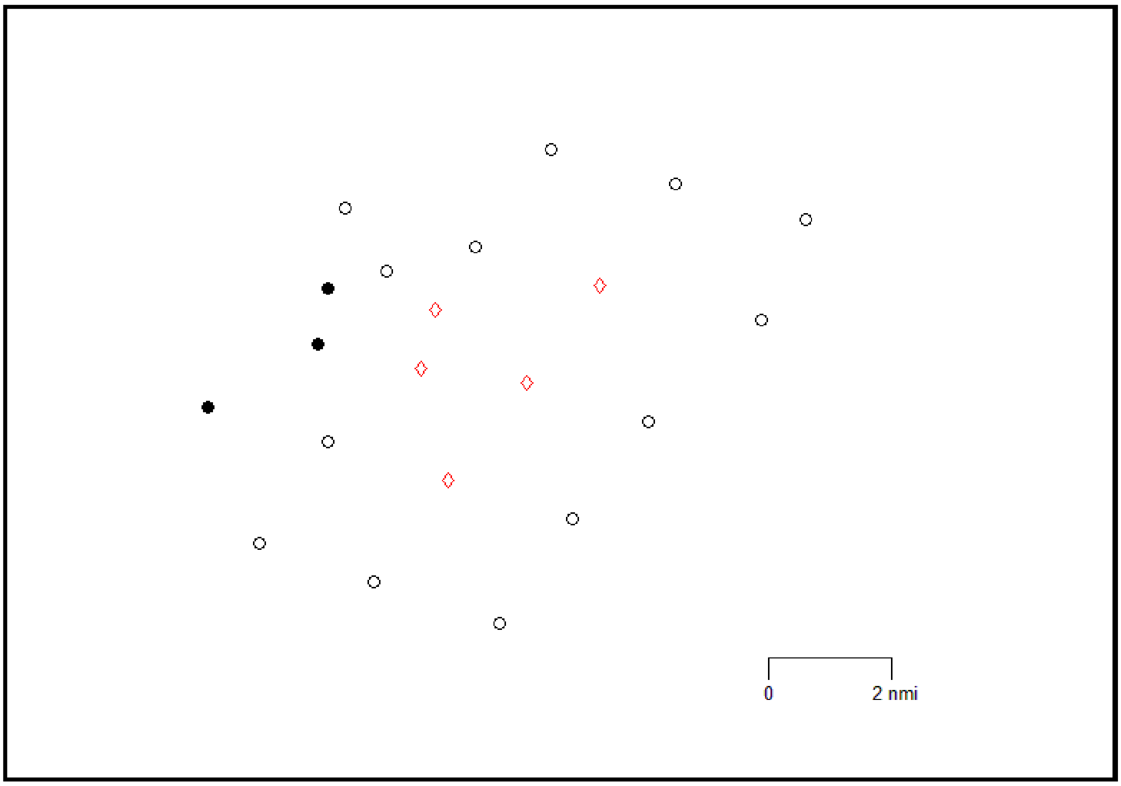

Figure A.3.1.5. Female Md518 dive 3

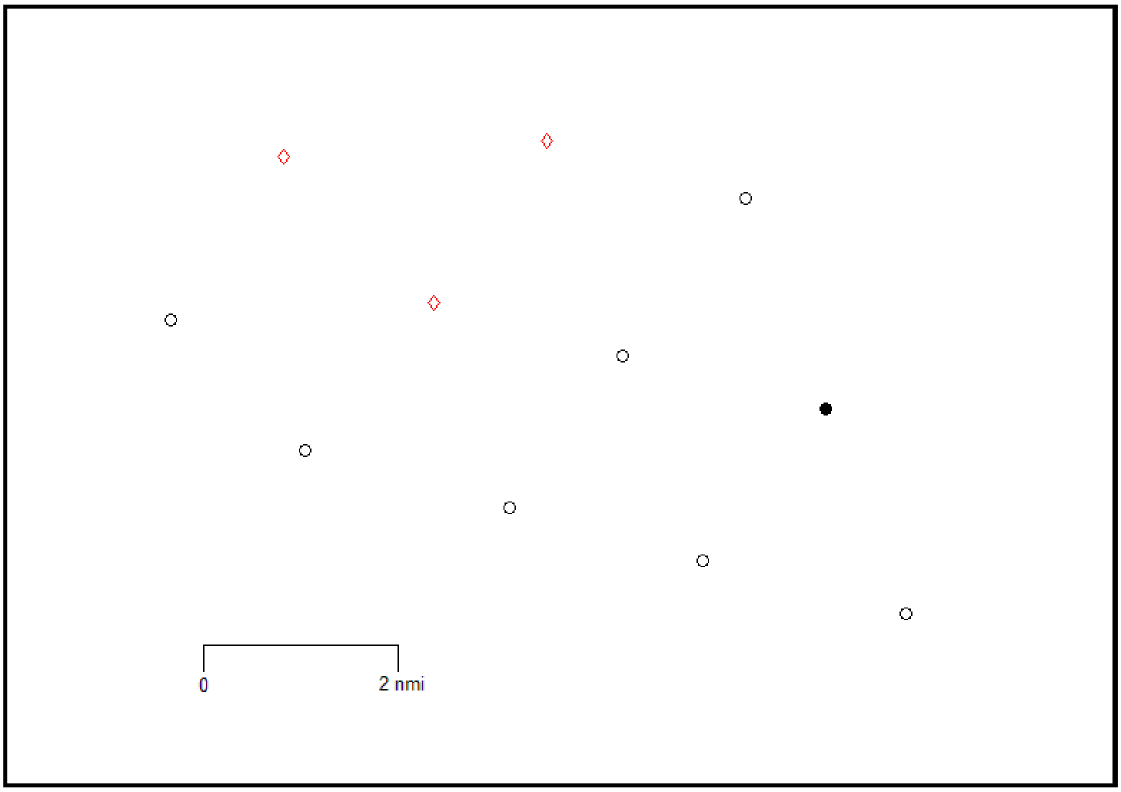

Figure A.3.1.6. Female Md524 dive 2

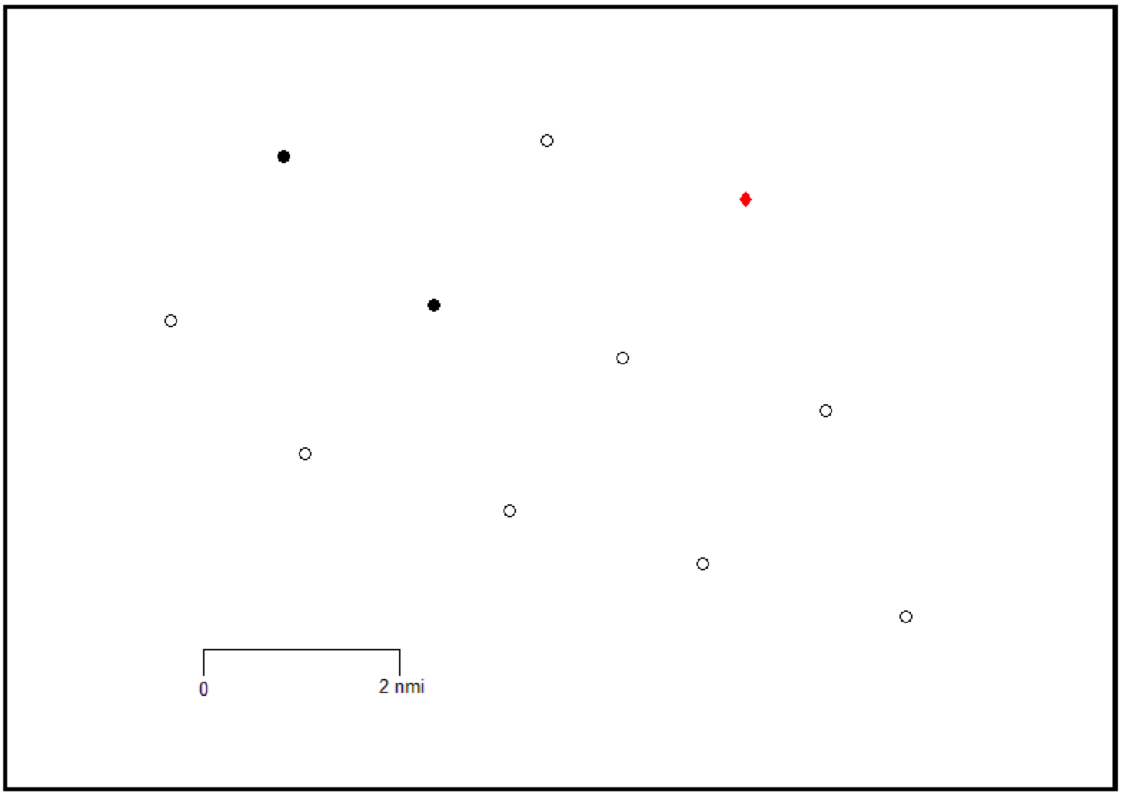

Figure A.3.1.7. Female Md524 dive 5

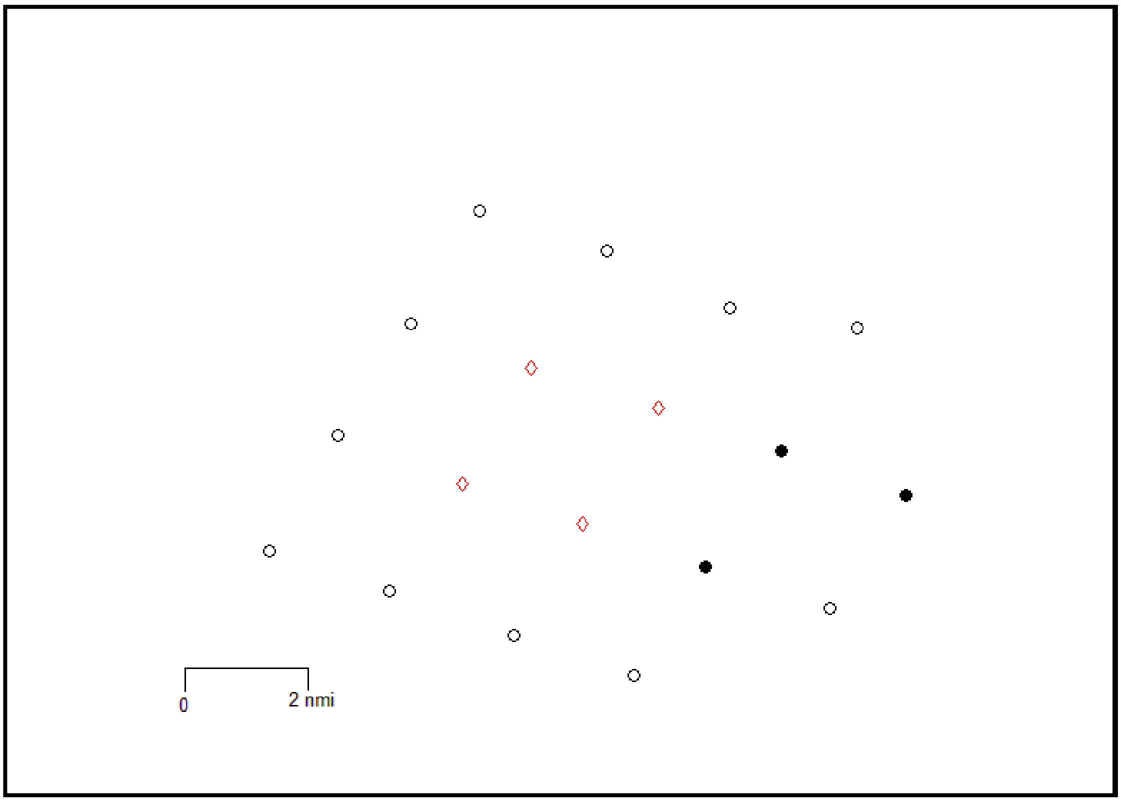

Figure A.3.1.8. Female Md527 dive 3

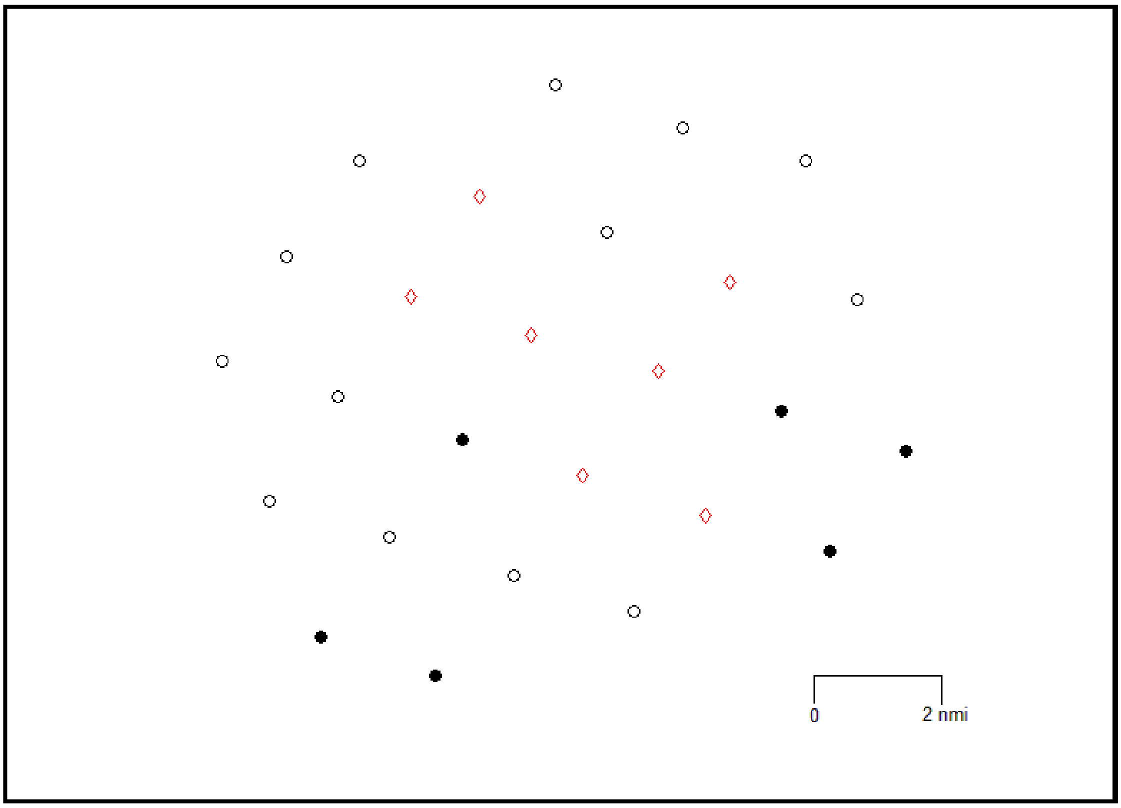

Figure A.3.1.9. Female Md527 dive 4

Appendix 4.1. Nearby beaked whale detections.

The recordings highlighted in grey in the table below (Table A.4.1) indicate recordings used in this analysis while other beaked whale groups were being detected on nearby hydrophones. These hydrophones are shown in the following five figures. Red empty diamonds represent the hydrophones being used in this analysis, solid black