

REPEATED CALL SEQUENCES IN LONG-FINNED PILOT WHALES: SOCIAL  
SETTING, MODIFICATION, AND BEHAVIOURAL CONTEXT

by

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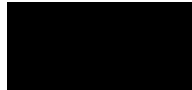
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*To my beloved family, who always encourages me to pursue my dreams no matter how challenging they might be.*



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## **Abstract**

Long-finned pilot whales (*Globicephala melas*) are matrilineal group-living cetaceans. They often produce repeated call sequences: the same call type repeated three or more times, roughly evenly spaced with six seconds or less between calls. I used recordings from 1998-2014 from a population off Cape Breton, Canada, to examine repeated call sequence function. I found no evidence that these calls were specific to individuals or social units or could be used to allocate social units into clans. However, there was some evidence for the horizontal transmission of call types between social units. Modifications of calls (both embellishment and morphing) were common within repeated call sequences. The rate of production of repeated calls increased with group size but not with calf presence and varied with group behaviour and between years. Thus these sequences are likely not individual or unit identifiers, or primarily mother-calf contact calls, instead possibly functioning as group contact calls.

## List of Abbreviations and Symbols Used

% – percent

dB – decibel

hrs – hours

Hz – hertz

kHz – kilohertz

km – kilometre

m – metre

min – minute

$Q$  – quality assessment (photo identification) and modularity coefficient (clustering)

s – second

SD – standard deviation

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# CHAPTER 1 - INTRODUCTION

## 1.1 Animal Communication and Function

Animal communication comes in many forms. Some species rely heavily on sound to share information amongst individuals, while others use vision, touch, or alternate sensory methods as their primary means instead. When such an interaction takes place, it can be described at its most basic level as the transfer of a signal from a sender to a receiver, with the latter then having to decide what course of action to follow with the information they have received (Bradbury & Vehrencamp 2011). Communication is used to solve the challenges of day-to-day life, with examples ranging from the contact calls of ringtail lemurs (*Lemur catta*) employed to maintain cohesion within group settings (Oda 1996) to the use of ultraviolet colour patterns in Ambon damselfish (*Pomacentrus ambionensis*) for conveying territorial signals (Siebeck 2004) and the infrasonic vibrations of African elephants (*Loxodonta africana*) that relay social identity to conspecifics as far as 2.5 km away (McComb et al. 2003). Species that are highly social are often found to have more complex communication systems, which help facilitate intra-specific interactions such as mating and caring for offspring, as well as maintaining contact and coordination within group settings, socializing, coordinated hunting, and other challenges that may arise alongside social complexity (Freeberg et al. 2012; Krams et al. 2012). These vocal repertoires can even include components that delineate levels of social organization (Ford 1991; Gero, Whitehead et al. 2016).

## 1.2 Cetacean Communication

As sight cannot be as dependably used to communicate and convey information – except at the shortest ranges – in an oceanic environment, and olfaction’s usefulness is even more reduced, cetaceans have come to depend on sound as the primary means for transferring information between individuals (Tyack & Clark 2000; Bradbury & Vehrencamp 2011). Toothed whales, odontocetes, are able to use a wide and varied range of sounds to communicate, navigate, and hunt (Tyack 2000), most notably evolving echolocation that allows them to ‘see’ in the dark and often murky waters they live in. Many odontocetes species live in social groups, having developed ways to overcome the challenges of coordinating movement among individuals and facilitating social interactions between many animals (Tyack 2000; Bradbury & Vehrencamp 2011).

Among cetaceans, we find a number of examples of complex social dynamics and intricate communication systems. Within this taxon vocal behaviour is often strongly linked to the social nature of a particular species (Tyack 2000). Some small delphinids that live in fission-fusion societies, where groups are relatively ephemeral, use individually specific signature whistles to mediate interactions with conspecifics (Van Parijs & Corkeron 2001; Sayigh et al. 2007; de Figueiredo & Simão 2009). Bottlenose dolphins (*Tursiops truncatus*) have been found to use these whistles for multiple purposes such as identification and contact (Smolker et al. 1993; Sayigh et al. 2007), as well as conveying the emotional state of the signaller (Esch et al. 2009).

A contrasting type of vocal behaviour is shown by the ‘resident’ killer whales (*Orcinus orca*) of the Pacific Northwest where call repertoires are group-specific. The smallest unit in the social structure of these killer whales is a matriline, which is made up



of a matriarch and several generations of her offspring (Bigg et al. 1990). They show binatal philotropy, where neither male nor female offspring disperse from their mothers during their lives. At this level of social structure matriline have been observed to have their own special calls (Ford 1989; Ford 1991). The next level of social organization is a pod, which is made up of several matriline that are genetically related, share a similar set of discrete calls, and are seen associating together on occasion (Bigg et al. 1990; Ford 1991; Barrett-Lennard 2000). The next level of social structure is an acoustic clan, which is composed of a number of pods that have similar dialects and are thought to have a common maternal heritage (Ford 1991; Strager 1995; Miller et al. 2000). The highest social level of these killer whales is a community, which consists of clans that interact, yet do not share vocal patterns (Bigg et al. 1990; Ford 1991).

Sperm whales also have repertoires that parallel their social structure. In the Pacific there are five known acoustic clans, which geographically overlap, but do not associate, and can be identified by their distinctive coda repertoires (Rendell & Whitehead 2003). Codas are sequences of clicks that are produced by female sperm whales in social settings (Watkins & Schevill 1977; Whitehead & Weilgart 1991). These clans may contain thousands of whales and are not genetically determined (Rendell & Whitehead 2003; Rendell et al. 2012). At the base of this structure are social units that are generally matrilineal and consist of around 10-12 females along with their immature offspring (Whitehead and Weilgart 2000). These units are quite stable, though transfer of individuals between them is possible (Christal et al. 1998). Multiple units of the same acoustic clan form temporary associations called groups that last for several days or more (Christal et al. 1998, Whitehead and Weilgart 2000). Sperm whales also have unit and

individual identity cues in addition to the overall clan repertoires (Gero, Whitehead et al. 2016).

Such dialects – which are defined in this thesis as intra-specific vocal differences resulting from a process of social learning as opposed to reproductive or geographic isolation (Mundinger 1982) – are rare in non-human taxa, and tend to be found in species with stable social groupings. Group-specific calls in killer and sperm whales are believed to be learned by offspring from their mothers, as well as from other family unit members (Ford 1991; Weilgart & Whitehead 1997). In addition to being the result of social learning, it is also possible that dialects in cetaceans act as a form of symbolic marker for different societal levels. Symbolic marking is an important element of human societies, involving the recognition of a social tier by its members through the use of learned cultural characteristics such as symbols, language, or behaviour (Boyd & Richerson 1987). Different matrilineal lines of northern ‘resident’ killer whales were found to exhibit parallel temporal changes in the structure of discrete call types they use, which suggest there may be culturally-driven horizontal transmission of modifications between these family units (Deecke et al. 2000). There is some evidence that sperm whales may also use their coda dialects as symbolic markers, with greater vocal distinctions between sympatric clans than between allopatric ones (Cantor & Whitehead 2013). These constitute the first evidence that these group-living cetaceans may be using calls as symbolic markers of groups, a phenomenon that has so far been only widely studied and identified amongst human cultures.

The observation of these complex interactions between the social structure and acoustic repertoire in killer and sperm whales leads to the question of whether other

species of socially complex odontocetes living in long-term social groups also exhibit similar repertoires that mirror different levels of their social structure?

### **1.3 Long-finned Pilot Whale Ecology and Social Structure**

The long-finned pilot whale (*Globicephala melas*) is a large member of the ocean dolphin family, found in the temperate north Atlantic (subspecies *Globicephala melas melas*) and southern hemisphere (subspecies *Globicephala melas edwardii*) (Bernard & Reilly 1999). A third unnamed subspecies used to live in the northwestern Pacific, but is now extinct (Rice 1998). This species shares the genus *Globicephala* with the short-finned pilot whale (*Globicephala macrorhynchus*). Long-finned and short-finned pilot whales are often hard to tell apart at sea. However, the long-finned pilot whale can be distinguished by longer pectoral fins, and by a higher tooth count. The two species have limited overlap worldwide as the long-finned pilot whale is found in cooler temperate waters while the distribution of short-finned pilot whales is largely tropical and subtropical (Jefferson et al. 2015). This thesis uses ‘pilot whale’ to refer to *G. melas* unless otherwise obviously stated, as no short-finned pilot whales have ever been documented in and around the waters where this study took place.

Long-finned pilot whales are classified as “data deficient” by the International Union for the Conservation of Nature (IUCN) because of a lack of available information on this species’ distribution and abundance (Taylor et al. 2008). Estimates from surveys conducted in 1987 and 1989 gave an estimated abundance of 780,000 pilot whales in the North Atlantic (Buckland et al. 1993), with an earlier study suggesting that the eastern Newfoundland and southeastern Labrador populations are made up of around 13,000 individuals (Hay 1982). A more recent survey in 2007 that covered much of the Canadian

eastern seaboard, including the Gulf of the St. Lawrence, suggested an abundance of just over 6,000 pilot whales (Lawson & Gosselin 2009). The movements of long-finned pilot whales into coastal waters off eastern Canada during the summer and fall are thought to coincide with prey abundance, particularly of squid species such as northern shortfin squid (*Illex illecebrosus*) and longfin inshore squid (*Loligo pealei*), as well as small fish such as Atlantic mackerel (*Scomber scombrus*) (Mercer 1975; Desportes & Mouritsen 1993; Payne & Heinemann 1993; Abend & Smith 1997). However, much remains unknown about the population dynamics and movement of pilot whales in the northwestern Atlantic.

Long-finned pilot whales form long-term matrilineal social units like killer and sperm whales (Amos, Schlotterer, et al. 1993; Ottensmeyer & Whitehead 2003; de Stephanis et al. 2008), and it has been suggested that in this species both sexes display natal philopatry (Amos, Bloch, et al. 1993; Amos, Schlotterer, et al. 1993), similar to ‘resident’ killer whales (Bigg et al. 1990; Barrett-Lennard 2000). There have been three studies on the social structure of long-finned pilot whales. Genetic analyses of animals from Faroese drive hunts, called ‘grinds’, showed that members of the herds of whales driven ashore together were closely related, and that males tended to breed outside of their own group, presumably briefly associating with other groups to mate (Amos et al. 1991; Amos, Bloch, et al. 1993; Anderson & Siegismund 1994). In the Strait of Gibraltar, a population of around 200 resident pilot whales contains small ‘line units’ that consist of several well marked individuals who regularly are sighted with one another (de Stephanis et al. 2008). These would then join up with other line units to form larger groups.

The third study was carried out on the population of pilot whales that is the subject of my research. Ottensmeyer and Whitehead (2003) found evidence for 7 long-term social units averaging about 11-12 individuals each. These were made up of key individuals – seen on four or more days together with a minimum separation of 30 days between sightings – and constant companions – seen on three or more days with a key individual with a minimum separation of 30 days between sightings (Ottensmeyer & Whitehead 2003). More recent analysis has resulted in 21 units with an average of 7 individuals in each (Augusto et al. submitted). Approximately 30-35% of individuals off the coast of Cape Breton can be identified by the unique pattern of nicks, notches, protrusions, and permanent scars on their dorsal fins (Auger-Méthé & Whitehead 2007). Individual social units may join up with others in ephemeral groups that last anywhere from a few hours to many days (Ottensmeyer & Whitehead 2003; Jankowski 2005).

### **1.3.1 Expectations for Vocalizations**

Given the similarity of the social structure of the long-finned pilot whale to those of killer and sperm whales, Rendell and Whitehead (2001) predicted that in this species social levels would be marked by distinct portions of their acoustic repertoire. If the calls of pilot whales function in a similar nature to the discrete calls of ‘resident’ killer whales or the codas of sperm whales, I would expect unit-specific dialects as well as clusters of social units sharing sets of calls – as in pods or clans.

It also may be the case that long-finned pilot whales have individual specific identifiers, similar to the signature whistles of bottlenose dolphins and other small delphinids (Van Parijs & Corkeron 2001; Sayigh et al. 2007). This would manifest itself with call types being specific to a particular unit of long-finned pilot whales and not heard

when that unit – representing the individual’s presence – is not around during the recording.

#### **1.4 Long-finned Pilot Whale Vocalizations**

There is limited information on the vocalizations of long-finned pilot whales. Their calls can contain frequencies as low as 140 Hz and range to well above 20 kHz (Nemiroff & Whitehead 2009). The long-finned pilot whale vocal repertoire was first described by Busnel and Dzedzic (1966) after an encounter with a group of individuals where one was harpooned, with an introductory description of their echolocation coming a few years later (Busnel et al. 1971). Both these summaries were relatively brief, but showed that the pilot whale repertoire included clicks, whistles, and pulsed calls. Taruski was the first to give a comprehensive study of the whistles produced by long-finned pilot whales, concluding that they were graded and could be arranged on a continuum ranging from simple to more complex in seven broad classes (Taruski 1979). Weilgart and Whitehead (1990) came to the same conclusion that their whistles could be arranged on a gradient with seven different contour types. It was found that the whistles of long-finned pilot whales were distinctive when compared to seven other odontocetes: *Lagenorhynchus acutus*, *Stenella frontalis*, and *Stenella longirostris* (Steiner 1981); as well as *Pseudorca crassidens*, *Globicephala macrorhynchus*, *Grampus griseus*, and *Lagenorhynchus albirostris* (Rendell et al. 1999).

Studies on the pulsed calls of long-finned pilot whales were not conducted until recently, when Nemiroff and Whitehead (2009) described the structural characteristics of these call types, and discussed the presence of biphonated calls in the pilot whale repertoire. Biphonic calls have an overlying high-frequency component, in addition to a

low-frequency component that is produced simultaneously, and those produced by long-finned pilot whales are similar to those found in the vocal repertoire of killer whales (Filatova et al. 2009). Many of the vocalizations produced by this species are made up of a mix of both tonal and pulsed elements, which can be difficult to distinguish from one another.

Nemiroff (2009) found that the structure of the pulsed calls produced by long-finned pilot whales seemed to vary with the social unit that produced them, and suggested that certain clusters of units produce similar calls that could indicate a higher level of social organization. There has also been some evidence that call structure is related to behaviour (Weilgart & Whitehead 1990; Nemiroff 2009), with Weilgart and Whitehead (1990) showing that vocalizations were more complex when whales were displaying energetic surface active behaviours, such as breaching and lunging.

#### **1.4.1 Repeated Call Sequences in Long-finned Pilot Whales**

The rhythmic repeated call sequences produced by long-finned pilot whales were briefly mentioned by Busnel and Dziedzic (1966) and can be heard prominently throughout the recordings made in the presence of these whales off Cape Breton. However, studies of the vocal repertoire of this species have never focused on these vocal repetitions, instead breaking the repertoire up into echolocation, whistles, and pulsed calls (Taruski 1979; Nemiroff 2009; Eskesen et al. 2011). Unlike acoustic studies of killer whales (Ford 1989), no attempt has been made to separate possible discrete calls from aberrant or variant forms. However, many of the call types made in the vocal repetitions of pilot whales bear resemblance to the group-specific pulsed calls and complex whistles of killer whales (Ford 1989; Ford 1991). The repetitive nature of these calls is similar to vocalizations

described in other cetaceans such as short-finned pilot whales (Sayigh et al. 2013), melon-headed whales (*Peponocephala electra*) (Kaplan et al. 2014), and northern right whale dolphins (*Lissodelphis borealis*) (Rankin et al. 2007), where the function of these calls is unknown. Repeated call sequences produced by pilot whales also share some structural similarities with the vocal repetitions of bottlenose dolphin signature whistles that are used for individual identification. These often are produced in rhythmic sequences with a gap of up to ten seconds between whistles (Janik et al. 2013). Similarities to known group and individual identification calls in other species make this part of the pilot whale's vocal repertoire the ideal candidate for studying whether or not these vocalizations are group-specific, while also exploring other possible functions of these sequences.

## **1.5 Why Study Function?**

Specific signal types and vocal patterns have been linked to function for a wide range of terrestrial species, such as bats (Gillam and Chaverri 2012; Matsumura 1981; Wilkinson and Boughman 1998), primates (Delgado 2006; Wheeler 2008), birds (Mammen & Nowicki 1981), anurans (Grafe 1996), and even insects (Ryder & Siva-Jothy 2000). However, this is a much more challenging task when a species cannot be visually observed for long periods of time. Such is the case with long-finned pilot whales, where individuals spend the majority of their time beneath the surface of the oceans. But why study function?

Recognizing the variety of signals used by a species and the context in which they are produced allows us to form some basic understanding of life on a day-to-day basis. It is through building up this fundamental knowledge over time that we are able to learn



how individuals vocally mediate interactions with members of other social groups, maintain contact – especially among certain demographics such as mothers and offspring – within their own units, and even how they may delineate between different social tiers through the use of acoustic signals. It is through the study of call function that we have learned that the signature whistles of bottlenose dolphins are used for individual identification (Janik & Slater 1998; Sayigh et al. 2007) and contact during separations and reunions (Smolker et al. 1993), as well as likely indicating the emotional state of the signaller (Esch et al. 2009).

Determining the functional role of cetacean vocalizations can be a challenging task, especially when playback experiments – often used in similar studies of terrestrial species, and frequently highly informative – are not practicable and the signallers themselves are not directly observable much of the time. With animals whose behaviour is as cryptic as that of most cetaceans, the acoustic realm can be our clearest insight into the social structure, diurnal cycles, and behavioural states. We can use the social, behavioural, and environmental context that these vocalizations are produced in, as well as the nature of the calls themselves, as an alternate way to investigate possible functions of the repeated call sequences produced by long-finned pilot whales.

### **1.5.1 Functions Being Tested**

This thesis investigates potential functions, four in particular, of the repeated call sequences of long-finned pilot whales to determine if there is support for some or evidence that may make others unlikely. Firstly, I will look at the link between these vocalizations and what is known of this species' social structure to determine if they may display a socio-acoustic structure similar to those found in either killer or sperm whales –

in which case the sequences are acting as group-identifiers to us, and maybe the whales themselves. At the same time, I will also look at the potential for these calls to be individual specific, like the signature whistles of bottlenose dolphins – in which case the sequences could be acting as individual identifiers. I will also test to see if these vocal repetitions may function as contact calls, through looking at modifications within sequences as well as the social and environmental context of these vocalizations to see if there are predictors that may support or refute the use of these calls for cohesion and coordination. Finally, the above analyses also allow me to investigate the possibility that they may serve primarily in mother-calf contact.

## **1.6 Thesis Overview**

In this thesis I am asking the fundamental question: Why do long-finned pilot whales put so much time and effort into producing repeated call sequences? To investigate the function of these vocal repetitions, I examine whether they could be identifiers comparable to the group-specific dialects of ‘resident’ killer whales or the individual signature whistles of other small delphinids through looking at the use of call types from these sequences across known pilot whale social units (Chapter 2). Secondly, I look at types of modification, including ornamentation, found within repeated call sequences (Chapter 3). In the final part of my thesis I investigate the context of these vocal repetitions to see if there are specific behavioural or environmental predictors of when they are produced (Chapter 4). The final chapter synthesizes what I have learned from my studies, along with their limitations, and directions that future work could take to increase our understanding of long-finned pilot whale vocalizations and their role in the daily lives of this species.

## **CHAPTER TWO – LONG-TERM SOCIAL UNITS OF LONG-FINDED PILOT WHALES DO NOT SHOW GROUP-SPECIFIC REPERTOIRES OF REPEATED CALLS**

### **2.1 Abstract**

Long-finned pilot whales (*Globicephala melas*) have been described as living in stable familial groups, termed social units, which are thought to be analogous to matriline groups found in killer whales (*Orcinus orca*) and the social units of sperm whales (*Physeter macrocephalus*), species whose societies also include social levels delineated by acoustic similarities. A significant portion of the pilot whale's vocal repertoire consists of calls made in rhythmic repeated sequences. These are good candidates for individual- or unit-specific vocalizations, or signals that might delineate other social levels, such as acoustic clans. In this study I explored the acoustic similarity among 19 known social units of long-finned pilot whales that were recorded opportunistically over a period of 16 years off Cape Breton Island, Nova Scotia, Canada. I visually catalogued 90 different call types with five of these being further divided into a total of 14 subtypes – together referred to as call categories – from 182 extracted repeated call sequences. Primary call types, as well as all call categories, heard on two or more days were then used to look for unit specificity. Little evidence of individual or unit-specific call types was found, with many units sharing call categories and few being specific to a single unit. The network of acoustic similarity between units had low modularity and thus no evidence for the organization of units into acoustic clans. However, tests on the temporal distribution of these call types showed that call categories were more often heard within the same field season, while overarching call types were heard more often than expected over a three to five-year period. This suggests horizontal transmission of call types across social units.

## 2.2 Introduction

Group-specific vocal variation has been found across an array of taxa, with examples including differences in the social calls of adjacent Kuhl's pipistrelle bat (*Pipistrellus kuhlii*) populations (Russo & Jones 1999) and regional variation in the contact calls of yellow-naped amazons (*Amazona auropalliata*) (Wright 1996). However, intraspecific vocal differences that are indicative of social learning and not the result of geographic or reproductive isolation – termed 'dialects' (Mundinger 1982) in this study – are far less common. It is in humans that we find the most recognized and studied examples of dialects where language variation has arisen through social learning (Piazza et al. 1995; Cavalli-Sforza 1997). Though rare in non-human taxa, there is compelling evidence for this kind of vocal variation in some species. Further genetic studies of yellow-naped amazons showed high gene flow between regions, suggesting that the specificity of their contact calls may be the result of social learning and pressures on individuals to conform to the local dialect instead of reproductive or regional isolation (Wright & Wilkinson 2001).

Research on cetaceans has also uncovered dialects. The best known example of this is the socio-acoustic structure of 'resident' killer whales (*Orcinus orca*) found off the western coast of North America, which is delineated by acoustic clans made up of matrilineally-based pods that each use a unique and temporally stable set of 7-17 discrete call types (Ford 1989). Here we see vocal differences at both a pod and clan level. A pod is a set of closely related matriline (Bigg et al. 1990), with matriline thought to represent the equivalent of social units found in other cetaceans such as sperm whales (*Physeter macrocephalus*) (Gero et al. 2013) and long-finned pilot whales (*Globicephala*

*melas*) (Ottensmeyer & Whitehead 2003). Following the discovery of dialects in killer whales, female sperm whales were also found to have acoustic clans that paralleled their social structure. In the Pacific there are five known clans, which geographically overlap and are not genetically distinct, that can be identified by their characteristic coda repertoires (Rendell & Whitehead 2003). Codas are sequences of clicks that are produced by female sperm whales in social settings (Watkins & Schevill 1977; Weilgart & Whitehead 1997). Further research has discovered social unit and individual specific coda variation in addition to the overarching differences between clans (Gero, Whitehead et al. 2016). Both killer and sperm whales are considered matrilineal where a female and her female offspring generally stay together in the same social unit (or matriline) for life. There is some variation in this general pattern between the two species and among different populations within them in factors such as unit size, whether social units contain multiple matrilines, and whether males disperse (Barrett-Lennard 2000; Gero et al. 2013). For example, 'resident' killer whales exhibit bisexual natal philopatry – where both sexes stay with their mother (Bigg et al. 1990; Barrett-Lennard 2000), while in sperm whales the males disperse from the unit as juveniles and only female offspring remain with their mothers long-term (Best 1979; Richard et al. 1996).

The study of dialects can provide important insight into the evolution of signalling and its relation to ecology and social structure. Dialects often arise in species with stable social groupings, which is especially evident in cetacean species with long-term matrilineally-based units (Weilgart & Whitehead 1997). Within killer and sperm whales, these vocal repertoires are learned by calves from their mothers, as well as from other members of their family unit (Ford 1991; Weilgart & Whitehead 1997). There is also the

possibility that group-specific calls in cetaceans function as symbolic markers of social tiers. An important part of human society and culture, symbolic marking is when individuals actively identify with and are recognized as part of a social level through a certain learned cultural trait, such as a language, behaviour, or symbol (Boyd & Richerson 1987). Deecke et al. (2000) found parallel changes in the structure of specific types of discrete call between matrilineal groups of northern 'resident' killer whales over time, suggesting that there is culturally-driven horizontal transmission of vocally learned modifications between matrilineal groups in addition to the already recognized vertical transmission from mother to offspring. Amongst sperm whales, Cantor and Whitehead (2013) noted a greater vocal difference between sympatric clans than allopatric ones. These two examples suggest the possibility that these species may use their vocalizations as symbolic markers (Deecke et al. 2000; Cantor & Whitehead 2013), for which there is little evidence among non-human species.

Long-finned pilot whales are found throughout the pelagic temperate waters of the North Atlantic and Southern Oceans, yet there are few known places where individuals show site fidelity to specific coastal regions. One such location is the inshore waters of Cape Breton Island, Nova Scotia, Canada, where approximately 1,500 individuals have been studied through the use of photo identification since 1998. Genetic studies of this species from Faroese drive hunts have suggested matrilineality (Amos, Schlotterer, et al. 1993; Amos, Bloch, et al. 1993), supported by the documentation of stable long-term units, not only off Cape Breton (Ottensmeyer & Whitehead 2003; Jankowski 2005), but also in the Strait of Gibraltar (de Stephanis et al. 2008). What we know of the social structure of long-finned pilot whales makes them an ideal model in which to look for

vocal dialects, given their similarities to other matrilineal cetaceans such as killer and sperm whales (Rendell & Whitehead 2001).

Repeated call sequences – the same call type repeated in sequence three or more times with a maximum of 6 seconds between calls (see Chapter 4) – make up a significant portion of calls produced by long-finned pilot whales. Seemingly more stereotyped than the rest of this species' vocal repertoire, these calls are superficially similar to the discrete call types produced by killer whales (Ford 1989; Ford 1991). The repetition of these call types in sequence also bears some structural similarity to the pattern of production of the individual signature whistles of several small delphinid species (Caldwell et al. 1990; Van Parijs & Corkeron 2001) that are also sometimes repeated in sequence (Janik et al. 2013). It has been suggested that repeated calls found in both short-finned pilot whales (*Globicephala macrorhynchus*) (Sayigh et al. 2013) and melon-headed whales (*Peponocephala electra*) (Kaplan et al. 2014) might function as individual or group identifiers, though there was not enough evidence in these studies to make strong conclusions. Repeated call sequences in long-finned pilot whales have also been linked to behaviour, being heard frequently when whales are socializing and rarely when they are resting, which lends contextual support to their possible role as group identifiers and contact calls (Chapter 4). For these reasons combined, I believe that call types found in the repeated call sequences of long-finned pilot whales are the best candidates for investigating the presence of group specific dialects in this species.

If pilot whales use sets of call types that are unit specific (as in the pods of 'resident' killer whales), I expect that I would find evidence of these call types in the recordings of repeatedly encountered social units. If the units are clustered into socio-

acoustic clans, similar to those found in killer and sperm whales, this would be indicated by clusters of units sharing call types. Alternately, if call types within repeated call sequences function as individual signature whistles I would expect them not to be shared amongst different social units. With these data I was also able to look at the possibility of horizontal learning amongst social units of pilot whales. As horizontal learning tends to produce relatively temporally-unstable behaviour—fads (Cavalli-Sforza et al. 1982) —, this could be indicated by temporal clustering of specific call types. In this study I use ten years of opportunistic recordings of known long-finned pilot whale social units to isolate calls used in repeated sequences. This is the first time that call types from the repeated sequences produced by long-finned pilot whales have been catalogued and compared to look for evidence of unit-specific calls, acoustic clans, individual identifiers and horizontal learning.

## **2.3 Methods**

### **2.3.1 Field Work and Data Collection**

Both acoustic recordings and photo-identification data were collected simultaneously from a population of long-finned pilot whales found along the northwestern coast of Cape Breton Island, Nova Scotia, Canada, during the months of July and August from 1998-2000, 2002-2003, 2005, 2007-2008, and 2013-2014. Whale-watching vessels were used as research platforms, being based out of the port of Pleasant Bay (46°50'N, 60°47'W) from 2002-2014 and the port of Bay St. Lawrence (47°02'N, 60°29'W) in previous years. These sites are only 31 km apart and many of the same individuals were photo identified in both locations, suggesting that whales regularly use both study areas. Upon



encountering pilot whales, the vessel was opportunistically stopped and hydrophones were placed at a depth of approximately 10-15m. A VEMCO hydrophone (10Hz-20kHz frequency response) was used to collect recordings from 1998-2003 along with a Sony TCM 5000 eV analog cassette tape recorder, while a Cetacean Research C55 hydrophone (8Hz-100kHz frequency response) was used for those collected from 2005-2014 along with a Zoom H4n 4-channel Handy Recorder. Recordings on cassette tape were digitized using CoolEdit Pro (ver. 2.0). Final audio files had a 44.1 kHz sampling rate and 16-bit sample size.

### **2.3.2 Assignment of Calls to a Social Unit**

The social units used in this analysis were delineated through observed associations between photo-identified individuals (in this case using data collected annually from the years 1998-2011) in a study by Augusto et al. (submitted) following methods described by Ottensmeyer and Whitehead (2003) for the same Cape Breton population of long-finned pilot whales. To be included in the study, photographs had to have a quality rating,  $Q \geq 3$  on a scale of one (poor) to five (excellent) based on focus, orientation, exposure, size and fin percentage visible (Ottensmeyer & Whitehead 2003; Auger-Méthé & Whitehead 2007). From these photographs, individuals were identified based on the position and number of mark points on and around the dorsal fin. These mark points included nicks, internal corners of notches, and protrusions found on the dorsal fin (Auger-Méthé & Whitehead 2007). Only images with at least 3 mark points were considered. These were compared with the population catalogue using Finscan (Araabi et al. 2000). Approximately 33% of individuals from this population can be photo identified by the mark points on their dorsal fins (Auger-Méthé & Whitehead 2007). Encounters for

which photographic effort resulted in less photographs taken than the number of whales counted, as well as those in which poor photographic coverage was noted, were excluded (Ottensmeyer & Whitehead 2003).

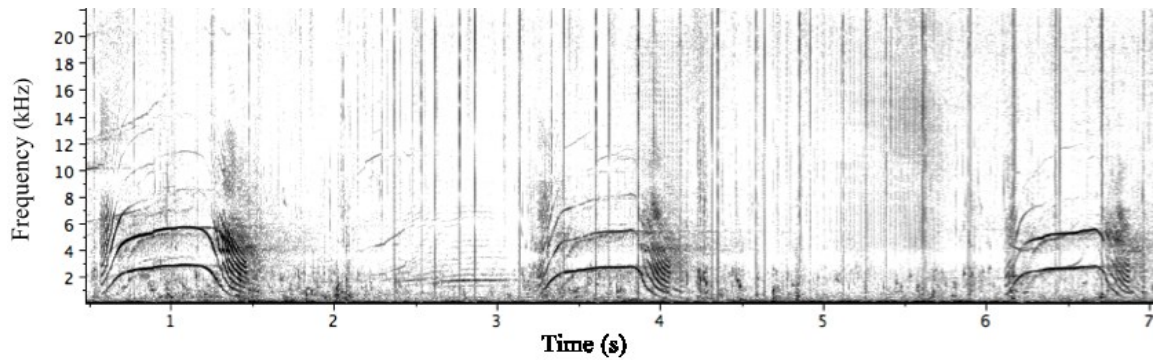
Social units were made up of key individuals – who had been seen at least four times with a minimum 30-day gap between consecutive pairs of sightings – and all of their constant companions – who had been seen on the same day as a key individual at least three times, with a minimum 30-day gap between sightings (Ottensmeyer & Whitehead 2003). The original study found seven units with average unit size of 11-12 individuals (after correcting for the proportion of individuals that can be photo-identified) using data from 1998-2000 (Ottensmeyer & Whitehead 2003). This has since been updated to a total of 21 units with an average group size of 7 individuals by Augusto et al. (submitted) using a larger dataset that spanned 1998-2011 (Appendix I).

Recordings were associated with social units when at least one key individual of that unit was photographically identified during the encounter in which the recording took place, and all identified individuals in that encounter that could be assigned to a unit belonged to only one unit.

### **2.3.3 Call Extraction and Categorization**

The recordings where a single known social unit was identified to be present amounted to 19.45 hrs of recordings including a total of 20 units. Raven Pro (Bioacoustics Research Program 2014) was used to extract repeated call sequences (defined in Chapter 4) (Figure 2.1). A spectrogram example of one call with good signal to noise ratio and minimal overlapping of other calls was created for each extracted sequence. If no calls matched these criteria, the sequence was discarded. All spectrograms had a 600-point (13.6 ms)

Hann window (3 dB bandwidth = 106 Hz) and overlap set to 50%, with a DFT size of 1024 samples and grid spacing of 43.1 Hz. Call spectrograms were visually compared between units and categorized into call types, in which sets of calls show similar frequency contours and other characteristics allowing them to be categorized into a single type. Human visual categorization was used as it has been found to be more reliable in distinguishing between call types than automated methods (Janik 1999; Sayigh et al. 2007; Kershenbaum et al. 2013), with one study showing that signature whistles recorded from a number of isolated bottlenose dolphins were reliably classified to each individual without the classifiers knowing the context of these calls (Janik & Slater 1998). Several of these call types were separated into subtypes, but only in cases when clear groupings of calls that showed distinctive characteristics were present within a broader call type. Call types were double-checked aurally to see if calls within types shared similar acoustic characteristics. To ensure that categorization was repeatable, two naïve volunteers independently performed visual classification using a randomly selected subset of 25 calls that made up approximately 14% of the overall sample for this study. Each volunteer's classification of each pair of calls as either being in the same or different categories was scored against the primary author's allocation. The number of pairwise allocations that agreed between myself and the first volunteer was 298/300, while the number that agreed between myself and the second volunteer was 297/300. This shows the reliability of the classification method.



**Figure 2.1** Example of a repeated call sequences produced by long-finned pilot whales, which is defined as the same call type repeated in a rhythmic and roughly evenly spaced sequence with no more than 6 seconds between calls (see Chapter 4)

### 2.3.4 Call Repertoire Similarity Among Social Units

To investigate whether long-finned pilot whales have unit-specific calls, I checked whether there were any call types and subtypes unique or characteristic (heard very often) from each unit.

To evaluate whether units were organized into acoustic clans, I searched for sets of units that shared specific call types or subtypes more than would be expected. Acoustic similarity between pairs of units was calculated as the number of call types shared between units divided by the combined number of unique calls heard from both units. I used modularity, calculated using Newman's (2006) eigenvector algorithm, to look for clustering of social units according to acoustic similarity. Modularity values  $Q > 0.3$  suggest a reliable partition (Newman 2006), here interpreted as evidence for organization into acoustic clans. In addition to modularity, both average linking cluster analysis and non-metric multidimensional scaling (Manly 1994) were used to illustrate patterns of acoustic similarity between social units in a two-dimensional space.

To investigate whether call types or subtypes from repeated sequences may be clustered temporally, I performed three different tests as follows. In all cases, I compared a summary statistic of the real data with a theoretical distribution of this statistic generated by 10,000 permutations of the dates on which each repeated call was heard. P-values (one-sided) were calculated as the proportion of times the statistic for the real data was greater than the permuted ones.

- a) Median of time span between first and last recording of each call type. Here the time delay – in days – between the first and last detection of each call type was calculated. The median of these ranges across all call types was then calculated, and compared to the expected median as computed from permuted data to see if it was significantly smaller than expected. This tests the null hypothesis of random ordering of call types over time, against the alternative that a call type appears in the populations, stays for some time (less than the 16-year duration of the study) and then disappears.
- b) Median across call types of the standard deviation of dates of detection. Here the standard deviation of the dates of detection for each call type was calculated. The median of standard deviations across all call types was then calculated, and compared to the expected median as computed from permuted data. This tests the null hypothesis of random ordering of call types over time, against the alternative that a call type appears and disappears in the populations as a Gaussian wave – where a call type gradually appears, becoming more and more used amongst the whales, then slowly fading out of the repertoire after a period of time

- c) Proportion of pairs of calls of the same type or subtype that were both heard in the same summer field season (two-month period), within a 1 to 2-year period, within a 3 to 5-year period, or within a 5 to 13-year period. This tests the null hypothesis of random ordering of call types over years, against the alternative that a call type was preferentially heard over a specific temporal period as mentioned above. This alternative thus allows a particular call type or subtype to appear and disappear two or more times over the full 16-year study instead of only being heard during a single temporal period.

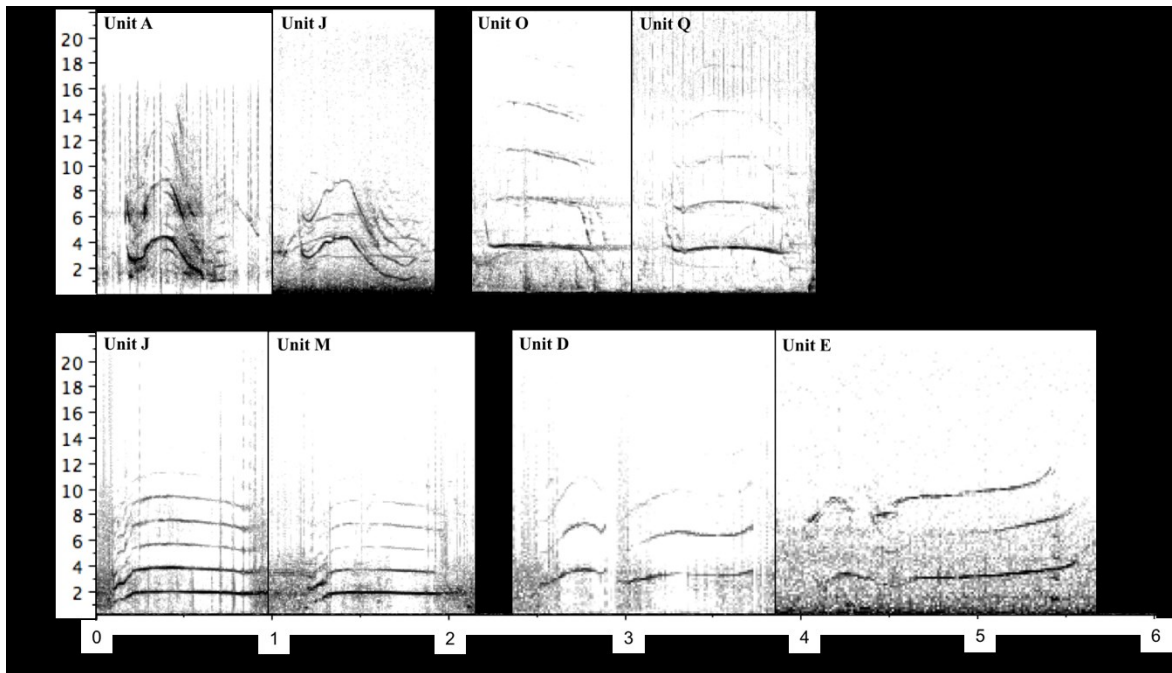
All analyses were performed using only call types that were heard on two or more days over the duration of this study. These analyses were performed twice: using only call types, and using call categories (i.e. both call types and subtypes), in MATLAB (MATLAB and Statistics Toolbox Release 9.0 2016).

## **2.4 Results**

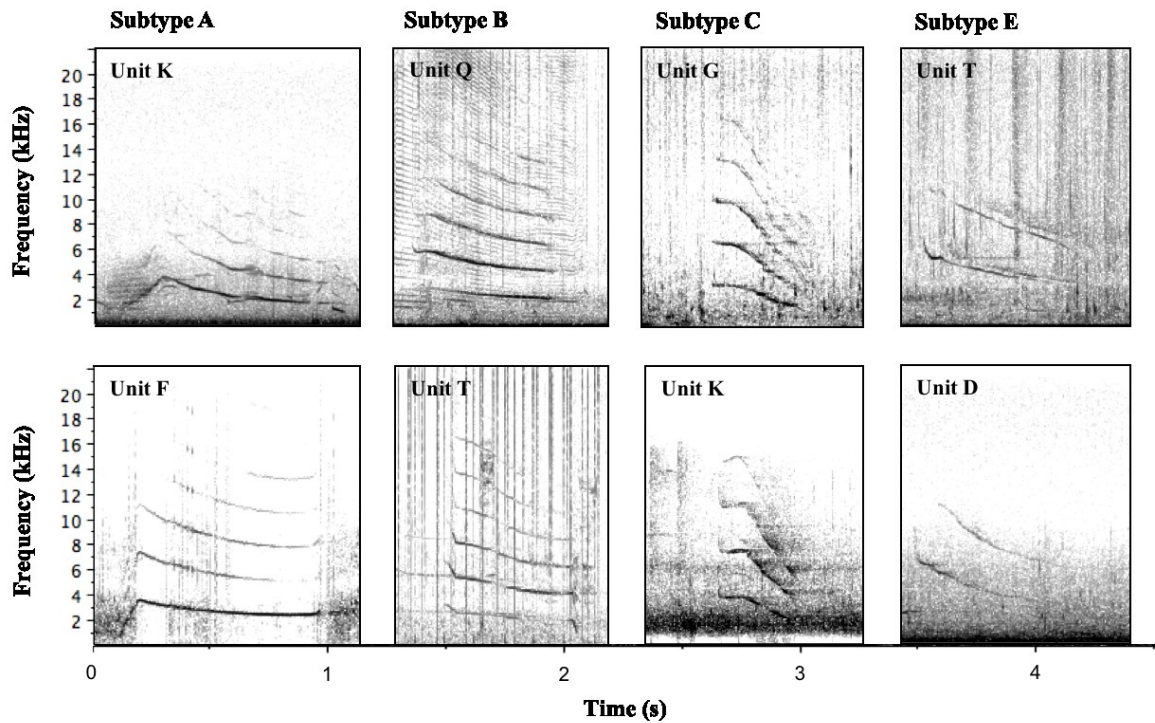
A total of 182 calls from repeated sequences were classified into 90 call types across 19 different social units, with recordings of the twentieth unit not containing any repeated call sequences. Of these call types, 5 were further divided into one or more subtypes. In total, 36 call categories from 27 call types were heard on more than one day across the 10 years of recordings spanning the 16-year duration of the study, with an average of 5.0 call categories – or approximately 4.5 (range = 0-24) call types – heard per social unit recorded.