circles represent nearby hydrophones, and solid red diamonds represent nearby hydrophones with Blainville's beaked whale detections.

Table A.4.1.1. The dataset for this analysis showing nearby temporally overlapping sounds (Md = *Mesoplodon densirostris*).

Group	Dive Vocal Start (Local)	Hydrophones with focal group sounds	Nearby sounds temporally overlapping
1	17:39	8, 10, 13, 35, 36	Delphinid clicks and whistles on H25/26
2	9:40	49, 56	Sperm whale on H25/35
2	11:43	42, 49	Md group on H3/6/25
2	13:18	49, 56	Md group on H8/10/13/35
2	16:28	42, 43, 49	4-12 kHz noise, Md group on H25/26
3	14:10	24, 29, 30	8-24 kHz broadband noise on H30/24
4	10:20	82, 83, 89, 90, 91, 92, 93	Sperm whale on H63/70/74/82
4	11:58	45, 46, 47, 52, 53	Whistles on H28, pinger on H28/39
5	13:47	12, 27, 28, 31	Md group on H33
6	16:25	64	Md group on H43/44/50
7	12:50	44, 45, 50, 51	Sperm whale on H38/45/46
8	9:41	2, 4, 1, 5, 7,17	Delphinid whistles on H18/19/22/17

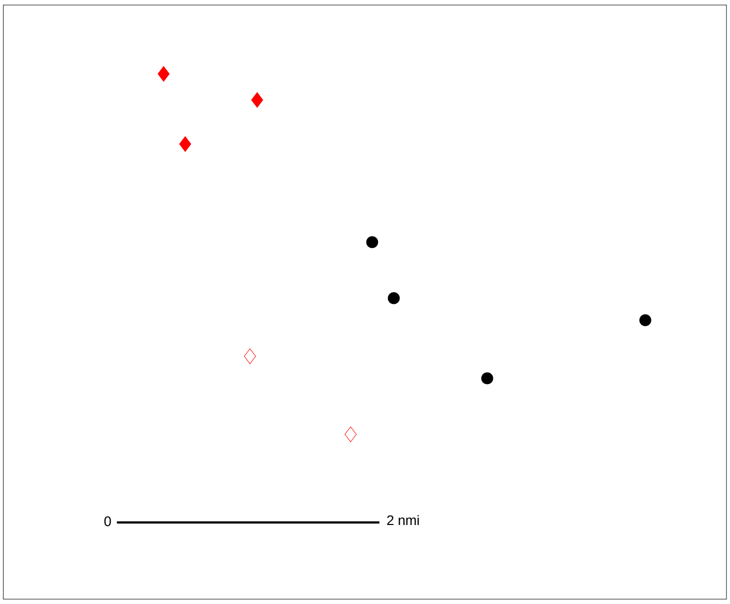

Figure A.4.1.1. Hydrophones with nearby beaked whales being detected during the recordings made on 27th September 2008 (group 2) on the second foraging dive of the encounter. This dive was removed from this study as the hydrophones with a nearby Md group vocalising were adjacent to the hydrophones being used for this analysis. (Red empty diamonds represent the hydrophones being used in this analysis, solid black circles represent nearby hydrophones, and solid red diamonds represent nearby hydrophones with Blainville's beaked whale detections).