## 2.4.1 Unit or Individual Call Specificity

There was a low rate of unit-specific calls that were heard on two or more days, with only one call type (type 25) being made by a single unit (unit Q). In addition to this, two call subtypes – 7c and 10a – were heard only from units K and J respectively. All other call categories were produced by two or more units over the duration of this study. There was only one call type, 8, heard on more than three days from a single unit, being heard on 8 different days from unit K, and 4 different days from unit Q. In total, this call type was heard 23 times from 10 different social units. The most shared call category was 8c, which was produced 11 times by 6 different social units. Figure 2.2 shows 4 examples of shared call types, while Figure 2.3 displays four subtypes from call type 8.



**Figure 2.2** Four sets of spectrograms, each showing a different call type produced in the presence of two different social units of long-finned pilot whales off Cape Breton, Nova Scotia



**Figure 2.3** Call type 8 with four examples of different subtypes, each produced in the presence of two different social units of long-finned pilot whales off Cape Breton, Nova Scotia

#### 2.4.2 Acoustic Similarity of Social Units

For both the analysis of only call types and for call types and subtypes the modularity values were below the 0.3 threshold (types:  $Q=0.210$ ; types and subtypes:  $Q=0.278$ ).

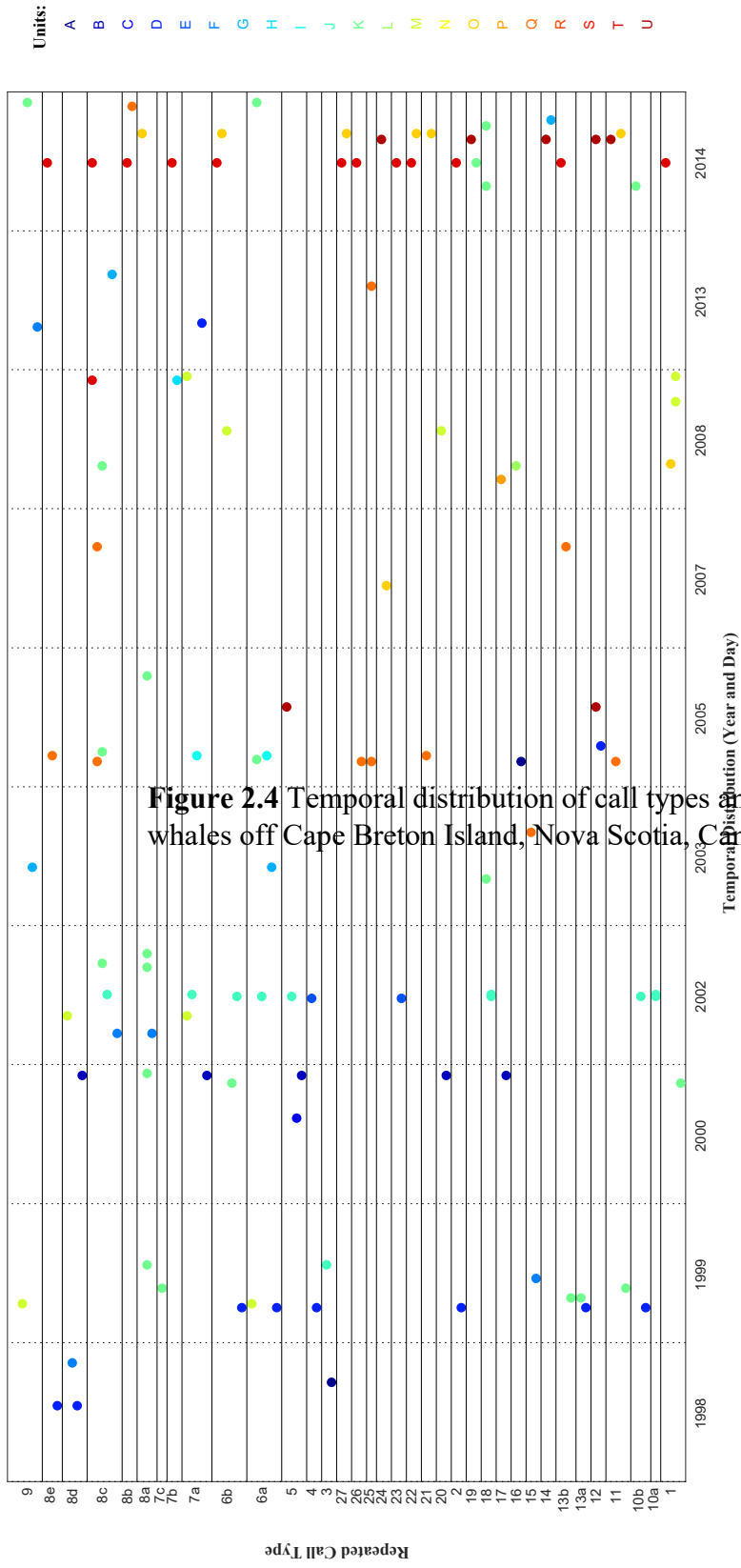
These results suggested there were no clear partitions of the matrix of acoustic similarity among units into clusters (Newman 2006). Both hierarchical clustering and non-metric multidimensional scaling supported the lack of acoustic clusters (see Appendix II). Thus, I found no strong evidence for acoustic clans among social units of long-finned pilot whales.



### **2.4.3 Temporal Distribution of Repeated Sequence Call Types**

There was no obvious temporal clustering of call categories heard on more than one day (Figure 2.4).

However, tests for temporal clustering of call categories (Table 2.1) indicated that calls of a particular type or subtype occurred together more frequently than expected by chance. Our data supported the third alternative hypothesis, that a call would be preferentially heard over a summer field season, disappear and then maybe reappear later. An example of this would be call subtype 6a that was clustered in 1999 and then in 2005 (though it was also heard on two occasions in between), and was not recorded again until 2014. Call subtype 13a also showed such within-season clustering, being heard only during the 1999 season. Tests for temporal clustering using only call types (Table 2.1) also supported the third alternative hypothesis, but showed that call types were heard more often than expected by chance over a period of 3 to 5-years before disappearing. For example, call type 8 was overall clustered mainly in 2002, but also occurred sporadically in previous and later years, while call type 5 is heard during 2000-2005, but never before or after.



**Figure 2.4** Temporal distribution of call types and subtypes (n=119) made by different species of whales off Cape Breton Island, Nova Scotia, Canada

**Table 2.1** Permutation tests for clustering of both call types and call categories of long-finned pilot whales over different time scales. Real: value of the summary statistic for the empirical data; Expected: value expected from a theoretical distribution created from 10,000 permutations; SD: Standard Deviation

Statistic	Call Types			Call Categories		
	Real	Expected	P (one-sided)	Real	Expected	P (one-sided)
Last – first detection of call, median (d)	3309	3526	0.333	2924	3677	0.071
SD detections of call, median (d)	1926	1931	0.429	1760	1968	0.164
Proportion of pairs of detections within in same summer season	0.130	0.119	0.256	0.167	0.122	<b>0.036*</b>
Proportion of pairs of detections in a 1 to 2-year period	0.114	0.119	0.588	0.125	0.116	0.351
Proportion of pairs of detections in a 3 to 5-year period	0.222	0.165	<b>0.030*</b>	0.190	0.172	0.265
Proportion of pairs of detections in a 5 to 13-year period	0.436	0.453	0.707	0.440	0.447	0.586

\* significant at  $p < 0.05$

## **2.5 Discussion**

### **2.5.1 Lack of Evidence for Individual or Group-specific Calls**

I found no evidence of individual or group-specific vocal signals in the repeated call sequences of long-finned pilot whales, contrary to our expectations that these vocal repetitions could function as identifiers such as the repeated discrete calls of other delphinids. I expected the vocal repertoire of pilot whales to present such vocal markers (Rendell & Whitehead 2001) since their social structure contains stable matrilineally-based social units (Amos, Bloch, et al. 1993; Ottensmeyer & Whitehead 2003; de Stephanis et al. 2008) similar to that found in killer whales and sperm whales (Bigg et al. 1990; Rendell & Whitehead 2003). Vocal identification, at various social levels, seems to be an important component of these social systems (Ford 1991; Rendell & Whitehead 2003; Gero, Whitehead et al. 2016). The pulsed calls and complex whistles of pilot whales make up a significant portion of their vocal repertoire and are aurally and structurally very similar to those produced by killer whales. This suggests these calls may have evolved to solve communication challenges – such as cohesion, coordination, and group interactions – shared by both of these species (Nemiroff & Whitehead 2009). However, I found no evidence of group-specific dialects – unique sets of call types – heard repeatedly throughout the years from a particular social unit, as would be expected if they were sharing a limited and temporally stable repertoire of these repeated sequence call types similar to pods of ‘resident’ killer whales (Ford 1989; Ford 1991). If pilot whales had group-specific dialects, I would have also expected to see some call types or subtypes unique to specific units. It is possible that these units share very similar sets of repeated calls indicating a higher order social structure such as a geographic clan, which

all social units in this study belong to. More recording effort or studies over a larger spatial scale may be needed to find the subtle differences between units, as was the case with sperm whales off Dominica, where variation between acoustically similar units became more apparent as more data was collected over the years (Gero, Whitehead et al. 2016).

Alternatively, I predicted that call types found in these vocal repetitions could represent individual identifiers similar to the signature whistles of some smaller delphinids (Van Parijs & Corkeron 2001; Sayigh et al. 2007). Bottlenose dolphins (*Tursiops truncatus*) produce individual signature whistles in rhythmic sequences, with an interval between calls of 1-10 seconds (Janik et al. 2013). If the vocal repetitions of long-finned pilot whales functioned in a similar manner, I would have expected call types to be limited to one social unit and only recorded when a particular individual was present. However, our data provided no evidence for individual specific vocalizations, as all but one call type and two subtypes were shared amongst multiple social units, making it unlikely that these calls represent individual identifiers.

### **2.5.2 Absence of Acoustic Clans**

I also did not find any obvious clustering of social units based on the similarity of their repertoires, which would be indicative of acoustic clans. This was an unexpected outcome when considering the long-term stability of long-finned pilot whale social structure (Ottensmeyer & Whitehead 2003; de Stephanis et al. 2008), and is contradictory to the socio-acoustic structure of killer and sperm whales where social units can be clearly clustered based upon their vocal repertoire (Ford 1991; Rendell and Whitehead 2003). If pilot whales had group dialects analogous to those found in ‘resident’ killer

whales, I would have expected to observe clusters of social units with a high degree of acoustic similarity representing the equivalent of pods. I also may have found some cases where a cluster of units has almost no acoustic similarity to another cluster representing different acoustic clans or perhaps even separate populations. If pilot whale group dialects were similar to sperm whale clans, I would have expected clusters of social units with a high acoustic similarity representing clans, but low similarity between different clusters resulting from the absence of shared call types (Rendell & Whitehead 2003). However, analyses provided no evidence for clustering of known social units that would indicate different acoustic clans or other multilevel acoustic structure as seen in killer or sperm whales.

There are several possible explanations for the lack of evidence for clans in the repeated calls of long-finned pilot whales. It could be that vocal differences between units are far subtler than those found in killer and sperm whales, in which case a much larger dataset would be required to find evidence of them. An alternate explanation for the observed absence of acoustic clans would be that the social units in this study are all part of a single acoustic clan, as had been reported for sperm whale social units found off Dominica (Antunes 2009; Gero, Whitehead et al. 2016) until the recent discovery of a second acoustic clan (Gero, Böttcher et al. 2016). The movements of pilot whales off Eastern Canada are not well understood, nor is it known whether I may have multiple populations. Evidence for geographical structure has been found in Europe, where stable isotope analysis of stranded long-finned pilot whales off Scotland and the Iberian Peninsula showed that the former hunted mainly pelagic prey while the latter had a coastal benthic diet (Monteiro et al. 2015). Acoustic studies of pilot whales elsewhere in

the northwest Atlantic may lead to the discovery of different geographically-based acoustic clans or even populations.

### **2.5.3 Evidence for the Temporal Clustering of Calls**

I provided some evidence for temporal clustering of use of call types and subtypes. Tests including call types and subtypes showed evidence of the same calls being more commonly observed within a given 2-month field season, while the overarching call types were generally heard over longer periods of 3 to 5 years. This temporal distribution may be indicative of horizontal learning, where specific call types are shared among units, preferentially produced by these units for a period, and then disappear.

There has been evidence of behavioural fads in cetacean, similar to those observed amongst humans (Cavalli-Sforza et al. 1982). The ‘southern resident’ community of killer whales had a behaviour of pushing dead salmon that spread amongst members of all three pods for a few months and then disappeared (Whitehead et al. 2004), as well as a spell of recreationally killing harbour porpoises (*Phocoena phocoena*) (Baird 2011). The latter fad was observed over a longer period, including a sharp spike in incidences in 2005.

A particularly well-studied example of temporal change in the vocalizations of cetaceans is the songs of humpback whales, *Megaptera novaeangliae*, which change from year to year, but remain quite consistent within any given year across a population (Payne & Payne 1985). Could long-finned pilot whales also be demonstrating some form of temporal vocal modification? Though the observed temporal clustering of call types and categories is interesting, more recording effort and analysis is needed to determine whether these could be the result of cultural vocal learning, or whether these may be due

to other factors such as which groups of whales – social units as well as all others that have not yet been assigned to units – are present during a given field season. Units seem to associate with one another inside the study area over periods of hours to days (Ottensmeyer & Whitehead 2003). Over larger spatial and temporal scales, I do not know whether their entries and exits from the Cape Breton study area, or large scale movements, are coordinated. However, if taken at face value, the results suggest call types sweep through the population for several years, with subtypes generally lasting about one 2-month field season, before perhaps returning years later.

#### **2.5.4 Future Directions and Summary**

It has become clear through this study that the pilot whales produce a great range and diversity of communicative sounds, with 90 distinct call types being found in just under 20 hrs of recordings. A larger dataset would be useful for building up call catalogues and may lead to the discovery of subtler differences between units, perhaps beginning with analysing all call types produced in the presence of two units. Suction cup digital acoustic recording tags (Johnson & Tyack 2003) and focal follows of both groups and individual whales are needed to learn more about social units, to look at possible short-term dispersion of individuals, and to investigate the detailed relationship between social behaviour and vocal output. Future studies should also compare recordings made over a range of both spatial and temporal scales to determine if there may be regional differences in the calls of long-finned pilot whales.

In summary, I did not find any evidence for identification calls at an individual or unit specific level for the call types or call categories, and the majority of these were shared amongst different social units. There was also no noticeable clustering of units



based on their acoustic similarity, and thus no evidence for acoustic clans. However, call categories and overarching call types appear and then disappear over a period of time, which suggests the possible horizontal transmission of these vocalizations between social units.

## **2.6 Acknowledgements**

I would like to thank everyone involved during the 16-year duration of this study, including graduate students, honours students, and research assistants in the field, as well as the coop students and volunteers who provided the manpower behind organizing much of the data used in this study. A special thanks to the captain and crews on both whale-watching vessels, the *Double-Hookup* (Captain Mark's Whale and Seal Cruise) and *Northern Gannet* (Captain Cox's Whale Watch), for facilitating our field work. I thank Luke Rendell, Mauricio Cantor, and Andy Horn for manuscript comments and suggestions. Thanks also to the Natural Sciences and Engineering Research Council of Canada (NSERC) for providing the funds needed to conduct many of these field seasons.

## **CHAPTER THREE – THE BAROQUE POTHEADS: CALL MODIFICATION AND EMBELLISHMENT IN REPEATED CALL SEQUENCES OF LONG-FINNED PILOT WHALES**

### **3.1 Abstract**

Patterns of vocal variation, particularly within calls that are generally stereotyped and stable in nature, lead us to question the function of such modification. In this study we characterized and described two fundamental call transition types leading to vocal variation, embellishment – a discrete change to a specific part of a call – and morphing – non-discrete small changes over a call, found in repeated call sequences of long-finned pilot whales (*Globicephala melas*) from a population found off Cape Breton, Nova Scotia, Canada. I found a high rate of modification, 51%, for transitions between consecutive calls with 31% being embellished and 20% morphed. A Pearson Chi Square test was used to determine that transitions were non-independent with modifications between pairs of consecutive calls often being followed by another modification of the same type. For embellished call transitions in sequence I described the dominant pattern of alternating between ornamentation and simplification, as well as 10 subtypes of embellishment which varied in rate of occurrence as well as temporal location within a call. Most common were the addition/deletion of buzzed, pulsed or tonal elements. Functions of these modifications could include conveying information on location, emotional state of the signaller, or be purely the result of vocal innovation.

### **3.2 Introduction**

Vocal variation – specifically in reference to changes over time seen in stereotyped calls and sequences made by an individual or set of individuals – has been described in a vast

number of different species. These changes range from the vocal response of the northern cricket frog (*Acris crepitans*) to intruders (Wagner 1989) and the modification of contact calls in budgerigars (*Melopsittacus undulatus*) (Farabaugh et al. 1994), to the learned development of stereotyped calls during the first year of life for beluga whales (*Delphinapterus leucas*) (Vergara & Barrett-Lennard 2008). One type of vocal variation, which I refer to as embellishment throughout this study, is the addition of details or features to a call. Also described as ornamentation, this form of call modification is perhaps best known from studies of bird song, where it has found to be correlated with cognitive abilities such as vocal learning (Boogert et al. 2008; Sewall et al. 2013). In some species the females show a preference for males with more complex song, leading to the hypothesis that they use ornamentation as an indicator of the intellectual performance of the singer when choosing mates (Nowicki & Searcy 2011) and perhaps even an individual's cognitive weaknesses (Sewall et al. 2013). Embellishment is also seen in anurans, such as is the case in the calls of the Tungara frog (*Engystomops pustulosus*). This species is found to make a basic “whine” vocalization, that can be made more complex with an addition of up to six “chucks” afterwards (Rand & Ryan 1981). The chucks are added to the call in the presence of other singing males, as females are not as attracted to the individuals producing only whines.

Large portions of the known vocal repertoire of several cetacean species are made up of highly stereotyped vocalizations. These range from the temporally stable individual signature whistles of bottlenose dolphins (*Tursiops truncatus*) (Caldwell et al. 1990) and the dialects of different families of ‘resident’ killer whales (*Orcinus orca*) (Ford 1991; Ford 1989), to the distinctive sets of codas produced by sperm whale (*Physeter*

*macrocephalus*) units and clans (Gero, Whitehead et al. 2016). Perhaps due to the often stereotypic nature of cetacean calls, the concept of embellishment has not been extensively explored within this taxon despite there being a number of studies that have described modifications to calls. One example of cetacean vocal modification observed in bottlenose dolphins, termed ‘looping’, happens when individuals alter their signature whistles through varying the number of repetitive elements, known as “loops”, within the whistle (Caldwell et al. 1990). This has been linked to stress, and may relay other important information about emotional state (Esch et al. 2009). Another possible expression of embellishment in cetaceans is the production of multi-component calls, where the individual components can be heard by themselves at other times. Killer whales have been found to produce compound vocalizations like these, where the relative positions of the sections remain unchanged even though not all sections are used every time the call is produced (Strager 1995). For many cases of vocal variation in cetaceans we do not understand the purpose of the modifications being made. This is because understanding the function of call modification in this taxa is challenging due to the difficulty of linking vocalizations to individual callers and their behaviours in the field. However, by looking at cetacean vocal modification types, such as embellishment, and how they manifest themselves we can begin to gather clues as to the kinds of information being transferred by different types of acoustic signals.

Relatively little is known about the vocalizations of long-finned pilot whales (*Globicephala melas*), a voluble delphinid species found in temperate waters of the North Atlantic and Southern Oceans. Though pilot whales are generally thought to have a very fluid, graded repertoire, where distinctions between specific call types are hard to

establish (Taruski 1979), I observed that stereotyped repeated call sequences – formally defined as the same call type made three or more times in sequence with roughly even spacing and a maximum of six seconds between them – make up a substantial portion of this species’ acoustic repertoire in a population off Cape Breton, Nova Scotia, Canada (Chapter 4). The calls in sequence are generally non-overlapping and have similar amplitude, supporting the hypothesis that the sequences are generally made by a single pilot whale (Busnel and Dziedzic 1966; Sayigh et al. 2013). While broad descriptions of both pulsed calls (Nemiroff 2009) and whistles (Taruski 1979) are available, there has been very little work on the function of different parts of this species’ vocal repertoire.

In this study I describe and characterize for the first time the transitions found between repeated calls within sequences. I also develop descriptive categorization tools that can be used in the investigation of call modification for other cetacean species. If non-random, characterizable forms of modification are found in pilot whale repeated call sequences, then it would suggest that the way whales alter their calls may be done with intention and for specific purposes, rather than simply being the result of a fluid repertoire.