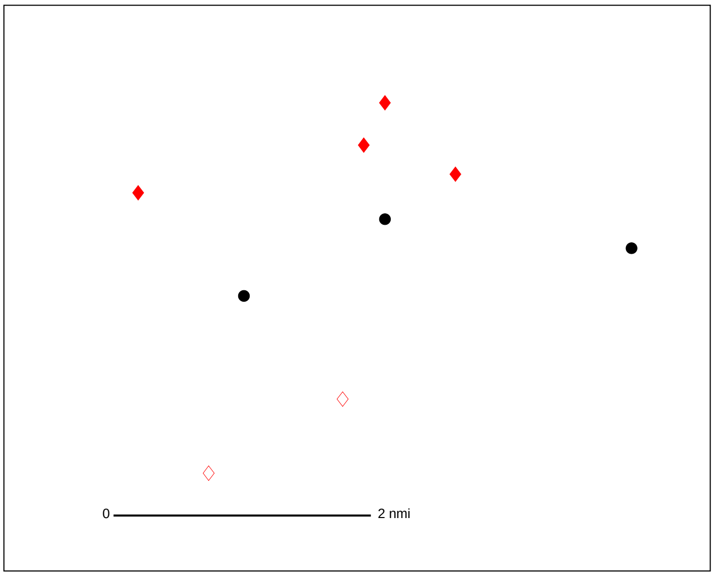

Figure A.4.1.2. Hydrophones with nearby beaked whales being detected during the recordings made on 27th September 2008 (group 2) on the third foraging dive of the encounter. (Red empty diamonds represent the hydrophones being used in this analysis, solid black circles represent nearby hydrophones, and solid red diamonds represent nearby hydrophones with Blainville's beaked whale detections).

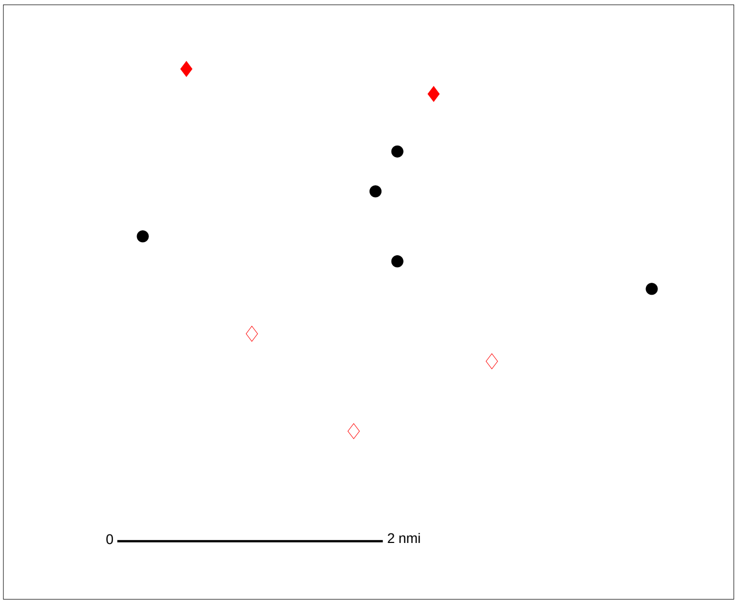

Figure A.4.1.3. Hydrophones with nearby beaked whales being detected during the recordings made on 27th September 2008 (group 2) on the fourth foraging dive of the encounter. (Red empty diamonds represent the hydrophones being used in this analysis, solid black circles represent nearby hydrophones, and solid red diamonds represent nearby hydrophones with Blainville's beaked whale detections).

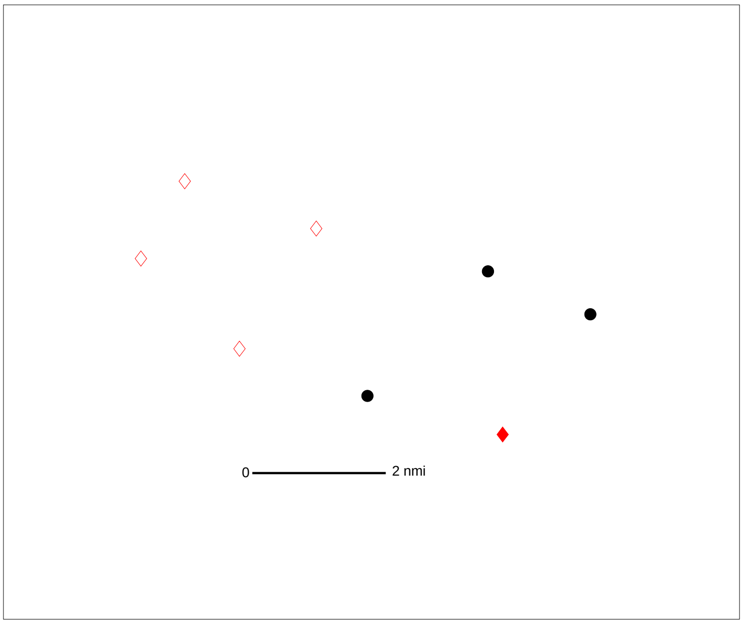

Figure A.4.1.4. Hydrophones with nearby beaked whales being detected during the recordings made on 27th April 2005 (group 5). (Red empty diamonds represent the hydrophones being used in this analysis, solid black circles represent nearby hydrophones, and solid red diamonds represent nearby hydrophones with Blainville's beaked whale detections).