### **3.3 Methods**

#### **3.3.1 Field Work and Data Collection**

Recordings of a population of long-finned pilot whales found in the Gulf of St. Lawrence off Cape Breton Island, Nova Scotia, Canada were collected opportunistically during the months of July and August during 1998, 1999, 2000, 2013 and 2014. The research was conducted using whale-watching vessels based in the ports of Bay St. Lawrence

(47°02'N, 60°29'W) from 1998-2000 and Pleasant Bay (46°50'N, 60°47'W) from 2013-2014, which are separated by a distance of 31 km. Many photo-identified pilot whales used both areas. In Bay St. Lawrence recordings were collected using a VEMCO hydrophone (10Hz-20kHz) and a Sony TCM 5000 eV analog cassette tape recorder. Those collected in Pleasant Bay (46°50'N, 60°47'W) used a Cetacean Research C55 hydrophone and a Zoom H4n 4-channel Handy Recorder. The early recordings were digitized using CoolEdit Pro (ver. 2.0). All audio files used in this study had a 16-bit sample size and a 44.1 kHz sampling rate. Recordings were taken after the vessel had encountered a group of pilot whales and the engine had been turned off. Hydrophones were deployed to a depth of 10-15m. A total of 62 hrs of recordings were used for this analysis.

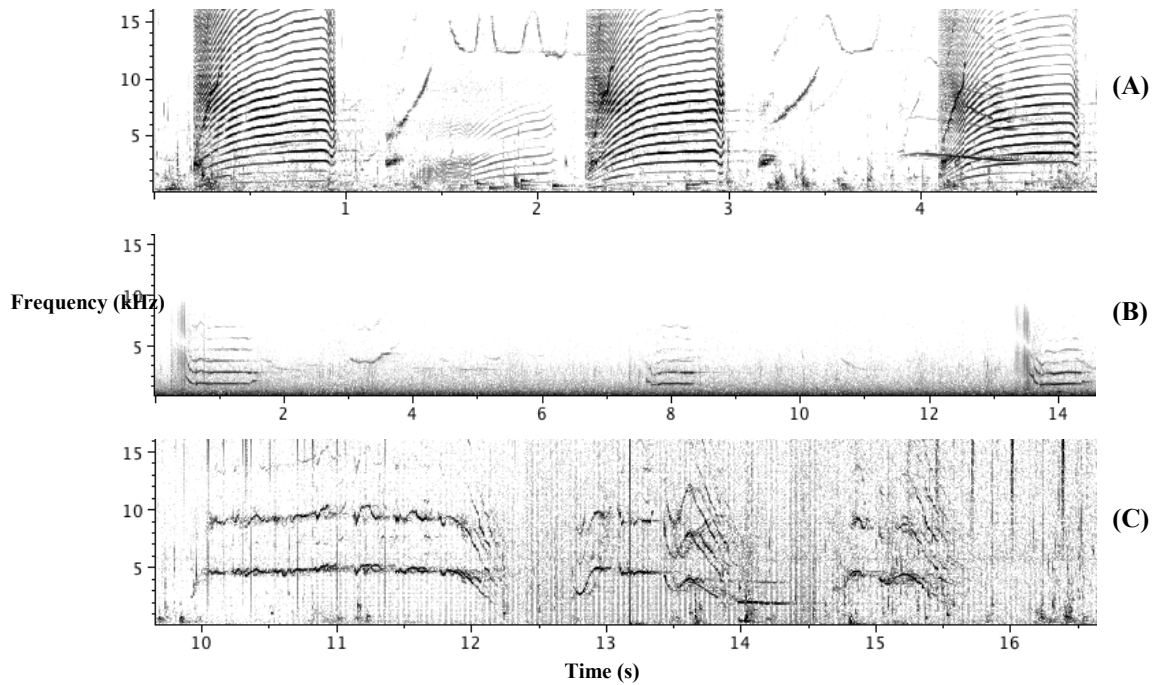
### **3.3.2 Recording Analysis**

Raven Pro (ver. 1.5) (Bioacoustics Research Program 2014) was used to create spectrograms with a 600-point (13.6 ms) Hann window (3 dB bandwidth = 106 Hz), with a 50% overlap and 1024-point DFT. All recordings were visually scanned and any repetitive vocalizations that matched the definition of repeated call sequences were extracted. Repeated call sequences are defined as the same call type made three or more times at roughly regularly spaced intervals with up to six seconds in between calls. These sequences had to have a good signal to noise ratio and minimal or no overlap with other calls for at least three calls in succession. Out of 188 repeated call sequences that met these criteria, 174 were scored for transition type for both the first and second call transitions as either stable, embellished, or morphed (Table 3.1, Figure 3.1). The remaining fourteen sequences could not be accurately categorized as they showed

discrete as well as non-discrete changes and these sequences were omitted from further analysis.

**Table 3.1** Definitions of transition type classifications for long-finned pilot whale repeated call sequences

Transition	Definition
Stable	Call remains conserved with no major changes
Embellished	Discrete additions or subtractions made to call. Can include gaps, buzzes, inflections, new tonal sections, etc.
Morphed	A combination of non-discrete small changes made across call, often involving simultaneous changes in fundamental frequency, length, number of inflection points, and other elements



**Figure 3.1** Spectrogram examples of sequences with (A) stable (B) embellished – with a buzz before the first and last calls – and (C) morphed transition types for repeated call sequences made by long-finned pilot whales

Analysis was done using IMB SSPS Statistics (IBM Corp. 2013). Contingency tables were used to look at the relationship between the first and second transition types (i.e. the transitions between the first and second, and second and third, calls in the sequence), with a Pearson Chi Square test being performed to test the null hypothesis that the second call transition type is being made independently of the first transition type. Further, both contingency tables and chi squared tests were used to investigate patterns of embellishment in sequences where both the two transitions looked at were classified as embellished, testing the null hypothesis that the second embellished transition type - ornamentation or simplification – is made independent of that which was used in the embellished transition type found before it. Embellished transitions were then categorized according to type, which can be found in Table 3.2 and Figure 3.2, and the location of

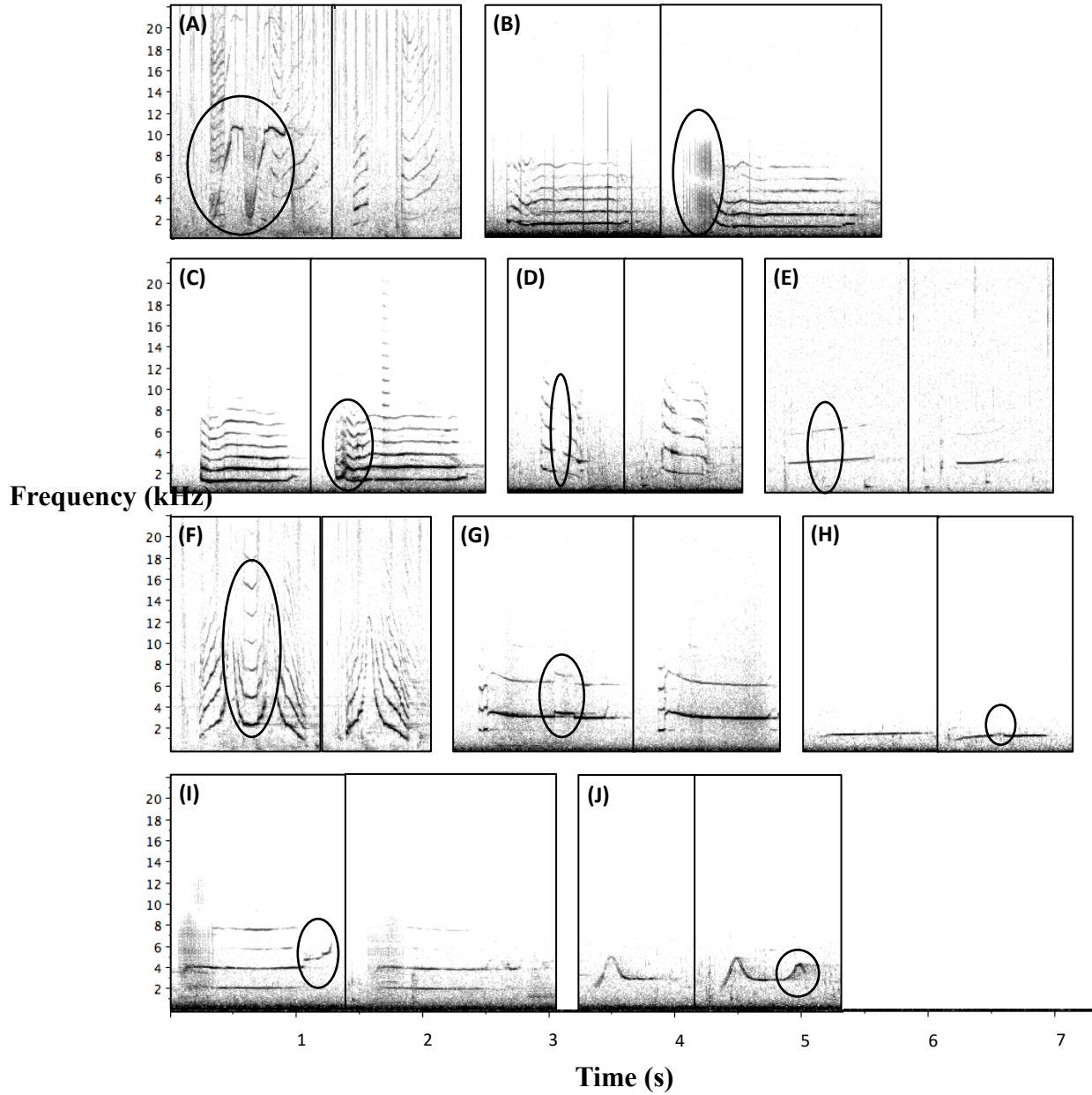


these embellishments within the call was noted. This was done by dividing the call into thirds and then determining whether the embellishment was made at the beginning, middle, or end.

In order to test the repeatability of the categorizations for transition and embellishment types, two untrained volunteers were given a random subsample of spectrograms of calls (N=15) and asked to complete the same task (see Appendix III). The answers matched those of this study by over 80% for this small sample size, showing agreement in categorization methods and that call transition types can be reliably distinguished.

**Table 3.2** Classifications for long-finned pilot whale repeated call sequence embellishment transitions

Embellishment Type	Definition of addition/subtraction
Biphonation	Addition of upper or lower frequency component resulting in biphonation and an increased complexity of the call
Buzz/Pulse	A buzz, brief pulsed component, or click
Change	An already existing section of call is modified, while the rest remains the same and the change does not fit into one of the other categories
Gap	Call is segmented by a gap where the whale briefly stops emitting the call
Lengthening	One section of the call is significantly lengthened or shortened
Looping	Akin to what has been described in signature whistles, where the number of repetitive elements – “loops” – are varied within a call
Step	A jump up or down in the fundamental frequency of the call which is visualized as a step-like contour on a spectrogram
Upsweep	An upwards sweep in frequency of a call
Wobble/Hump	Inclusion of new inflection points to create fluid wobble or hump in a section of the call
Unclassified Add/Sub	A new section is added to or subtracted from call that does not fit into any of the other add/sub categories mentioned



**Figure 3.2** Spectrograms of different types of embellishment found in the repeated call sequences of long-finned pilot whales including (A) biphonation (B) buzz/pulse (C) change (D) gap (E) lengthening (F) looping (G) step (H) wobble/hump (I) upswEEP and (J) unclassified tonal additions, presented in the order in which they were found - embellished areas circled

## **3.4 Results**

### **3.4.1 Transition Types in Repeated Call Sequences**

Transitions between stereotyped calls within a repeated sequence were most often stable in nature, with little or no differences between consecutive calls occurring in 49% (N=170) of transition types, but modification between calls was also frequent with embellishment of a call occurring in 31% (N=109) of transitions types analysed and morphing found in 20% (N=69). When looking at the second transition in relation to the preceding one in the sequence, whales tend to use the same type of transition more often than expected by chance (Table 3.3). If a whale begins the repeated call sequence using a stable transition it most often continues that way, if it embellished then it continues to do so, and if it morphed the call it often will continue in the second transition with the same pattern. Morphed transitions between calls were rarely followed by stable ones, and even less commonly by embellished transitions, with these patterns in reverse being uncommon as well. However, stable transitions were followed by embellished ones occasionally and embellished by stable, though these were less frequent than repeated call sequences where only a single transition type was noted. Therefore, transitions types within a sequences do not appear to be made independently of one another.

**Table 3.3** Contingency table of first (A→B) and second (B→C) transition types with Pearson Chi-Square value of the null hypothesis that first and second transition types in the repeated call sequences of long-finned pilot whales are made independently of one another

		B→C			Row Total
		Stable	Embellished	Morphed	
A→B	Stable	<b>63</b>	21	4	88
	Embellished	13	<b>35</b>	3	51
	Morphed	6	2	<b>27</b>	35
	Column Total	82	58	34	<b>174</b>

$\chi^2=126.8$   $p<0.001$

### 3.4.2 Embellishment Patterns and Categorization

Looking specifically at the 35 sequences where an embellished transition was followed by another of the same type, it appears that the majority of these were characterized by an alternating addition and subtraction pattern, where a call would be ornamented, then simplified or vice versa (Table 3.4). Only seven sequences did not have this alternating pattern.

All embellished transitions in this study were then categorized into types and the relative locations within the calls were noted (Table 3.5). The most common types of embellishments in repeated call sequences were general tonal additions and subtractions that did not fit into defined categories, as well as buzzes and pulses. Other embellishment modifications observed were: the addition of a higher or lower frequency component, a specific section of the call being changed, the addition of a gap, a significant increase in length of a section of the call, looping patterns, addition of steps, upsweeps at the beginning or end, and finally a wobble in one section of the call. Some embellishment types were seen in specific locations within the call, such as buzzes which were almost

always observed at the beginning, looping and upsweeps at the end, and wobbles in the middle (Table 3.5). Others seemed to be relatively equally distributed over the length of a call, such as the unclassified tonal additions and subtractions and the step embellishment. For three call transitions there were two embellishments made to the call simultaneously, which resulted in a total number of 112 embellishments categorized.

**Table 3.4** Contingency of embellishment for first (A→B) and second (B→C) transition types (addition and subtraction) with Pearson Chi-Square value of the null hypothesis that the second embellished transition type – addition or subtraction – is made independent of that which was used in the first embellished transition

		<b>B→C</b>		Row Total
		<i>Addition</i>	<i>Subtraction</i>	
<b>A→B</b>	<i>Addition</i>	<b>4</b>	17	21
	<i>Subtraction</i>	11	<b>3</b>	14
	Column Total	15	20	<b>35</b>

$\chi^2_1=12.2$   $p<0.001$

**Table 3.5** Chart of types of *embellishment* contrasted with *location* in the call for embellished transitions in repeated call sequences of long-finned pilot whales with the most commonly observed location within a call highlighted in bold

	<i>Beginning</i>	<i>Middle</i>	<i>End</i>	<i>All</i>	<i>Other</i>	Row Total
<i>Biphonation</i>	0	1	0	<b>5</b>	0	6
<i>Buzz/Pulse</i>	<b>19</b>	0	1	0	0	20
<i>Changed</i>	<b>3</b>	0	<b>3</b>	0	0	6
<i>Gap</i>	5	<b>8</b>	1	0	0	14
<i>Length</i>	1	2	<b>3</b>	0	0	6
<i>Looping</i>	0	2	<b>7</b>	0	0	9
<i>Step</i>	1	<b>3</b>	<b>3</b>	0	0	7
<i>Upsweep</i>	3	0	<b>7</b>	0	0	10
<i>Wobble</i>	2	<b>10</b>	2	0	0	14
<i>Unclassified Add/Sub</i>	6	4	<b>8</b>	0	2	20
Column Total	40	30	35	5	2	112

### **3.5 Discussion**

Though the repeated call sequences produced by long-finned pilot whales are often stable in nature, this study found that modification, embellished or morphed, between repeated calls occurs in over 50% of transitions observed. These vocal repetitions show characteristic patterns - particularly the use of a single transition type over consecutive transitions within a repeated call sequence and the alternating of embellished transitions between simplified and more complex calls - yet at the same time the amount of variation found within these sequences is remarkable. The ubiquity and arrangement of embellishment, along with the non-independence of transitions in repeated call sequences leads us to question whether there are underlying functions behind these patterns or if this is simply artefacts of the pilot whale's fluid vocal repertoire (Taruski 1979; Weilgart & Whitehead 1990).

#### **3.5.1 The Nature of the Signal Producer**

Past studies have suggested that the repeated call sequences of pilot whales are usually produced by a single individual, based on the non-overlapping nature of calls as well as their consistent amplitude (Busnel & Dziedzic 1966; Sayigh et al. 2013). However, it is possible that some sequences involve more than one signaller. A sequence of repeated calls can result when one individual is making a sequence of calls, and another attempts to match each call of the first. We refer to this as 'call matching' following the definition given by Gerhardt et al. (2000). Call matching has been observed in several species of cetaceans such as 'resident' killer whales (Miller et al. 2004) and sperm whales (Schulz et al. 2008), and there is evidence in short-finned pilot whales for multiple whales producing the same call in close temporal proximity (Sayigh et al. 2013). Alternately, a

sequence of repeated calls can also result from two individuals vocally interacting with each other in a reciprocal manner. This is called ‘antiphonal duetting’ when both signallers enter into a temporally coordinated exchange of repeated calls characterized by a consistent time lag between the individuals (Langmore 2002; Mann et al. 2003). These vocal interactions could have interesting functional implications for some of the modification being observed. Our definition of repeated call sequences includes only those where calls are roughly equally spaced and thus likely excludes the majority of sequences where two or more whales are vocalizing. However, occasionally, the timing between calls of the two individuals making the same call may be roughly evenly spaced leading to these repetitions being included among the repeated call sequences used for this study. If two whales engage in a temporally synchronized call exchange where spacing is roughly even between calls, it would most likely be the result of antiphonal duetting as it suggests that both whales are coordinating their calls with one another in a fashion that makes it sound as if a single individual was producing the sequence (Mann et al. 2003). This phenomenon has been observed in many other taxa, including in insects (Bailey 2003), frogs (Klump & Gerhart 1992; Grafe 1996) and birds (Voigtl et al. 2006; Wright & Dahlin 2007). It can have a variety of functions such as territorial displays (Vehrencamp et al. 2007), advertisement of fertility (Tobias et al. 1998) and locational information (Bailey 2003). It is also thought a duetting individual may time the signal it produces to avoid overlapping calls from other individuals and the signal masking that can result from this (Brumm & Slater 2006). Future studies focused on the timing of call sequences of long-finned pilot whales, including both sequences that fall under our definition as well as those that do not, will help determine if this species engages in



antiphonal duetting. I will consider the possibility of multi-signaller sequences and what this phenomenon could mean for pilot whales, even though the discussion will focus on functions pertaining to sequences produced by a single individual.

### **3.5.2 Patterns and Potential Functions of Embellishment**

Perhaps the most intriguing observation of this study is the high frequency of the embellished transition type, where only one section of the call is altered. It has been suggested that repeated call sequences like these in other species may function in identification (Sayigh et al. 2013; Kaplan et al. 2014) as is the case with the structurally similar vocal repetitions of bottlenose dolphin signature whistles (Sayigh et al. 2007). Studies of known cetacean identification vocalizations show some modification, but these calls are more often stereotyped in nature (Ford 1989; Ford 1991; Esch et al. 2009; Gero, Whitehead et al. 2016). Why then is call modification, particularity embellishment, so common in the repeated call sequences of long-finned pilot whales? One possibility is that the embellishment of calls may relay specific information to signal receivers. If this is the case, the patterns and nature of these transitions may give insight into the reason behind these modifications. Another possibility is that the modification observed is the result of the fluid nature of their vocal repertoire (Taruski 1979). However, patterns of embellishing and denuding found in many repeated call sequences suggest that there may be other reasons for these modifications, which are worth considering.

There are several possible explanations for the alternating addition-subtraction pattern of ornamentation and simplification, which vary according to the type of embellishment that was added. One reason for embellished call modification may be that these changes are an indicator of the emotional state of the signal producer. In 8% of

embellished transitions I observed a variation in the number of repetitive elements within the call which was being repeated, similar in nature to what has been described as looping in the signature whistles of bottlenose dolphins (Caldwell et al. 1990). Though these made up only a small percentage of categorized embellishments, it is possible that they could function in a similar manner to looping, which has been linked to stress (Esch et al. 2009). Another possible explanation for the observed pattern of ornamentation and simplification found in embellished call sequences is that whales add certain features to their calls in order to send locational information to other whales. It was observed that the upper frequency component of the biphonated calls made by killer whales was directional, leading to the hypothesis that these calls are used to help with coordination (Miller 2002). Clicks and buzzes – which can be used for communicative purposes beyond their well-established echolocation functions (Whitehead & Weilgart 1991; Rankin et al. 2007) – are also directional in nature (Bradbury & Vehrencamp 2011), and could be therefore used to give other individuals information on the location and orientation of the caller. It is worth mentioning that an artefact of recording with an omnidirectional hydrophone is that there is the possibility that in some instances these vocalization types may only being heard when the whale is oriented in a manner that allows the hydrophone to pick up this signal due to their directional nature. However, because of the alternating patterns of ornamentation and simplification found in many sequences along with the consistent amplitude of other sections of the call, this is likely seldom the case for our study. Together buzzes and pulses, along with biphonation, accounted for 23% of embellished transitions observed in this study. Given that pilot whales are a very social species living in a group setting where coordination would be

important, a reasonable explanation for embellishments involving buzzes or clicks as well as upper frequency components is that these modifications function in conveying locational information to signal receivers.