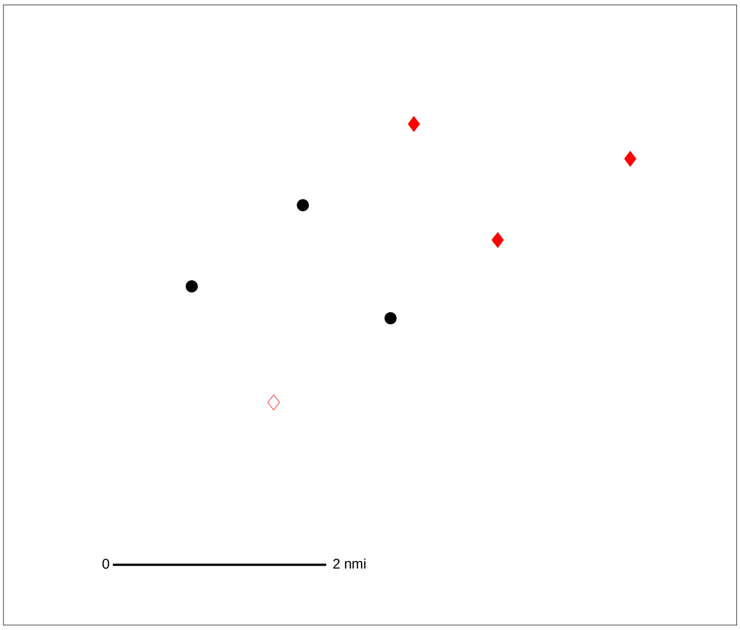

Figure A.4.1.5. Hydrophones with nearby beaked whales being detected during the recordings made on 26th July 2012 (group 6). (Red empty diamonds represent the hydrophones being used in this analysis, solid black circles represent nearby hydrophones, and solid red diamonds represent nearby hydrophones with Blainville’s beaked whale detections).

Appendix 4.2. Histograms of the data from group 5 showing the mean, and the 2.5% and 97.5% quantiles. Data below the 2.5% and above the 97.5% quantiles were filtered out for this and all groups.

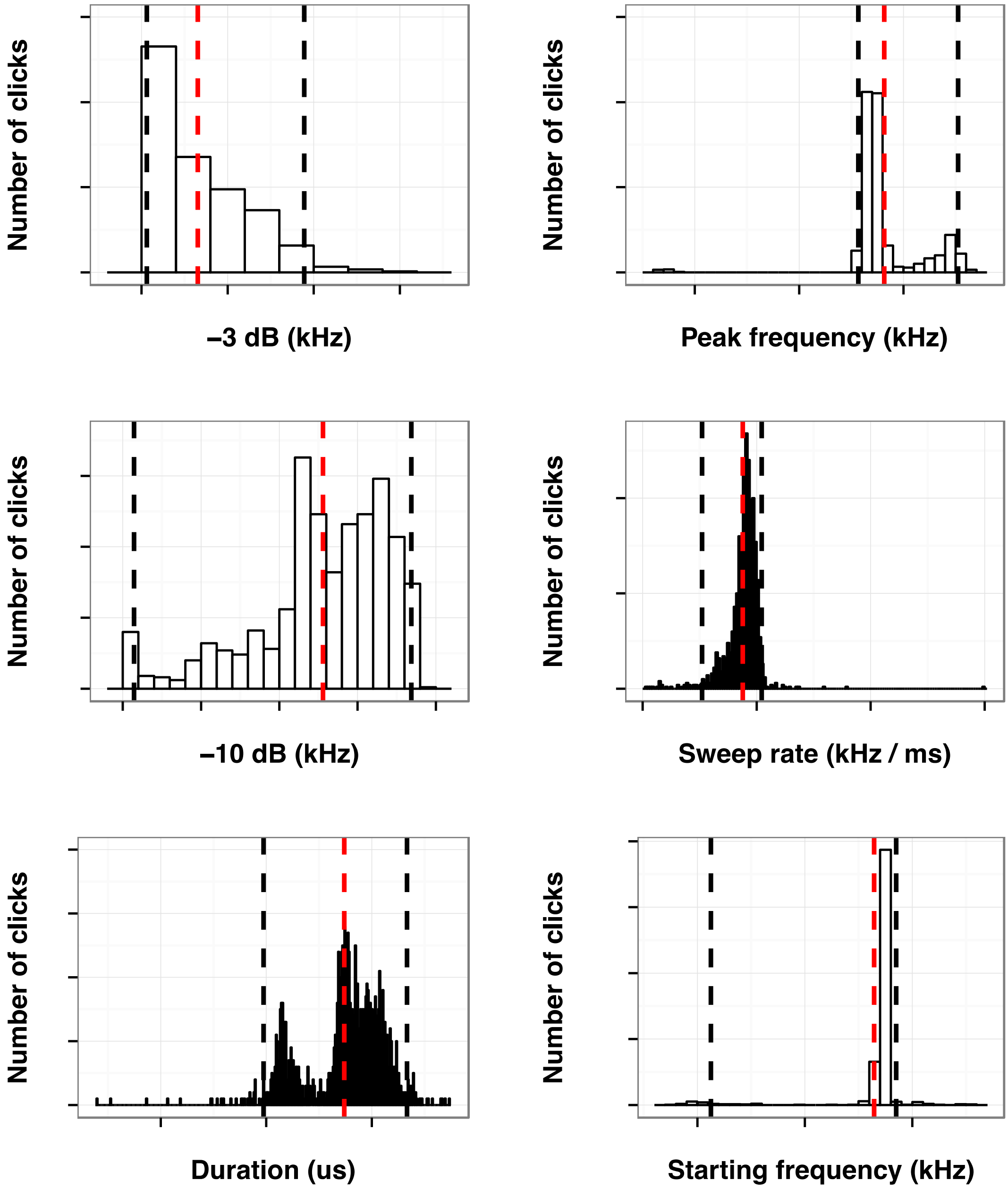

Figure A.4.2.1. Histograms for all parameters from group 5 with the mean of the data shown by the red verticle line, and the 2.5% and 97.5% quantiles shown by the black vertical lines, 2.5% on the left and 97.5% on the right of each histogram. Bin width was set to 1 for each histogram.

Appendix 4.3. PCA loadings for each click parameter for both PC1 and PC2, for six groups of whales whose clicks underwent cluster analysis.

Table A.4.3.1. The loadings from PCA for six groups of whales' click parameters, with the dominant variables shown in bold.

Group	PC	-3dB	-10dB	Duration	Peak frequency	Sweep rate	Starting frequency
1	1	0.22	**0.55**	**0.55**	0.24	**0.52**	-0.09
1	2	**-0.65**	-0.14	0.15	0.37	0.20	**0.60**
2	1	0.24	**0.55**	0.51	0.24	**0.53**	0.22
2	2	**0.59**	0.15	-0.40	**0.43**	-0.38	0.37
3	1	0.37	**0.55**	0.43	0.33	**0.50**	0.12
3	2	0.10	-0.17	-0.18	**0.55**	-0.22	**0.77**
4	1	-0.27	0.37	**0.50**	0.46	**0.54**	0.19
4	2	**0.59**	**0.45**	0.18	-0.39	0.29	-0.42
5	1	0.10	**0.58**	**0.54**	0.28	0.52	0.14
5	2	**0.58**	0.13	-0.14	-0.33	-0.12	**0.70**
6	1	0.30	**0.57**	0.39	0.33	**0.53**	0.20
6	2	**0.52**	-0.04	-0.47	**0.51**	-0.35	0.35

Appendix 4.4. Frequency distributions of randomised error rates.

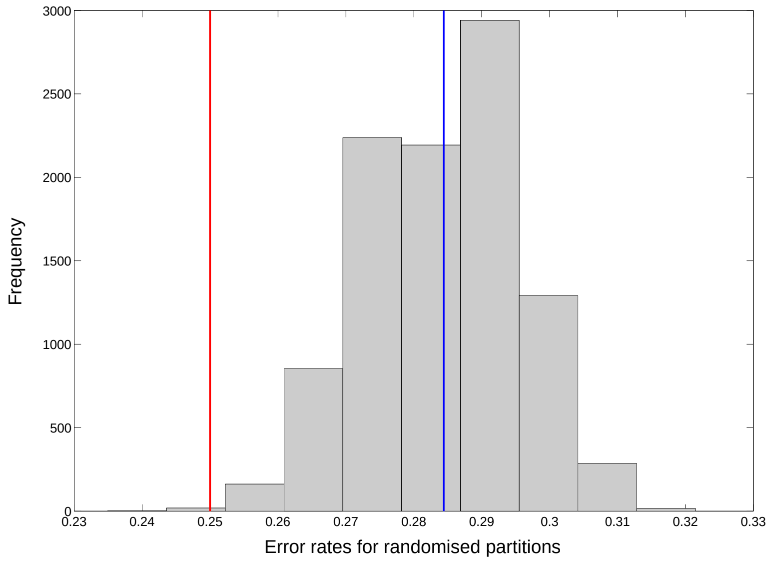

Figure A.4.4.1. Frequency distributions of the 10,000 randomised error rates for the pair of whales from groups 8 and 10. The red line indicates the error rate from the cluster analysis, and the blue line is the median of the randomised error rates.

Appendix 4.5. Plots for each pair of whales whose clicks are known to belong to them.

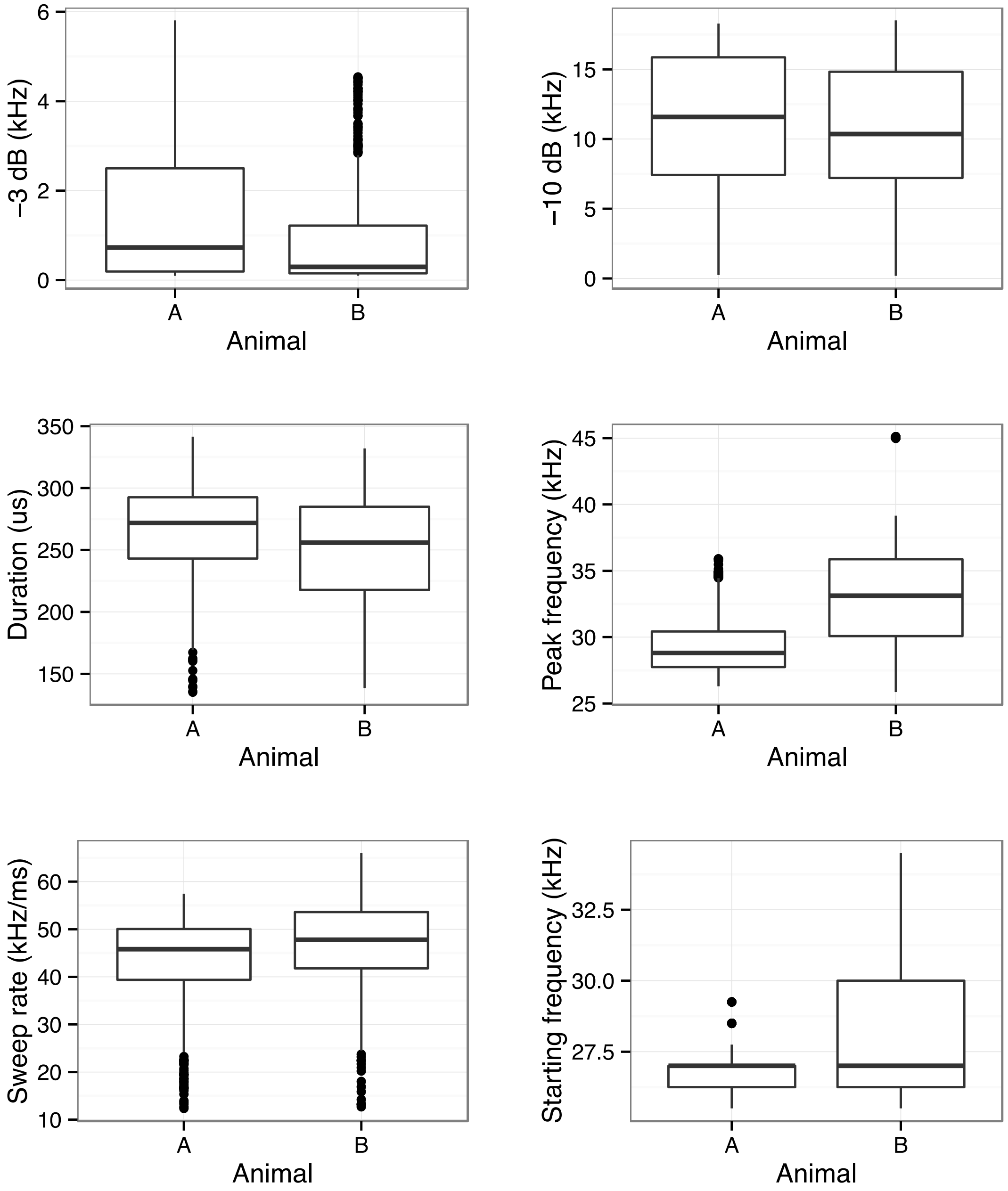

Figure A.4.5.1. Boxplots for each parameter for groups 7 (A), an adult female, and 8 (B), an adult female.