The alternating pattern of ornamentation and simplification may also be explained in some cases by two whales producing similar, but at the same time distinctive, versions of the same call type in a non-overlapping rhythmic pattern. Though antiphonal duetting has not been well established or studied in cetaceans, call-matching has been observed in a variety of species and has an assortment of proposed functions ranging from providing locational information (Janik 2000; Miller et al. 2004) to social bonding (Schulz et al. 2008). In order to determine whether some of these cases, such as in sperm whales, are coordinated duets rather than simply the response of one individual to another's signal, studies focusing on timing and specific context of both individuals are needed. While considering the possibility of two signallers in some sequences, it is important to note that mimicry has been well documented in a variety of cetacean species. One example of such is found in bottlenose dolphins, which have been found to mimic not only another individual's signature whistle (Tyack 1986), but sounds found outside the vocal repertoire of this species such as human voice (Lilly 1965) and computer generated sounds (Richards et al. 1984). Belugas have also been found to imitate human speech (Ridgway et al. 2012). The precision of the vocal imitations observed in cetaceans suggest that in a few cases it may be difficult to differentiate between one whale modifying calls and the alternative where one whale is precisely imitating the call of another if the latter happens to be in a stereotyped temporal pattern with similar amplitude between calls.

### **3.5.3 Potential Functions of Morphing**

Morphed transitions between consecutive calls in sequence were less common than both stable and embellished, but nonetheless made up a substantial portion of transitions.

Several possible reasons for the high frequency of morphing include the phenomenon of infant babbling and alteration due to the emotional state of the individual. In regard to infant babbling, we know that many species show vocal development in young that involves learning calls over time (Fripp et al. 2005). This phenomenon has been observed in many taxa, including cetaceans and primates (Elowson, Snowdon, and Lazaro-Perea 1998; Vergara and Barrett-Lennard 2008). Because of this, it is possible that some repeated call sequences with morphed transitions are the result of vocal learning in pilot whales calves, as many groups are seen with young. It has been observed that repeated call sequences as a whole are not more commonly heard from groups with calves (Chapter 4), but a more specific study of transition types in relation to group composition is needed to determine whether pilot whale calves may be a predictor for the presence of sequences with observed morphed transitions.

Another possibility for the presence of morphed call sequences would be that the transitions that are taking place are related to the emotional state of the signaller, with sequences displaying morphing perhaps indicative of an excited or stressed individual. Just as aberrant calls in killer whales were found associated with socializing and periods of high excitement (Ford 1989), perhaps the more variable calls heard from pilot whales in repeated sequences are representative of emotional state. Further study into the context of morphed transitions is needed to determine if this is the case.

### **3.5.4 Innovation as an Explanation for Call Modification in Pilot Whales?**

There is also a possibility that call modification observed in repeated call sequences may simply be a product of innovation for innovation's sake. Just as innovation is popular in many human cultures today, it has also been observed in non-human species such as chimpanzees (Ramsey et al. 2007) and swamp sparrows (Nowicki et al. 2001). In fact, many definitions of both culture and intelligence include innovation as a key component (Kummer & Loy 1971; van Schaik & Pradhan 2003). Innovation has not yet been studied in pilot whales, though examples from other cetacean species include the novel play behaviour of bottlenose dolphin calves, which is thought to have an important role in cultural innovation (Kuczaj et al. 2006), and the initiation of lobtail feeding amongst New England humpbacks (*Megaptera novaeangliae*) (Weinrich et al. 1992). An example of behavioural innovation for the sake of innovation was a short-lived fad seen amongst the southern 'resident' killer whales, where one whale began pushing dead salmon around with its head and it was not long before individuals from other pods were also seen exhibiting the same behaviour (Whitehead et al. 2004). If different kinds of innovation have been described amongst other species of cetaceans, might pilot whales be also doing this vocally?

### 3.5.5 Future Directions and Summary

Highly stable stereotyped calls have been the focus of many cetacean bioacoustics studies, while aberrant calls are often left to be looked at later when more tools become available. It has long been known that human visual (from spectrograms) categorization of cetacean calls is often more reliable at distinguishing between call types than automated methods, perhaps due to the similarities between what we perceive in calls and the characteristics that are used by cetaceans themselves (Janik 1999; Sayigh et al. 2007; Kershenbaum et al. 2013). This study is an example of how human perception can be used to explore differences and similarities amongst not only stereotyped calls, but also aberrant calls that were formerly omitted from analysis.

In summary, this study found that modification within the repeated call sequences of long-finned pilot whales occurs frequently, including morphed as well as a diverse range of embellished transitions types. This vocal variation may be linked to the information being transferred through these call repetitions or perhaps even a display of innovation in this species. Future research using a hydrophone array would make it possible to look at individual behaviour or location with respect to the larger group, and other data valuable for understanding call context. Even at a group level, an investigation into context as it is related to the frequency of different transitions types may give insight into whether there are differences in the situational use of stable, embellished, and morphed transitions, including more specifically the types of embellishments categorized in this study.

### **3.6 Acknowledgements**

Thanks to everyone who was involved in the field and lab during the 16-years of this study, especially the graduate students, research assistants, coop students, and volunteers who collected, organized, and analysed much of the data leading up to this study. A special thanks to the captain and crew of the *Double-Hookup* (Captain Mark's Whale and Seal Cruise) and *Northern Gannet* (Captain Cox's Whale Watch), who helped facilitate these field studies. Thanks also to the Natural Sciences and Engineering Research Council of Canada (NSERC) for the funding needed to run many of these field seasons.

## **CHAPTER 4 – REPEATED CALL SEQUENCES AND BEHAVIOURAL CONTEXT IN LONG-FINNED PILOT WHALES OFF CAPE BRETON, NOVA SCOTIA, CANADA**

### **4.1 Abstract**

Repeated calls are part of the vocal repertoire of a diverse array of species, often presented in sequences that take time and effort on the part of the signal producer. Rhythmic repeated call sequences make up a significant portion of long-finned pilot whale (*Globicephala melas*) vocal production, yet the function of these sequences has not been investigated until now. In this study I explored the relationship between behavioural context and the presence of these vocal sequences using recordings of a population of pilot whales found off Cape Breton, Nova Scotia, Canada. I applied a binomial logit-link generalized linear model to look for possible predictors of the presence of repeated call sequences. They were more common in recordings of socializing whales than in those of whales in other behavioural states, and least common in resting whales. These vocal repetitions were also more common with larger group size. These results suggest that sequences function in maintaining contact and cohesion within this social species, possibly also serving in individual or group identification. The context of repeated call sequences indicate that they are not primarily mother-calf interactions, as they are heard just as commonly from groups without young. Future studies of pilot whale repeated call sequences should include individual-level behaviour and detailed acoustic calling context.



## 4.2 Introduction

Repeated calls – stereotyped calls that are produced by an individual repeatedly over time, sometimes in regularly-spaced sequences – are an important part of the vocal repertoires of many different species, from the territorial chirping of Japanese burrowing crickets (*Velarifictorus micado*) (Alexander 1961) and interactive calling of male American green tree frogs (*Hyla cinere*) (Klump & Gerhart 1992), to the family-specific calls of stripe-backed wrens (*Campylorhynchus nuchalis*) (Price 1999) and ‘resident’ killer whales (*Orcinus orca*) (Ford 1991). When a species produces a significant portion of their calls in this manner, the often striking and stereotyped nature of repeated calls leads us to consider the function of the call that is being repeated, as well as that of the repetition. What is a signal’s purpose if a species is willing to invest much time and effort into repeating the same call again and again? While the metabolic cost of sound production for many aquatic taxa is thought to be minimal in comparison to the total energy used by an individual (Bradbury & Vehrencamp 2011), the indirect costs of detection by predators, prey, or social competitors can be ecologically important (Jensen et al. 2012). Some have suggested that repetition of calls is a redundancy used to reduce masking of the signal from background noise or calls from other individuals (Brumm & Slater 2006), when transferring important information such as about future actions and identity (Bradbury & Vehrencamp 2011). However, it can be a challenge to link repeated calls to a specific function.

Cetaceans are no exception, with sequences of repeated call types having been described across a broad range of species, but only well understood in a few. Melon-headed whales (*Peponocephala electra*) (Kaplan et al. 2014) and northern right whale

dolphin (*Lissodelphis borealis*) (Rankin et al. 2007) have both been recorded making repeated call sequences for which we do not yet have an explanation of function. One possible function of repeated calls is that they act as either individual or group identifiers. Signature whistles are individually distinctive stereotyped whistles found in some delphinid species (Caldwell 1965; Janik & Slater 1998; Van Parijs & Corkeron 2001) often produced in sequences with 1-10s intervals between calls (Janik et al. 2013). Individual vocal identifiers are not limited to cetaceans, being found in other taxa such as bats (Gillam & Chaverri 2012), birds (Mammen & Nowicki 1981), and primates (Bergman 2010). In contrast to the signature whistles found commonly in cetaceans that have fusion-fission societies, in which the composition and size of groups changes over time, other whale species that live in stable matrilineal units have been found to produce group-specific identification calls. Both 'resident' killer whales (Ford 1989) and sperm whales (*Physeter macrocephalus*) (Gero, Whitehead et al. 2016) have vocalizations linked to different levels of their social structures. With both of these species, their group-specific vocalizations can be repeated in rhythmic sequences.

Mother-calf contact is also a possible function for these repeated calls in cetaceans. With sound as the main source of communication in cetaceans, and a bond between mother and calf being generally the strongest, one might expect calves to contribute significantly directly or indirectly to the vocal soundscape. Studies of several delphinid species support this, showing that whistling is much more prominent in groups with calves (Van Parijs & Corkeron 2001), as well as demonstrating the importance of whistling during separation and reunion (Smolker et al. 1993). In both these cases specific whistle types were repeated, sometimes in sequence.

Repeated calls can also function in establishing contact and maintaining organization in large groups of cetaceans. Highly social species of whales and dolphins need vocal ways in which to share information such as location and movement decisions that keep groups of individuals coordinated and functioning as a cohesive unit (Janik & Slater 1998; Tyack 2000). In this case the context in which an individual repeats a call may be also important. It has been suggested that repetition of calls can provide enough detail to give the receiver a good estimation of the location on the caller (Krebs et al. 1981; Falls 1985; Naguib & Haven-Wiley 2001).

Identifying functions of repeated calls, which may not be exclusive, brings us back to the challenge of studying how social life and communication relate to one another, both in cetaceans and more broadly. One way of addressing the function of specific vocalizations is through studying the contextual cues surrounding them. Most studies on the context of cetacean vocalizations have taken place in just a handful of species. Bottlenose dolphins (*Tursiops truncatus*) produce bray-like feeding calls (Janik 2000) and individuals meeting at sea exchange signature whistles (Quick & Janik 2012). It has also been observed that mothers use specific acoustic signals – which incorporate their signature whistle, but also include additional features such as clicks or other whistles – to call their calves (Kuczaj et al. 2015). Sperm whales, though not making tonal vocalizations, have been found to make specific click patterns called “codas” while socializing at the surface (Whitehead & Weilgart 1991).

Some of the earliest published studies of both long-finned (*Globicephala melas*) (Busnel & Dziedzic 1966) and short-finned (*Globicephala macrorhynchus*) (Caldwell & Caldwell 1969) pilot whale vocalizations include descriptions of repeated call types,

some of these made in sequence. A more recent study of short-finned pilot whales showed that these repeated call types made up a significant portion of their repertoire, though their function is not yet understood (Sayigh et al. 2013). Listening to the population of long-finned pilot whales found off Cape Breton, Nova Scotia, Canada, I noticed not only that repeated call types were present in most recordings when the whales were vocal, but that rhythmic repeated sequences of these calls were also commonplace. These sequences were composed of the same call type made three or more times, with roughly equal spacing of six seconds or less between adjacent calls and could include tonal as well as pulsed elements. Because of the range of different call types that are repeated in sequences the repetition itself is a distinctive feature of the pilot whales' vocal repertoire. It is not yet known whether each of these sequences is produced by a single individual, but prior studies have concluded that these non-overlapping sequences, in which calls have consistent amplitude, generally seem to be made by a single pilot whale (Busnel & Dziedzic 1966; Sayigh et al. 2013). Our understanding of this species' calling context in the north-western Atlantic is limited to two reports, the first which found that frequency, duration, and calling rate of whistles varied between some contexts (Taruski 1979), and a second where whales were found to make more complex whistles and pulsed calls when displaying surface active behaviour than when resting or travelling without much activity at the surface (Weilgart & Whitehead 1990).

If repeated call sequences in pilot whales function primarily as individual or group identifiers, I would expect them to be more common when individuals are socializing or when more whales are present, than when whales are resting or involved in other behaviours for which identification seems less important. If they function primarily

as calls in a mother-calf relationship, then their presence should increase when the observed number of calves in a group increases. If they function as more general contact calls they would be expected to occur during times when cohesion and coordination are important, such as socializing or increased group size. To investigate why pilot whales repeat calls, I relate the repeated call sequences made by long-finned pilot whales to behavioural and environmental data, to provide the first detailed description of context for these repeated call sequences.

## **4.3 Methods**

### **4.3.1 Recordings and Acoustic Analysis**

Recordings, photo-identification, behavioural, and environmental data for this study were collected during July and August in 1998-2014 off the north-western coast of Cape Breton Island, Nova Scotia, Canada. Two whale-watching vessels, the *Northern Gannet* and the *Double Hookup*, were used as primary research platforms. Trips were made up to three times daily, each lasting approximately 2.5 hrs. There were between one and three trained observers on board the vessel depending on the year.

Recordings from 1998-2000 were collected off Bay St. Lawrence (47°02'N, 60°29'W) using a VEMCO hydrophone (10Hz-20kHz) and a Sony TCM 5000 eV analog cassette tape recorder. These were digitized using CoolEdit Pro (ver. 2.0) with a 16-bit sample size and a 44.1 kHz sampling rate. Those from 2013-2014 were collected off Pleasant Bay (46°50'N, 60°47'W) using a Cetacean Research C55 hydrophone and a Zoom H4n 4-channel Handy Recorder at the same bit size and sampling rate. The frequency response of these hydrophones was from 20Hz-20kHz for the VEMCO

hydrophone, and 8Hz-100kHz for the C55. These sites are separated from each other by a distance of 31 kilometres, and photo identification of pilot whales seen over the years shows that many individuals use both areas.

In both sites the recordings started after we encountered a group of pilot whales, cut the engine, and lowered the hydrophone down to a depth of 10-15m. Encounters began when a group of whales were sighted and included all individuals within 200m of the vessel and each other using the chain rule (see definition of party size in Clutton-Brock et al. 1982). The encounters ended when we left to return to harbour, when the whales stayed submerged for more than 10 minutes, or if the captain decided to observe another group that was at least 200m away from any of the members in the previous group. A total of 329 recordings were used for analysis, with a mean estimated group size of whales present of 24.5 (SD = 19.0).

Behavioural and environmental information was recorded opportunistically in Bay St. Lawrence, while in Pleasant Bay it was taken every 10 minutes. Data gathered consistently in all five years included time of day, group size, group behaviour, group composition (including presence of calves under three years of age and those under one year of age), specific surface behaviours, other cetacean species present, and Beaufort Sea State. Behavioural states were defined as the behaviour displayed by the majority of whales during the observation period and were recorded as outlined in Table 4.1

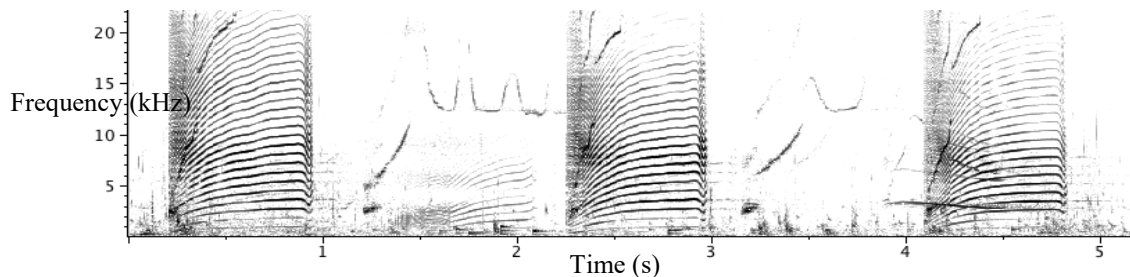
**Table 4.1** Definitions of long-finned pilot whale group behavioural states used in this study

<b>Behaviour</b>	<b>Definition</b>
Travelling	Steady directional movement, travelling faster than vessel's idle speed (ca. 5.5 km/hr), often displaying variable diving patterns
Socializing	Body contact between individuals, little to no directional movement, much activity at the surface, short dives
Foraging	Prolonged dives, lifting tails when diving, no directional movement, often characterized by birds feeding in association with group, little to no surface social activity with individual whales resurfacing on their own
Resting	Either logging most of the time or travelling at a rate slower than vessel's idle speed, individuals come to the surface as a group
Other	More than one behavioural state was predominant during the observation period or it did not fall into one of the four commonly observed behavioural states listed above

Group composition included the number of adults, as well as calves with their approximate ages. These were determined and classified by physical characteristics. Calves under one year of age had visible foetal folds visible along their sides, while those from one to three years of age were grey and smaller than the general population, but lacked these folds.

The recordings were analysed using the acoustics software Raven Pro (Bioacoustics Research Program 2014). Final analysed recording lengths varied between 1.5 and 6.0 minutes with a mean of  $3.58 \pm 1.1$  min, and only the first section of a recording was considered for those over six minutes in length. Spectrograms were made with a 600-point (13.6 ms) Hann window (3 dB bandwidth = 106 Hz), with a 50%

overlap and 1024-point DFT. Each recording was then scored for the presence or absence of repeated call sequences, which are defined as the same call type – showing similar frequency contour and overall acoustic characteristics that can be categorized as one type of call – made three or more times at roughly regularly spaced intervals with up to six seconds between consecutive calls (Figure 4.1). This definition separates repeated calls in sequences from others repeated sporadically throughout a recording, which may be of the same call type, but without a rhythmic nature.



**Figure 4.1** Example of a repeated call sequence made by a long-finned pilot whale. The same call type is made three or more times in a row with roughly even spacing and no more than six seconds between consecutive calls.

## 4.3.2 Statistical Analysis

### 4.3.2.1 Data Exploration

Potential behavioural and environmental predictors of repeated call sequences were explored statistically and graphically using IBM SPSS Statistics (IBM Corp. 2013). The following factors were chosen for analysis: (1) Group Behavioural State (categorical; as in Table 1); (2) Group Size (continuous); (3) Number of Calves under Three Years of Age (integer); (4) Presence of Other Delphinid Species (presence/absence); (5) Beaufort Sea State (categorical) (6) Time of Day (categorical: 10:00-13:00; 13:00-16:00; 16:00-



19:00; 19:00-22:00 local summer time); (7) Year (categorical) nested within Site (categorical: Bay St Lawrence or Pleasant Bay).

Recording length was included in initial exploration and modelling, in case it had significant impact on whether repeated call sequences were present. However, this measure was omitted from the final model as it had little effect on the presence of these sequences.

#### **4.3.2.2 Model Selection**

IBM SPSS Statistics was used to find social and environmental predictors for the presence of call trains using a binomial logit-link generalized linear model. Model selection was done manually using corrected AIC values (AICc). A backwards selection process was used, beginning with the inclusion of all predictors. The predictor dropped in each round was the one whose exclusion resulted in the lowest AICc, and the process stopped when excluding any predictor increased AICc.

To meet the independence assumption for modelling only the first recording was used for each encounter in cases where there was more than one recording taken. This gave 182 separate recordings. Data from all recordings were used for graphs and figures.

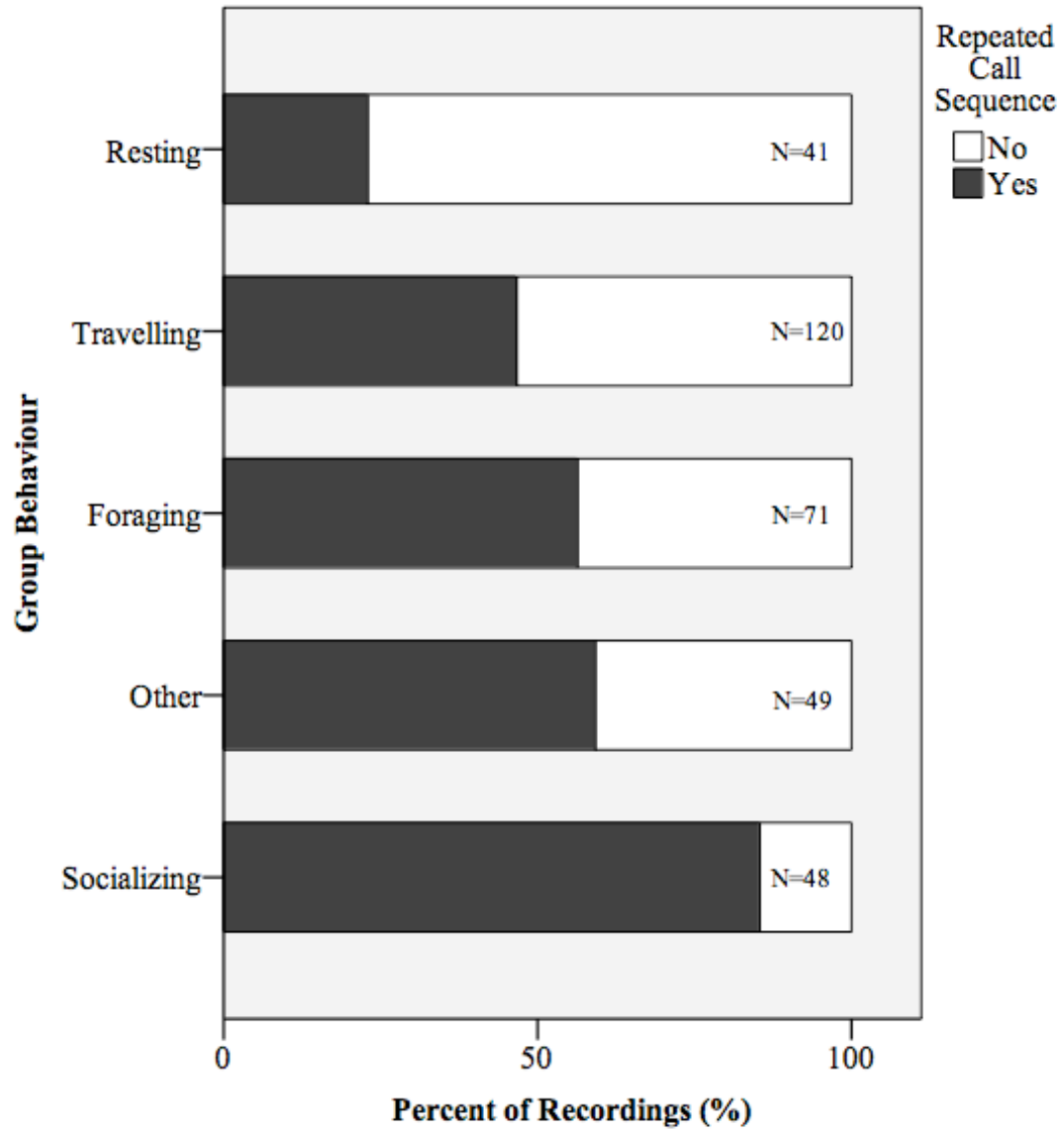
### **4.4 Results**

#### **4.4.1 Data Exploration**

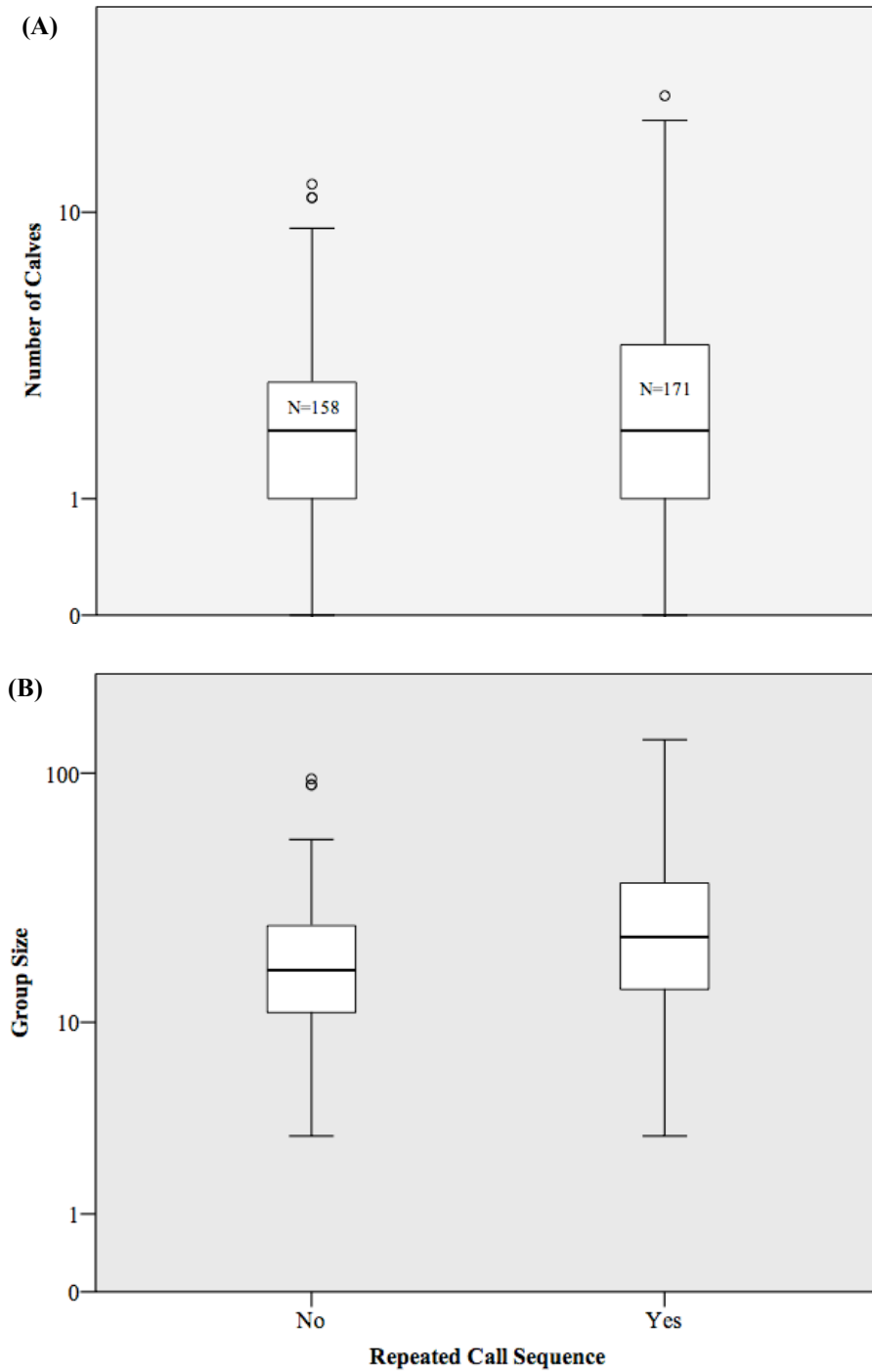
From over 100hr of collected recordings, a total of 450 individual recordings that could be linked to an encounter were scored for the presence or absence of repeated call sequences. These spanned 5 different years, 221 encounters, and totalled 16hrs. Of these,

329 recordings had recorded values for all chosen predictors and were used for final analysis and modelling.

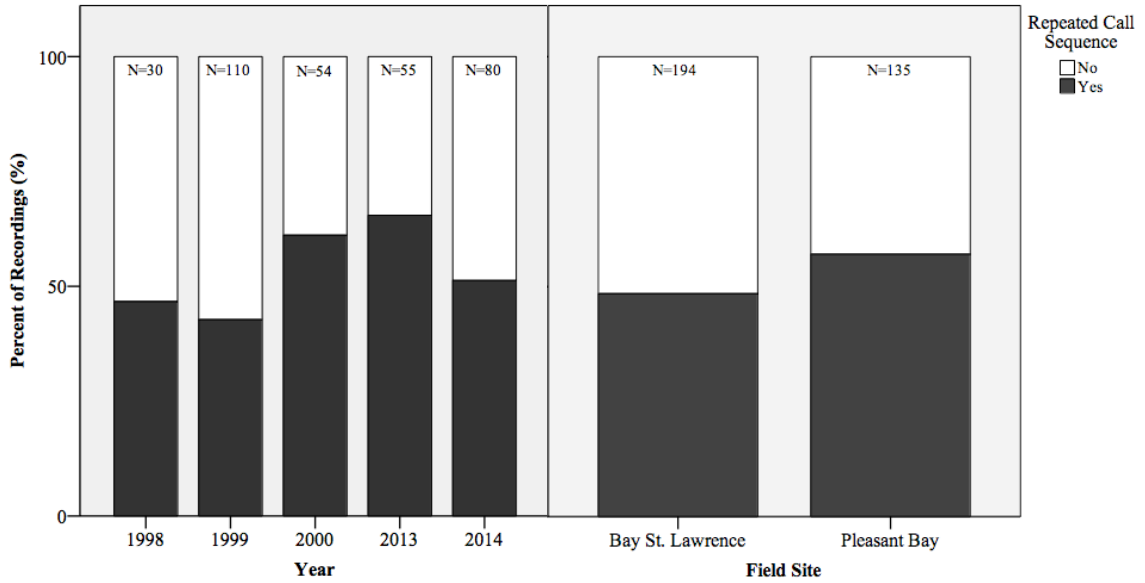
Repeated call sequences were present in 52% of recordings. The percent of recordings with repeated call sequences varied substantially between behavioural states, with 85.4% of recordings where whales were socializing having these calls and only 22.9% of recordings during which whales were resting (Figure 4.2). Group size was higher for recordings with repeated call sequences than those where repeated calls were absent (Figure 4.3). The former had a mean group size of 28.5 individuals with a median of 22.5, while the latter had a mean of 20.1 individuals with a median of 16.5. There is some difference apparent in the presence of repeated call sequences between years, with a higher presence of repeated call sequences in 2013 and lower in 1999 (Figure 4.4). The prevalence of repeated call sequences was not strongly related to calf number, presence of other delphinids, sea state, or time of day (Figure 4.3, Figure 4.5).



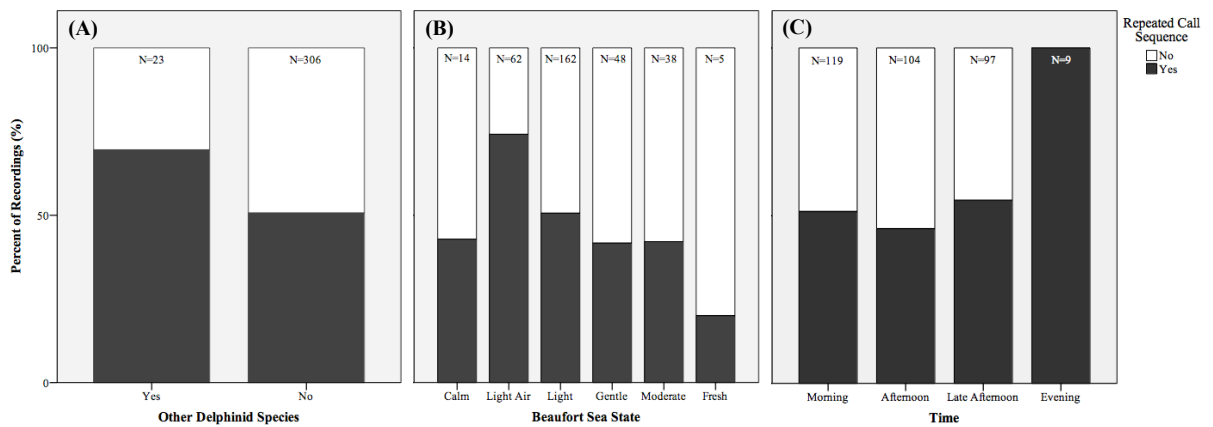
**Figure 4.2** Percent of recordings of long-finned pilot whales for each behavioural type that had repeated call sequences present (N=329)



**Figure 4.3** (A) Number of calves under the age of three in group and (B) size of group of long-finned pilot whales in relation to the presence and absence of repeated call sequences (N=329)



**Figure 4.4** Year of study and field site in relation to whether repeated call sequences were present for long-finned pilot whales (N=329)



**Figure 4.5** Percent of recordings of long-finned pilot whales with repeated call sequences for (A) the presence and absence of other delphinid species (B) each Beaufort Sea State with the following categories with corresponding Beaufort numbers: Calm (0), Light Air (1), Light Breeze (2), Gentle Breeze (3), Moderate Breeze (4), Fresh Breeze (5) (C) each time of day binned into morning (10:00-13:00), afternoon (13:00-16:00) late afternoon (16:00-19:00) and evening (19:00-22:00) (N=329)

#### 4.4.2 Repeated Call Sequence Presence/Absence Model

The final model chosen included behavioural state, group size, year nested within site (Table 4.2, Table 4.3), matching the results of the exploration of the larger dataset. Time of day, number of calves, sea state, and the presence of other odontocete species were excluded from the final model.

**Table 4.2** Manual backwards stepwise selection for repeated call sequence presence (REP) binomial generalized linear model with AICc values using predictors of group behaviour (GB), group size (GS), time of day (TD), number of calves under three years of age (CN), sea state (SS), presence of other delphinids (OD) and year nested within site (Y(S))

Step	Model	AICc	$\Delta$ AICc
1	REP ~ GB + GS + TD + CN + SS + OD + Y(S)	255.18	16.73
2	REP ~ GB + GS + CN + SS + OD + Y(S)	250.20	11.74
3	REP ~ GB + GS + SS + OD + Y(S)	247.99	9.54
4	REP ~ GB + GS + OD + Y(S)	240.26	1.81
5	REP ~ GB + GS + Y(S)	238.45	0.00
6	REP ~ GB + GS	238.62	0.16

**Table 4.3** Summary of final binomial generalized linear model predictors for the presence of repeated call sequences in long-finned pilot whales with the null hypothesis being that there are no differences in repeated call presence between different behavioural and environmental contexts (N=182)

Parameter	Coefficient	p-value
<b>Group Behaviour**</b>		0.034
Socializing	1.20	0.059
Other	0.18	0.766
Foraging	0.52	0.261
Travelling	0.00	
Resting	-0.79	0.124
<b>Group Size**</b>	0.03	0.011
<b>Year (Site)*</b>		0.078
1998	-0.60	0.410
1999	-0.84	0.097
2000	0.06	0.920
2013	0.57	0.277
2014	0.00	

\* significant at  $p < 0.10$  \*\* significant at  $p < 0.05$

**Table 4.4** Potential functions of repeated call sequences along with whether a positive ( $\uparrow$ ), negative ( $\downarrow$ ), or unknown ( $\downarrow\uparrow$ ), or no effect (-) relationship of repeated call sequences would be expected for each predictor, and the results of the model of the collected data.

<b>Predictor</b>	<b>Ind. Signature</b>	<b>Grp. Signature</b>	<b>Mother-Calf</b>	<b>Cohesion</b>	<b>Model</b>
Resting	$\downarrow$	$\downarrow$	$\downarrow$	$\downarrow$	$\downarrow$
Travelling	$\downarrow\uparrow$	$\downarrow\uparrow$	$\downarrow\uparrow$	$\downarrow\uparrow$	-
Foraging	$\downarrow\uparrow$	$\downarrow\uparrow$	$\downarrow\uparrow$	$\downarrow\uparrow$	-
Socializing	$\uparrow$	$\uparrow$	$\downarrow\uparrow$	$\uparrow$	$\uparrow$
Group Size	$\uparrow$	$\uparrow$	-	$\uparrow$	$\uparrow$
Calf Number	-	-	$\uparrow$	-	-
Other Delphinids	$\downarrow\uparrow$	$\downarrow\uparrow$	$\downarrow\uparrow$	$\downarrow\uparrow$	-
Sea State	-	-	$\uparrow$	$\uparrow$	-
Time of Day	$\downarrow\uparrow$	$\downarrow\uparrow$	$\downarrow\uparrow$	$\downarrow\uparrow$	-
Year (Site)	$\downarrow\uparrow$	$\downarrow\uparrow$	$\downarrow\uparrow$	$\downarrow\uparrow$	-



## **4.5 Discussion**

Repeated call sequences make up a substantial portion of the known long-finned pilot whale vocal production, with this study showing that these sequences are present in over fifty percent of recordings collected off Cape Breton, Nova Scotia. There has been no prior contextual description of these vocal repetitions in this species. Analysis of the social, behavioural, and environmental data collected alongside the recordings showed that group behavioural state, group size, and year are predictors of the presence of repeated call sequences, while time of day, sea state, calf presence, and other delphinid species present were not.

### **4.5.1 Possible Functions of Calls Repeated in Sequence**

In Table 4, I suggest expected trends in the rates of production of repeated call sequences with context for potential functions. The results are consistent with what would be expected if the calls within these sequences were to serve as identifiers, showing a strong link between the presence of repeated call sequences and group behaviour. Resting pilot whales are often found stationary at the surface in close proximity to the other members of their group where identification would likely not be necessary, but when whales are socializing it would likely be more important to know identity for the many interactions, and sometimes joining of groups, that occur during this behavioural state. There would also be an increased need for identification with an increased group size, especially on the individual level (Bradbury & Vehrencamp 2011; Tyack 2000). The framework of this study does not allow for the differentiation between individual and group identifiers, and as such I will discuss them together. Sayigh et al. (2013) suggested that calls within

repeated sequences in short-finned pilot whales off the Bahamas may represent individual identification akin to signature whistles found in other delphinid species, but their study itself was inconclusive on function. However, in contrast to the fission-fusion social organization of many dolphins that have signature whistles, long-finned pilot whales live in long-term social units consisting of approximately 11-12 individuals, which associate ephemerally, forming larger groups (Ottensmeyer & Whitehead 2003). It is thought that these units represent matriline, perhaps with neither male nor female offspring leaving their natal group (Connor et al. 1998), suggesting that these calls could serve a unit-specific identification function like those produced in other matrilineal species such as ‘resident’ killer whales (Ford 1989) or sperm whales (Gero, Whitehead et al. 2016). Initial exploration of long-finned pilot whale pulsed calls showed possible group-specific characteristics, but this has yet to be investigated further and to date there is currently no concrete evidence of group-specific call types (Nemiroff 2009). With a socially complex society where individuals form stable long-term groups, identifiers either on an individual or group level are likely to be desirable. The question remains as to whether the repeated calls found in sequences are identifiers for long-finned pilot whales, or whether other parts of their vocal repertoire serve this role. Further studies categorizing these calls within repetitions for specific repeatedly encountered groups are needed to determine whether these calls may function in identification and whether this would be at an individual or group level.

Our data did not support the hypothesis that repeated call sequences primarily function in maintaining contact between a calf and its mother, because the number of calves in a group had no effect on whether these vocal repetitions were present. Research

on infant pygmy marmosets (*Cebuella pygmaea*) showed a form of ‘infant babbling’ in which certain call types were repeated many times, while the mature animals in this species may make the same call only once or twice in sequence (Elowson et al. 1998). These calls were likely both important in the process of vocal development and essential for attracting the attention of the care giver. In cetaceans, beluga (*Delphinapterus leucas*) calves show the same babbling characteristics during vocal development (Vergara & Barrett-Lennard 2008). In long-finned pilot whales the calves stay with their mothers for many years, perhaps even both sexes remaining for life in this matrilineally-based species (Connor et al. 1998), making it interesting, therefore, that the number of calves in a group does not affect the presence or absence of these vocal repetitions. It is possible that mother-offspring contact calls are not part of these repeated call sequences, but take another form such as the low-frequency pulsed calls produced by beluga calves (Vergara & Barrett-Lennard 2008).

The calls within repeated sequences could also function as a form of contact call, a hypothesis which is also supported by the results of this study. The repeated sequences were made with higher frequency when whales are socializing, at moderate frequency when foraging and travelling, and at low frequencies when resting. This pattern supports their role in group coordination and cohesion, since socializing involves many interactions and pilot whale social gatherings, sometimes involving of hundreds of whales, can often create an apparently chaotic social environment. Resting whales are often grouped closely at the surface and would have little need of maintaining contact between whales already within visual distance who are not actively changing locations. Directionality found in the upper frequency component of killer whale repeated calls that

are biphonated – having both an upper and lower frequency component produced simultaneously – supports the theory that these calls may function in cohesion and coordination (Miller 2002). Similarly, pilot whales also use biphonated calls (Nemiroff 2009), which are found in many of the repeated call sequences they produce. Group size was also found to influence the presence of these repeated call sequences, which makes sense as more individuals means there would be a greater need for coordination, identification, and other potential functions that these calls may have (Bradbury & Vehrencamp 2011), as well as more individuals to produce them.