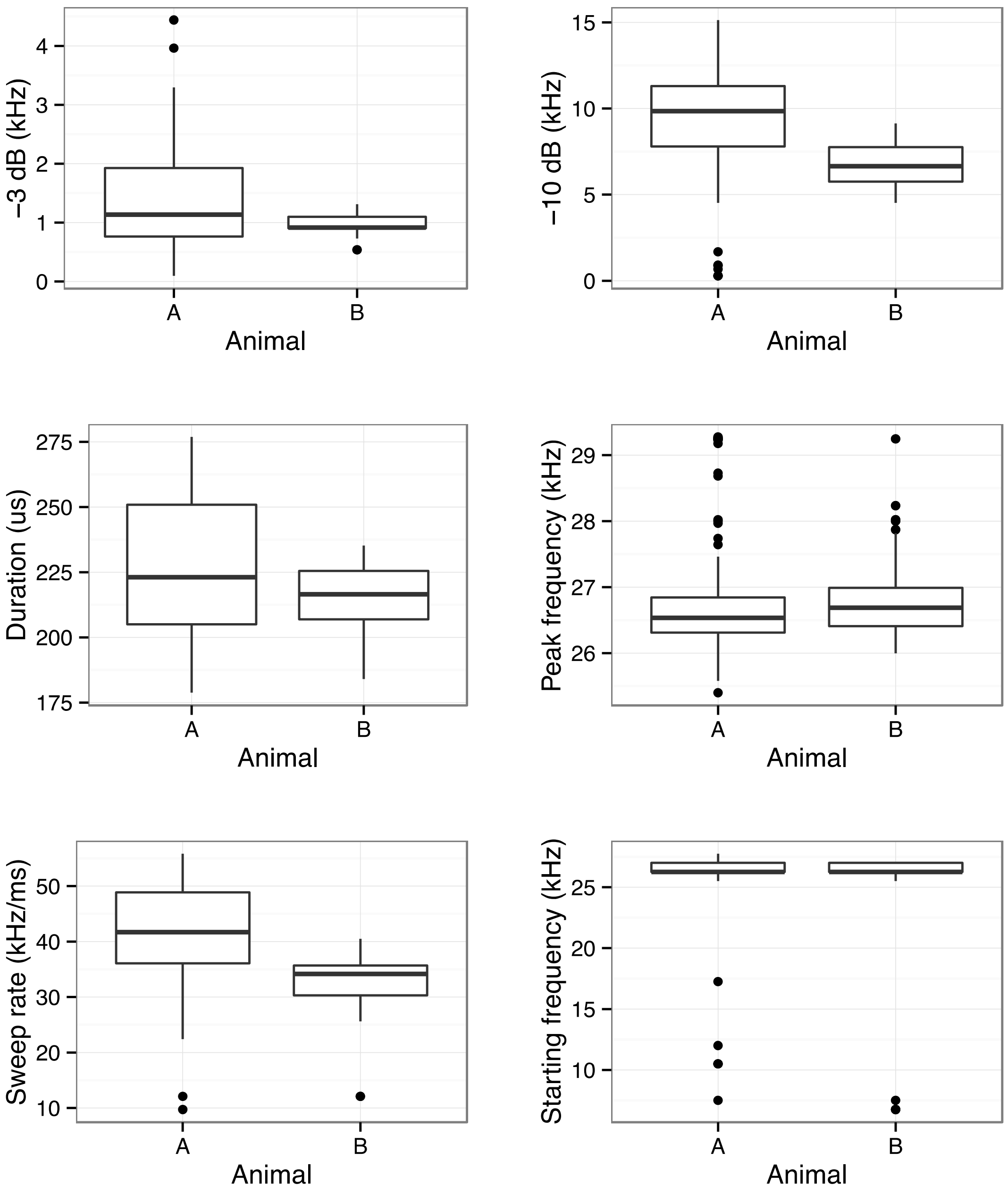

Figure A.4.5.2. Boxplots for each parameter for groups 9 (A) an adult male, and 10 (B), an adult female.

Appendix 6.1. Standardised random effects.

Using the ‘ranef’ command in R, I plotted the ‘predictors’ of the random effects divided by the estimated standard deviation of those random effects, for each species.

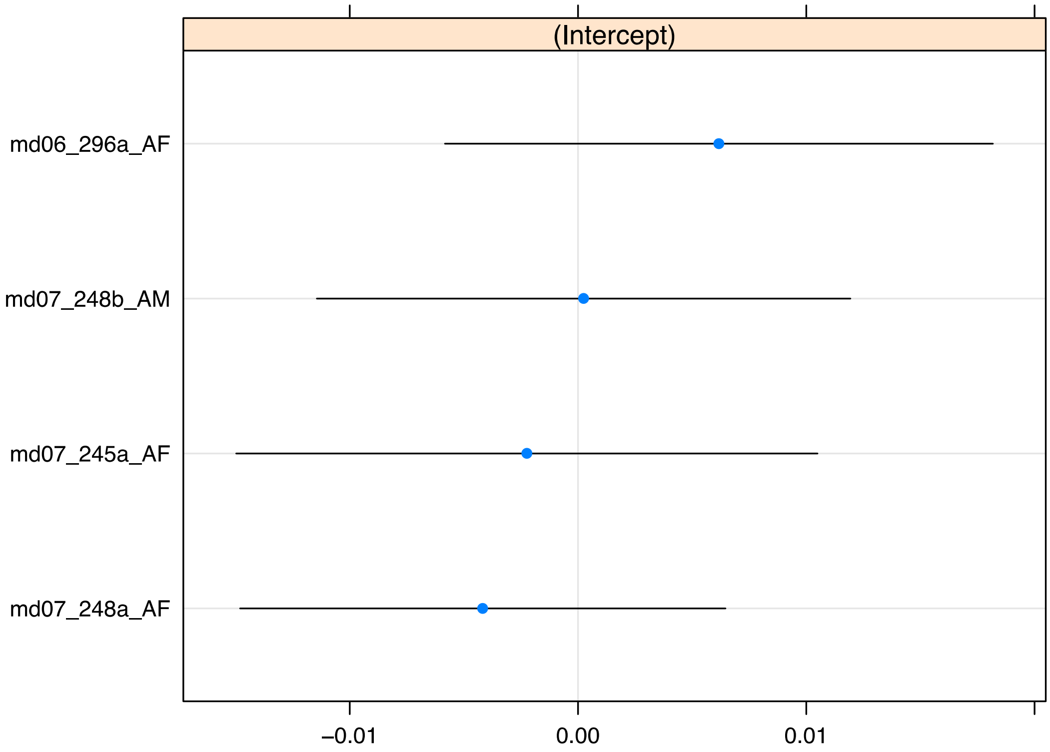

Figure A.6.1.1. 95% prediction intervals on the random effect between individuals (tag_id) for Blainville’s beaked whales, showing significant overlap with each other and therefore little difference should be expected between individuals for this species.