It is possible that the calls within repeated sequences could have multiple functions. Many contact calls have been found to also contain information on sender identity, which is especially important in ephemeral groups as individuals need to determine the identity of others as well as advertise their own (Kondo & Watanabe 2009). This is likely the case for bottlenose dolphins, who use signature whistles more frequently during socializing (Quick & Janik 2008) and separation (Janik & Slater 1998) than other contexts, suggesting that they also are important not only for identity, but also for cohesion and coordination within a group.

In addition to these inferences about function, the analysis of presence and absence revealed other attributes of repeated call sequences. Time of day was not indicated as a significant predictor, suggesting that pilot whales do not have a diel pattern associated with calls repeated in sequences, as has been found for specific types of calls for some other cetacean species (Risch et al. 2013). These patterns are often related to the behavioural context of the specific sounds, as is shown in studies of both echolocating odontocetes (Carlstrom 2005; Soldevilla et al. 2010) and calling blue whales

(*Balaenoptera musculus*) that indicated diel patterns in these vocalizations related to foraging behaviours (Wiggins et al. 2005). However, our research only covers daylight hours and a more comprehensive study including the nocturnal activities of this species will have to be conducted to determine if there are larger scale diel patterns present. Sea state and the presence of other delphinids were also not determined to be important predictors of repeated call sequences in pilot whales. Year nested within site was included in the final model, but the model without this term is also well supported, as it was not a strong predictor of sequence presence. The inclusion of year as a predictor may hint towards other important factors, perhaps environmental drivers, which were not included in the model.

#### **4.5.2 The Repetitive Nature of Calls in Sequence**

Regardless of the function of pilot whale calls repeated in sequences, the recurrent nature of the vocalizations themselves is striking. Repetition may be a measure to reduce signal masking due to background noise or the calling of others (Brumm & Slater 2006). In very vocal, group-dwelling species like pilot whales, this would seem a useful strategy to make sure one's voice is heard. It could also be that some of these sequences are the result of a form call-matching between two or more pilot whales, or perhaps even a type of rhythmic duetting, as is found in other species (Deecke et al. 2000; Miller et al. 2004; Schulz et al. 2008). There is evidence for call-matching in cetaceans being used as a means of contact between individuals that are not within sight of each other (Miller et al. 2004) leading to a potential purpose for the repeated call sequences found in pilot whales in maintaining group contact and cohesion. These sequences may also allow the whales

receiving the calls to estimate the approximate location of the calling whale as has been found in other species (Naguib & Haven-Wiley 2001; Miller 2002; Miller et al. 2004).

### **4.5.3 Future Directions and Summary**

The resolution of only using basic behavioural states and working with a groups instead of individual whales limits our knowledge of the specific contexts in which these repeated call sequences take place and the evaluation of alternate functions. The definition of ‘travelling’ in this study included both groups of whales travelling in a tight configuration with a pace barely above the vessel’s idle speed and groups moving fast (20 km/hr) and spread out over hundreds of meters. If repeated call sequences function in maintaining contact and cohesion within a group, it would be expected that there would be few of them heard in the former situation and more in the latter. Similarly, contact calls would seem to be most necessary when animals regroup after a dive while foraging, but perhaps not as important when everyone is down feeding. Future studies of the behavioural context of focal individuals relative to their production of repeated call sequences would give us a better understanding of the function of these vocal repetitions. In addition to this, localization of a calling individual’s respective position within a group could be used to further study the context of specific vocalization types in free-ranging pilot whales. In conclusion, repeated call sequences in long-finned pilot whales likely function as either identifiers, contact calls, or both. However, this study does not support mother-offspring communication as the main function of these vocal repetitions.

## 4.6 Acknowledgments

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## CHAPTER FIVE – CONCLUSION

### 5.1 Introduction

Highly social species often develop complex acoustic communication systems that help them deal with the challenges of everyday life such as maintaining contact with group members, mediating individual interactions, foraging, and navigation (Freeberg et al. 2012; Krams et al. 2012). Determining the functional role of these vocalizations can be an arduous task, especially when playback experiments are not feasible and the individuals producing the sounds are not directly observable. We can study the function of a particular portion of a species' repertoire by examining the social, behavioural and environmental context of the vocal production of those signals, as well as the nature of the signals themselves.

Prior to this study, there had been no focused investigation on the repeated call sequences produced by long-finned pilot whales (*Globicephala melas*). In fact, beyond descriptions of whistles (Taruski 1979; Weilgart & Whitehead 1990) and pulsed calls (Nemiroff & Whitehead 2009), very little is understood about the wide repertoire of vocalizations that this species produces. Briefly mentioned by Busnel and Dziedzic (1966), the sequences of rhythmically repeated calls produced by this species show similarities to those described in other cetaceans such as short-finned pilot whales (*Globicephala macrorhynchus*) (Sayigh et al. 2013), melon headed whales (*Peponocephala electra*) (Kaplan et al. 2014), and bottlenose dolphins (*Tursiops truncatus*) (Caldwell et al. 1990). Repeated calls can be made up of buzzed, pulsed, and tonal components. These vocal repetitions make up a significant portion of the calls produced by long-finned pilot whales, leading to many questions: Why is so much time



and effort spent making these repeated call sequences? Are they identifiers similar to the group-specific dialects of ‘resident’ killer whales or the individual signature whistles of bottlenose dolphins? How are they characterized and what sort of features do we see within them? Are they made in specific behavioural or environmental contexts? With fifteen years of fieldwork and ten years of recordings available from a population of this species found off Cape Breton Island, Nova Scotia, it was time to try and answer some of these questions and build upon our limited understanding of long-finned pilot whale vocalizations.

## **5.2 Summary of Key Findings**

### **5.2.1 The Role of Repeated Call Sequences in Pilot Whale Social Structure**

What is known of the social nature and long-term matrilineal units of the long-finned pilot whales has led to predictions that this species is likely to have a coupled socio-acoustic structure similar to those found in other matrilineal odontocetes (Rendell & Whitehead 2001). This may include unit specific dialects similar to killer whales (*Orcinus orca*) (Ford 1991), and perhaps even acoustic clans as found in both killer (Ford 1989; Ford 1991) and sperm whales (*Physeter macrocephalus*) (Rendell & Whitehead 2003). In contrast to this prediction, my analysis of call types produced in repeated sequences by long finned pilot whales in Chapter 2 indicated that different social units are sharing many of the call types, with no evidence of acoustic clustering that would denote higher levels of acoustic organization as is found in other matrilineal species of toothed whales. Only a few of the calls that were heard on more than one day over the duration of this study were produced in the presence of a single unit. These findings

suggest that the repeated call sequence of long-finned pilot whales do not function in a similar manner to those found in ‘resident’ killer or sperm whales. In these species I would expect to find clear socio-acoustic structures from analysis of the amount of data used in this study. However, it may be the case that there are regionally distinctive acoustic clans of pilot whales, of which I only have sampled one. It is also possible that there may be subtler acoustic differences between the repeated call sequences produced by social units that will take more time and recordings to determine, as was the case with those of the sperm whale units off the coast of Dominica (Gero, Whitehead et al. 2016).

Conversely, it has also been predicted that the vocal repetitions of the only congeneric species, the short-finned pilot whale, may be individual identifiers (Sayigh et al. 2013) akin to the signature whistles found in several dolphin species (Van Parijs & Corkeron 2001; Sayigh et al. 2007; de Figueiredo & Simão 2009). This idea was supported by the rhythmic sequences long-finned pilot whales produce these calls in, which are similar in nature to the observed sequences of bottlenose dolphin signature whistles (Janik et al. 2013). However, the sharing of conserved call types between social units of long-finned pilot whales found in this study suggests that the repeated calls are not individual identifiers that might function in a manner similar to the signature whistles found in some other small delphinids.

### **5.2.2 The Presence and Role of Modification in Repeated Call Sequences**

Many of the calls produced by cetaceans are highly stereotyped in nature (Ford 1991; Sayigh et al. 2007). When we see patterns of variation and modification in such stable vocalizations, it can bring in to question the function of such changes. In Chapter 3 I show that the calls in vocal repetitions of long-finned pilot whales are often modified

through two fundamental types of transitions: embellishment – where a discrete change is made to a specific part of the subsequent call – and morphing – where non-discrete small changes occur in the subsequent call. Transitions (either stable, embellished or morphed) between consecutive calls within a sequence were more often than expected followed by a transition of the same type. Finally, I also showed that sequences where succeeding calls were embellished tended to take on an alternating pattern of ornamentation and simplification (or vice versa) and these embellishments could be categorized into different types. It is possible that different types of modifications in these call sequences have diverse functions such as directional cues for conspecifics (Miller 2002) or that they may be indicative of the emotional state of the signaller (Ford 1989; Esch et al. 2009). However, it is also possible that this variation is simply the result of the fluid nature of this species' calls or even a product of pilot whale vocal innovation.

### **5.2.3 Behavioural Context and Its Link to the Production of Call Sequences**

The link between some vocalization types and the context in which they are produced has been demonstrated for several species of cetaceans. For example, there have been observed diel patterns in the calls of blue whales (*Balaenoptera musculus*) (Wiggins et al. 2005) and the production of echolocation by harbour porpoises (*Phocoena phocoena*) (Carlstrom 2005). Factors such as group size and behavioural context can also influence calling rates of some species (Quick & Janik 2008). When looking at the context of repeated call sequences of long-finned pilot whales (Chapter 4), I found that the production of these vocalizations was associated strongly with the behavioural state of the group recorded. Vocal repetitions were heard frequently when whales were

socializing, sometimes when they were foraging or travelling, and rarely when resting. Larger groups of whales were also more likely to result in the observed presence of repeated call sequences. These findings suggest that these sequences may play an important role in contact between individuals or groups, being used during behaviours such as socializing where a greater need for signals coordinating whales would be expected (Janik & Slater 1998; Tyack 2000). However, the context of these repeated call sequences did not give any suggestion as to whether they may also be used for identification.

Interestingly, the production of these repeated call sequences was not correlated with the number of calves in a group, rejecting the hypothesis that these vocalizations are mainly produced by young to facilitate contact between them and their caregivers during the first few years of life.

### **5.3 Painting a Picture of Pilot Whale Repeated Call Sequences**

#### **5.3.1 The Art of Elimination**

Though there is much still to be learned about the repeated call sequences produced by long-finned pilot whales, the analyses included in this thesis have begun to paint a picture of their nature, context and possible functions. Perhaps more importantly, I have provided evidence against some potential roles of repeated call sequences (Table 5.1). Firstly, these calls do not appear to be individual identifiers, as they are shared across multiple social units of pilot whales instead of being produced when only a specific whale (represented by only being heard when a particular long-term unit – that this individual is a member of – was present). Secondly, call types included in these vocal repetitions do

not seem to function in the same way as those found in killer and sperm whales, where there are distinctive group-specific repertoires and acoustic clans (Ford 1991; Rendell & Whitehead 2003; Gero, Whitehead et al. 2016). Thirdly, they do not appear to be exclusively involved in mother-calf contact, as there was no effect of the number of calves in a group on the production of these repeated call sequences. We can focus on the remaining possibilities as we go forward with studies of this species' vocal repertoire, knowing that the aforementioned functions are unlikely explanations for the repeated call sequences produced by long-finned pilot whales.

**Table 5.1** Potential functions of repeated call sequences produced by long-finned pilot whales along with whether a particular observation would be expected (✓), not expected (✗), or possibly expected (?) if these calls had one or more of these functions (↓ indicates decrease and ↑ indicates increase)

Observation	Unit Identifier	Individual Identifier	Mother-Calf	Cohesion	Thesis
Sequences ↓ when resting	✓	✓	✓	✓	✓
Sequences ↑ when socializing	✓	✓	?	✓	✓
Sequences ↑ with ↑ group size	✓	✓	✓	✓	✓
Sequences ↑ with ↑ calf number	✗	✗	✓	✗	✗
Social unit specific calls	✓	?	✗	?	✗
Individual specific calls	✗	✓	?	?	✗
Acoustic clans	?	✗	✗	?	✗

## **5.3.2 A Synthesis of Possible Functions for Repeated Call Sequences**

### **5.3.2.1 Contact Calls**

Given these results, some potential functions for the repeated call sequences of long-finned pilot whales seem improbable. However, there are other roles that these calls may play in the daily life of this species. My analyses suggest that one of the most likely roles of these vocal repetitions in pilot whales is that they are used in maintaining contact and cohesion between individuals (see Table 5.1). This species is not territorial and has no locational centres where they can be predictably found, such as the dens of wolves, instead being highly mobile and showing great variations in their patterns of movement like other species of cetaceans (Tyack 2000). In an aquatic environment where it is easy to lose sight of conspecifics, it is imperative that pilot whales have developed some sort of communication system that allows them to keep in contact with other individuals as they move about the oceans. This species is also highly social and has been shown to live in long-term stable units which are thought to be matrilineal (Amos, Schlotterer, et al. 1993; Amos, Bloch, et al. 1993), further emphasizing the need for contact calls to keep all members of a unit coordinated and together. I showed in Chapter 4 that vocal repetitions were associated with certain behaviours – such as socializing – where contact calls would be more necessary for group living cetaceans, especially in situations where more multiple units come together. This hypothesis is further supported by the increased presence of repeated call sequences with larger group size, which also would seem to warrant more vocal coordination. It has been observed that the contact calls of other species are often repeated in sequence (Miller et al. 2004; Janik et al. 2013), which makes this function a reasonable possibility for the vocal repetitions of long-finned pilot whales.

### **5.3.2.2 Identifiers**

Despite there being no evidence of individual-specific and unit-specific calls at this point in time (Chapter 2), there is still a chance that the call types found in the repeated sequences of pilot whales may play a role in identification. Social units of sperm whales off Dominica originally showed little inter-unit variation and were thought to be from a single clan (Antunes 2009; Gero, Whitehead et al. 2016), but analysis of the vocalizations of rarely-observed social units suggested clan-like partitions (Gero, Bøttcher et al. 2016), so it is possible that more detailed studies and a greater recording effort is needed to find acoustic differences between pilot whale social units. It could also be that the calls of this species are regionally specific or that there is another part of their vocal repertoire that is used as identifiers. The conclusion of this thesis is not that these calls have no identification purpose, but rather that their relationship with social structure is not what was expected in comparison to what is known of the complex socio-acoustic structure of other cetaceans, including killer and sperm whales, or the signature whistles of bottlenose dolphins and some other small delphinids.

### **5.3.3 The Voluble Nature of the Pilot Whale**

This study highlights the voluble nature of the long-finned pilot whale. Previously this species was thought to make the majority of their vocalizations on a graded continuum, including their whistles (Taruski 1979) and pulsed calls (Nemiroff & Whitehead 2009), without evidence for conserved call types. My finding of temporally conserved and shared call types and subtypes lead me to wonder whether the repertoire of long-finned pilot whales is as fluid as previously thought (Taruski 1979; Nemiroff 2009), or if it is



instead composed of both fluid and stereotyped components as suggested by my data.

One thing that has become apparent through these studies is the vast and diverse nature of pilot whale vocalizations. This includes not only the well-established clicks, whistles, and pulsed calls, but a sundry array of combinations involving all manner of these different kinds of calls. Biphonated vocalizations are sometime heard with one frequency component remaining the same, while the other changes between calls (see Appendix V for spectrogram example). Could this diversity and fluidity be the result of vocal innovation?

#### **5.4 Limitations and Suggested Future Studies**

There are a number of limitations to the studies that make up this thesis. Perhaps one of the most prominent is that we lack a detailed understanding of how long-finned pilot whale social structure functions. Are the long-term stable matrilineal units found in this species as strict as those observed in ‘resident’ killer whales? Is there short term dispersion from units or levels of social organization that present themselves differently to those we have found in other species of cetaceans? Do pilot whales behave differently in the inshore waters of Cape Breton than they do during other times of the year? A better understanding of social structure and other aspects of this species’ ecology will give a much stronger foundation to socio-acoustic studies.

Another concern is the limited geographical region in which these studies take place. It could be that whales using these waters are part of one acoustic clan, or maybe even a separate population, than those found in other regions of the north-western Atlantic. Analysis of the repeated call sequences of long-finned pilot whales over a broader spatial scale is needed to determine if vocalizations vary with region, and over

what spatial and temporal scales. It is not out of the question that cataloguing call types aside from those repeated in sequences may eventually reveal a socio-acoustic structure in this species.

For future research aimed at understanding the relationship between social context and vocal output in pilot whales, it would be invaluable to conduct suction cup digital acoustic recording tag studies of whales within known social units combined with focal follows, allowable through radio tracking of tagged whales, for observations of behaviour. Locational recordings in combination with aerial footage of long-finned pilot whale groups is another way in which we can learn more about the patterns of intra and inter unit call usage and its link with visually-observable behaviour.

Context allows us to learn more about the role that vocalizations play in the daily life of an individual. Though challenging, this can be feasible even when signallers are not directly observable. The nature, and variability in nature, of the calls themselves can also suggest, and rule out, certain functions. Sometimes it is through the art of elimination that we can narrow down the possible functions of specific vocalizations to learn more about the repertoire of a species.

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## APPENDIX I – Long-finned pilot whale social units and members

Key individuals and constant companions used for social unit comparisons in Chapter 2  
(from Augusto et al. submitted)

### Unit A

Size: 2 members (2 key)

Key: 1 246

### Unit B

Size: 6 members (5 key)

Key: 28 62 65 66 279

Constant: 345

### Unit C

Size: 3 members (3 key)

Key: 59 60 80

### Unit D

Size: 4 members (3 key)

Key: 82 280 876

Constant: 719

### Unit E

Size: 4 members (2 key)

Key: 123 243

Constant: 2 120

### Unit F

Size: 6 members (6 key)

Key: 139 140 142 248 254 701

### Unit G

Size: 2 members (2 key)

Key: 202 537

### Unit H

Size: 4 members (4 key)

Key: 205 496 531 808

### Unit I

Size: 3 members (2 key)

Key: 226 483

Constant: 679

### Unit J

Size: 4 members (4 key)

Key: 234 237 346 894

### Unit K

Size: 26 members (21 key)

Key: 260 261 262 302 311 312 314  
352 370 372 407 449 476 488 492 5  
07 511 599 697 871 923

Constant: 265 506 631 632 862

### Unit L

Size: 3 members (2 key)

Key: 265 506

Constant: 261

### Unit M

Size: 7 members (7 key)

Key: 270 466 473 513 543 569 617

### Unit N

Size: 4 members (3 key)

Key: 273 274 480

Constant: 261

### Unit O

Size: 8 members (5 key)

Key: 307 374 515 517 518

Constant: 508 570 637

## **Appendix 1, continued**

### **Unit P**

Size: 4 members (3 key)

Key: 363 482 887

Constant: 889

### **Unit Q**

Size: 10 members (9 key)

Key: 376 377 378 415 416 594 601

602 674

Constant: 375

### **Unit R**

Size: 2 members (2 key)

Key: 455 595

### **Unit S**

Size: 2 members (2 key)

Key: 489 490

### **Unit T**

Size: 2 members (2 key)

Key: 550 551

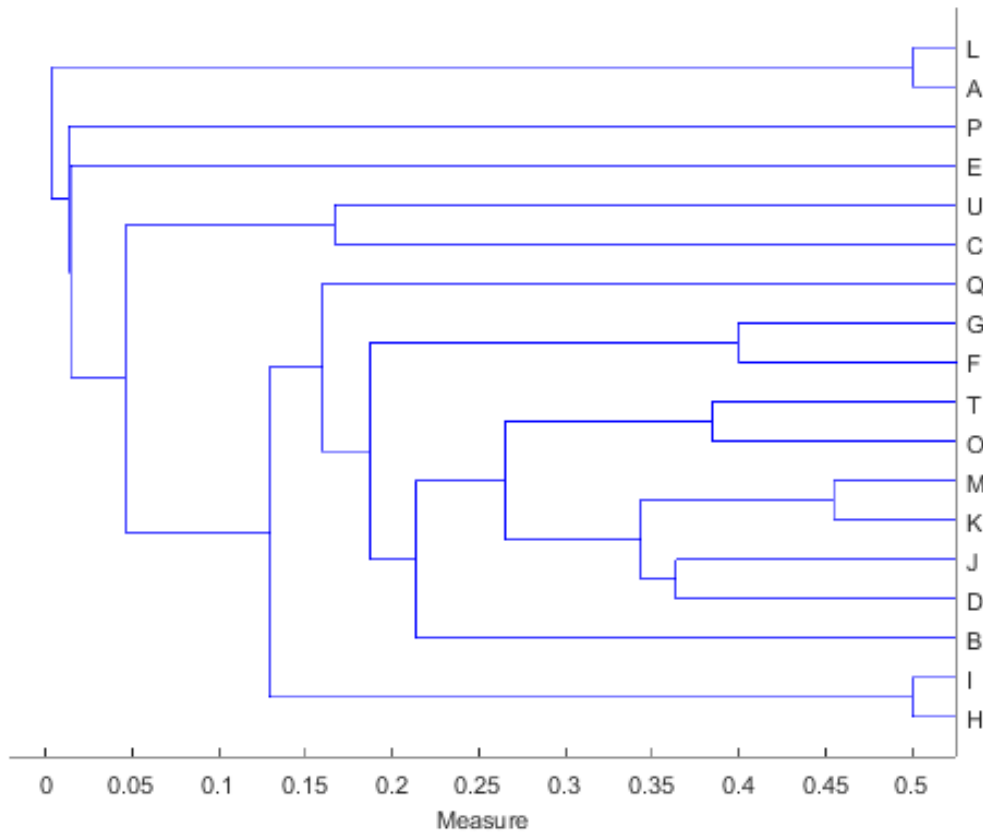
### **Unit U**

Size: 5 members (2 key)

Key: 632 862

Constant: 260 261 861

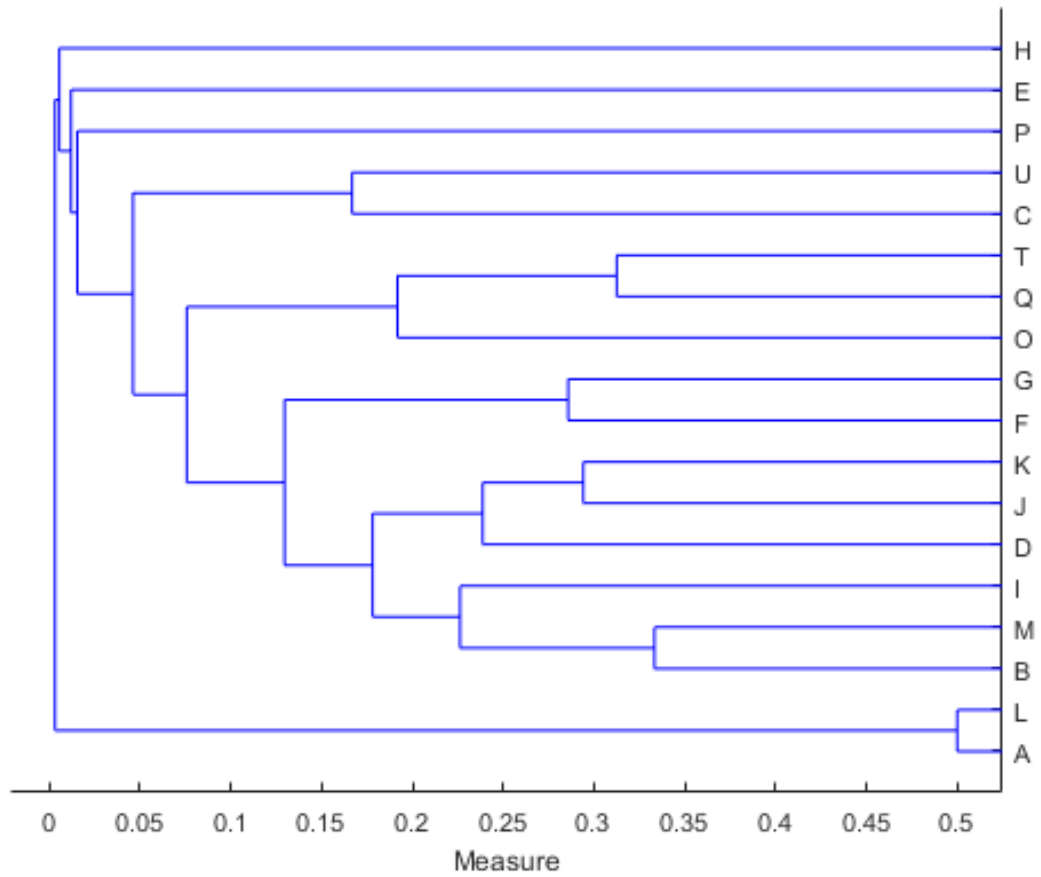
**APPENDIX II – Supplementary analyses for Chapter 2 including average linking cluster analysis and non-metric multidimensional scaling for both call types and call categories**



**Figure A2.1** Average linking cluster analysis of acoustic similarity between social units of long-finned pilot whales based on repeated sequence call type sharing with a phonetic correlation coefficient (CCC) = 0.8635

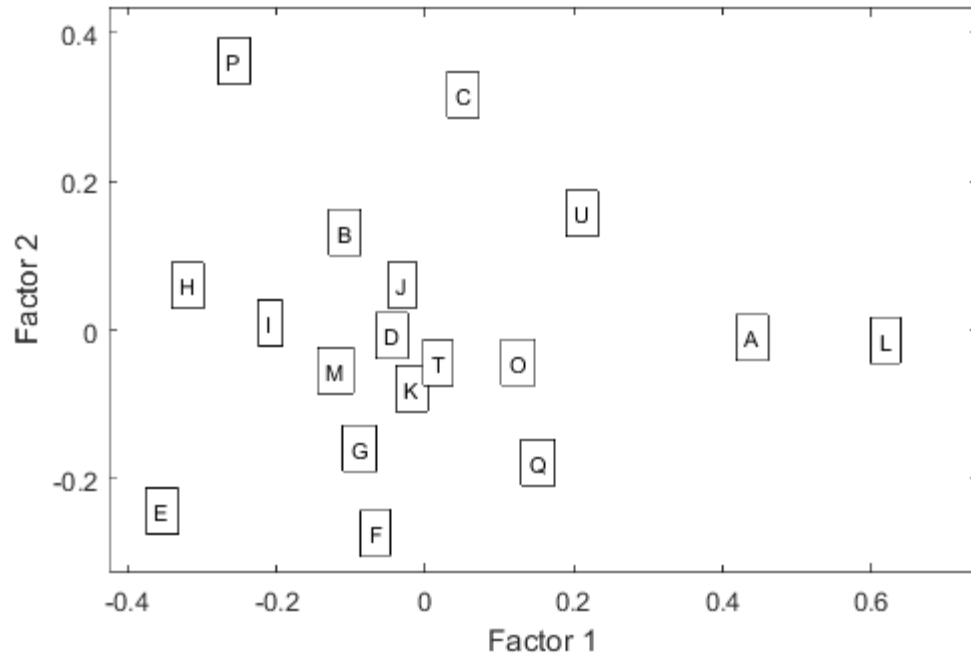


Appendix 2, continued



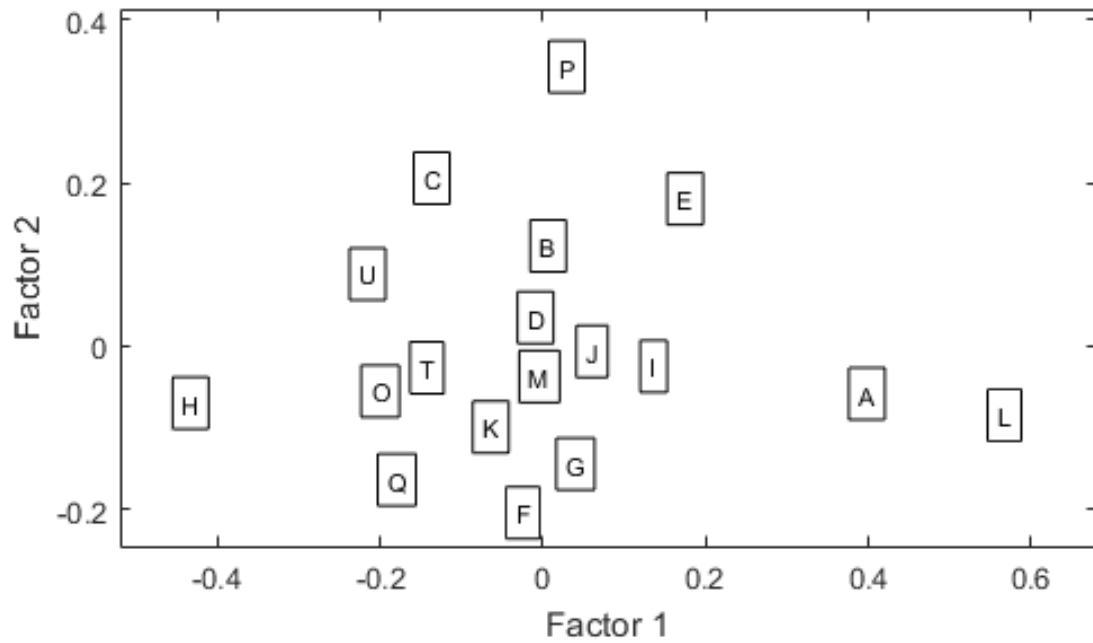
**Figure A2.2** Average linking cluster analysis of acoustic similarity between social units of long-finned pilot whales based on repeated sequence call category sharing with a phonetic correlation coefficient (CCC) = 0.8368

Appendix 2, continued



**Figure A2.3** Multidimensional scaling using non-metric stress criterion for the acoustic similarity between social units of long-finned pilot whales based on repeated sequence call type sharing (MDS Stress = 0.078554)

Appendix 2, continued

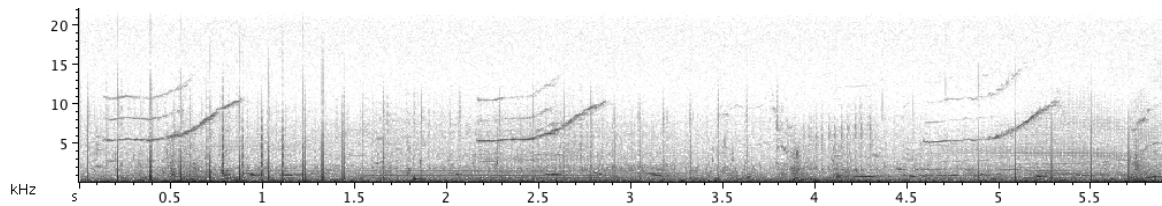


**Figure A2.4** Multidimensional scaling using non-metric stress criterion for the acoustic similarity between social units of long-finned pilot whales based on repeated sequence call category sharing (MDS Stress = 0.07579)

## APPENDIX III – Pilot whale repeated call sequence transition test instructions for volunteers

### STABLE:

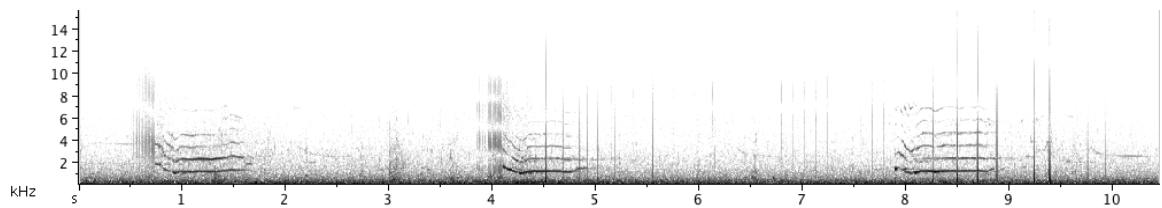
This is when the calls remain almost the same, with very little change if any.



The spectrogram above shows a call that is relatively stable. So the first transition would be STABLE and the second would be STABLE as well

### EMBELLISHED:

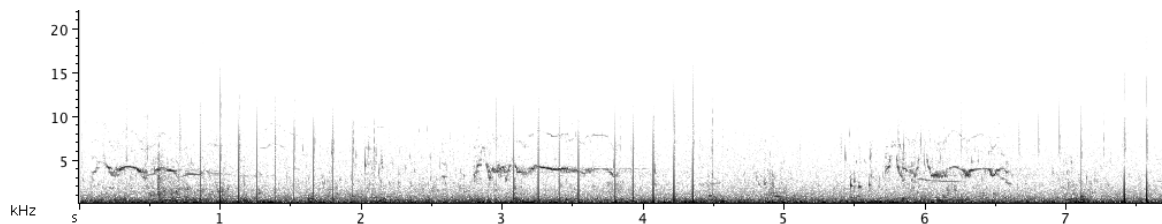
This is when the change that happens is discrete in nature, only happening to one or two parts of the call (E.g.: a buzz is added before the call, there is a gap inserted at a point in the middle of the call, one section of the call is wavy instead of straight, etc.) the rest of the call should remain conserved



In the call above you can see that there is a pulse before the first two calls, but not before the last. This is the case that the first transition is STABLE and the second is EMBELLISHED with the removal of the buzz.

### MORPHED:

Non discrete changes across most or all of the call



### Appendix 3, continued

Here a call is morphing, where the call is similar, but multiple things are changing in a non-discrete fashion over the duration of the call. This would be an example of MORPHED for the first transition and then MORPHED again for the second one.

#### EMBELLISHMENT TYPES

Embellishment Type	Definition of addition/subtraction
Biphonation	Addition of upper or lower frequency component resulting in biphonation and an increased complexity of the call
Buzz/Pulse	A buzz, brief pulsed component, or click
Change	An already existing section of call is modified, while the rest remains the same and the change does not fit into one of the afore mentioned categories
Gap	Call is segmented by a gap where the whale briefly stops emitting the call
Lengthening	One section of the call is significantly lengthened or shortened
Looping	Akin to what has been described in signature whistles, where the number of repetitive elements – “loops” – are varied within a call
Step	A jump up or down in the fundamental frequency of the call which visualized as a step-like contour on a spectrogram
Upsweep	An upwards sweep in frequency of a call
Wobble/Hump	Inclusion of new inflection points to create fluid wobble or hump in a section of the call
Unclassified Add/Sub	A new section is added to or subtracted from call that does not fit into any of the other add/sub categories mentioned

**Appendix 3, continued**

**PILOT WHALE REPEATED CALL SEQUENCE TRANSITIONS  
(EXAMPLE OF TEST)**

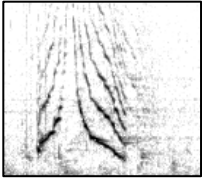
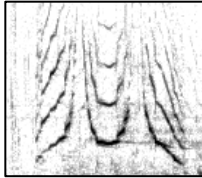
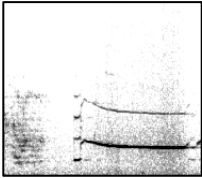
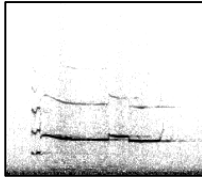
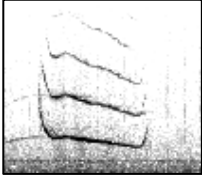

**S** - Stable: Very little change, remaining relatively constant

**E** - Embellished: A discrete change, the addition or removal of details to one part, while the rest of the call remains relatively unchanged the same

E.g.) Addition of a new part of call (pulse, whistle, gap), making part of the call wobbly while the rest is the same, noticeable upsweep to beginning or end, etc.

**M** - Morphed: a small change over multiple variables so that the majority of the call is changing, not discrete (frequency, duration, etc.)

***PLEASE USE THE SPECTROGRAMS TO MAKE YOUR DECISIONS***

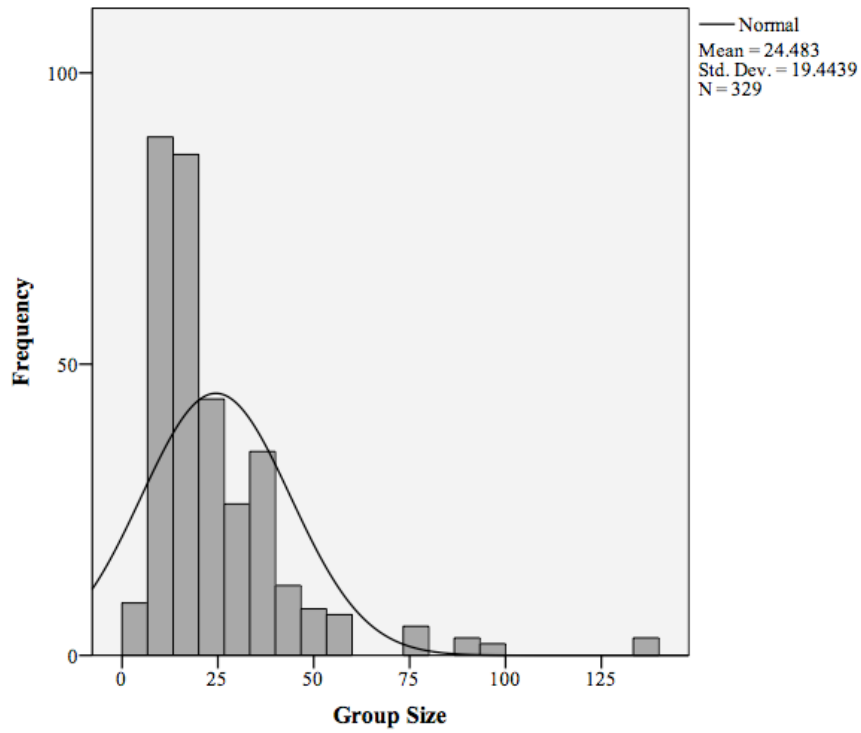
		Type of Transition (circle)	If Embellished... (type: gap, buzz, etc.)
1)			S E M _____
2)			S E M _____
3)			S E M _____

**APPENDIX IV – Summary of social, behavioural, and environmental predictors and response for all data explored (N=329) and histograms of group size**

**Table A4.1** Summary of social, behavioural, and environmental predictors and response for all data explored (N=329)

<b>Predictors</b>	<b>1998</b>	<b>1999</b>	<b>2000</b>	<b>2013</b>	<b>2014</b>	<b>All</b>
<b><i>Group Behaviour (%)</i></b>						
Foraging	16.7	36.4	7.4	29.1	7.5	21.6
Other	16.6	23.6	24.1	1.8	5.0	13.7
Resting	20.0	16.4	5.6	27.3	7.5	14.6
Socializing	6.7	3.6	9.3	25.5	20.0	12.5
Travelling	40.0	20.0	53.7	16.4	60.0	36.5
<b><i>Group Size</i></b>						
range	6-20	7.5-135	6.5-75	5-50	3-50	3-135
mean	15.4	32.1	30.0	18.1	18.1	24.5
median	16.0	25.5	25.0	15.0	14.0	
<b><i>Number of Calves Under Age 3</i></b>						
range	0-3	0-5	0-6	0-21	0-7	0-21
mean	0.9	2.2	2.6	5.4	2.4	2.7
median	1.0	2.0	3.0	4.0	2.0	
<b><i>Presence of Other Delphinids (%)</i></b>						
Yes	0.0	11.8	11.1	1.8	3.8	7.0
No	100.0	88.2	88.9	98.2	96.3	93.0
<b><i>Sea State (%)</i></b>						
0	20.0	5.5	3.7	0.0	0.0	4.3
1	3.3	7.3	16.7	40.0	27.5	18.8
2	40.0	61.8	51.9	36.4	42.5	49.2
3	0.0	14.5	18.5	14.5	17.5	14.6
4	33.3	10.0	9.3	7.3	10.0	11.6
5	3.3	0.9	0.0	1.8	2.5	1.5
<b><i>Time of Day (%)</i></b>						
Morning	33.3	35.5	24.1	30.9	31.3	31.6
Afternoon	40.0	20.9	33.3	36.4	30.0	29.5
Evening	26.7	43.6	42.6	30.9	28.7	36.2
Night	0.0	0.0	0.0	1.8	10.0	2.7
<b><i>Repeated Calls (%)</i></b>						
Yes	53.3	57.3	38.9	34.5	48.8	48.0
No	46.7	42.7	61.1	65.5	51.2	52.0

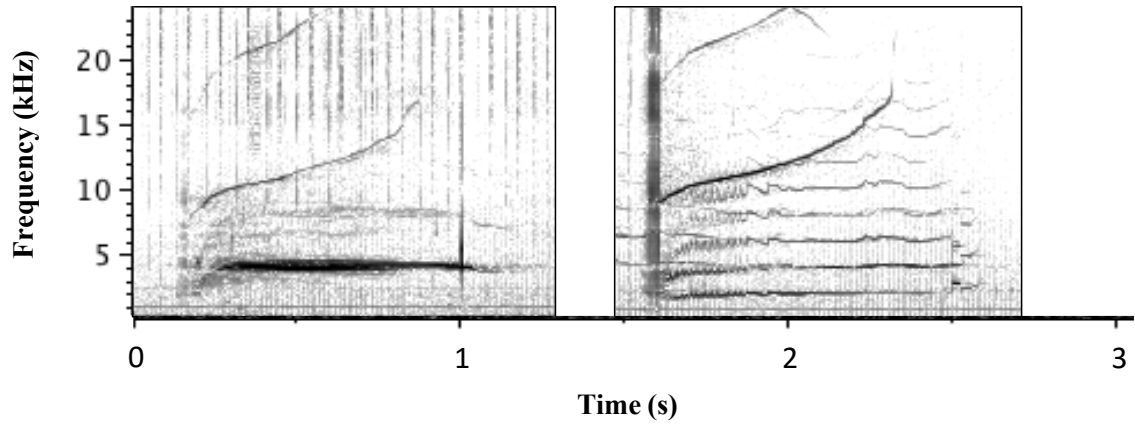
Appendix 5, continued



**Figure A4.2** Histogram of distribution of groups sizes of long-finned pilot whales encountered and recorded off Cape Breton, Nova Scotia



**APPENDIX V – Spectrograms showing biphonated calls where one frequency component is changed**



**Figure A5.1** Spectrogram example of a biphonated call produced by a long-finned pilot whale, where the lower frequency component is altered slightly