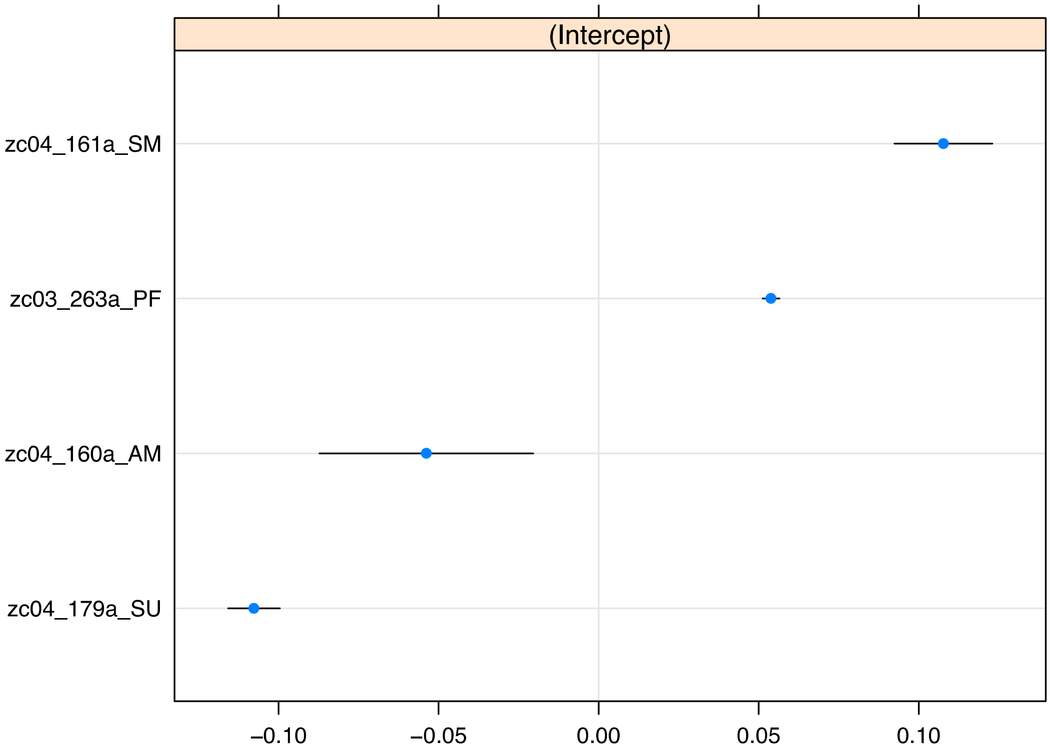

Figure A.6.1.2. 95% prediction intervals on the random effect between individuals (tag_id) for Cuvier's beaked whales, showing no overlap and therefore significant variability between individuals is expected.

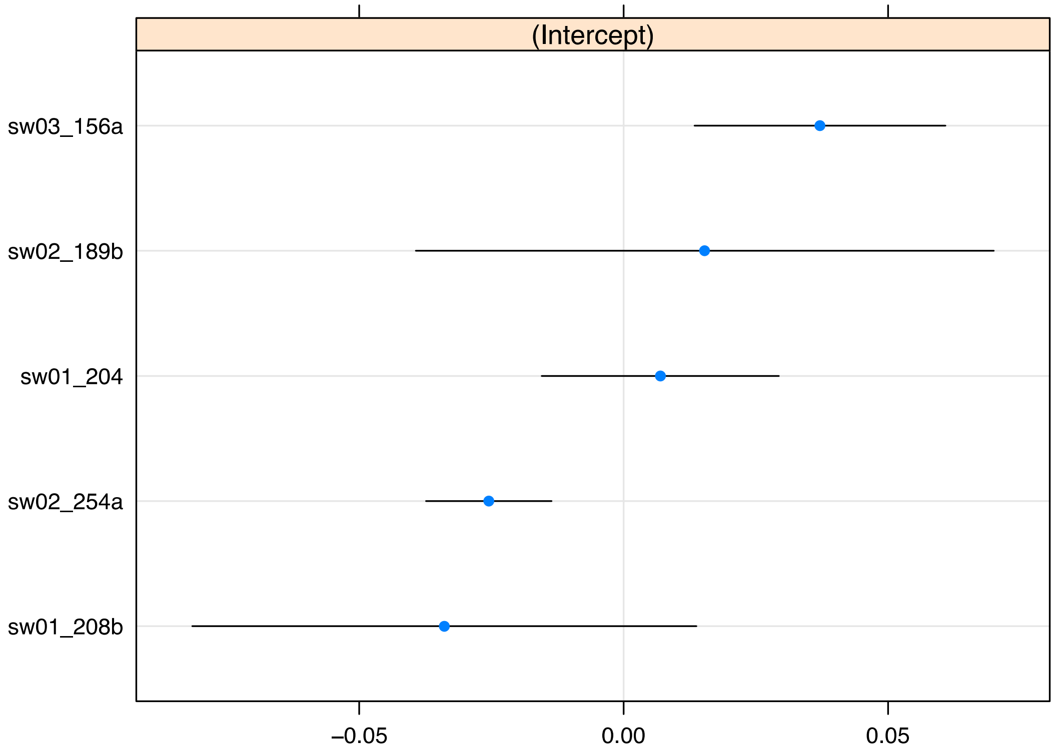

Figure A.6.1.3. 95% prediction intervals on the random effect between individuals (tag_id) for sperm whales, showing some overlap and therefore suggesting some individual differences for sperm whales.