

**BELUGA WHALE, *Delphinapterus leucas*, VOCALIZATIONS
AND THEIR RELATION TO BEHAVIOUR
IN THE CHURCHILL RIVER, MANITOBA, CANADA**

by

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ABSTRACT

The investigation of a species' repertoire and the contexts in which different calls are used is central to understanding vocal communication among animals. Beluga whale, *Delphinapterus leucas*, calls were classified and described in association with behaviours, from recordings collected in the Churchill River, Manitoba, during the summers of 2006-2008. Calls were subjectively classified based on sound and visual analysis into whistles (64.2% of total calls; 22 call types), pulsed or noisy calls (25.9%; 15 call types), and combined calls (9.9%; seven types). A hierarchical cluster analysis, using six call measurements as variables, separated whistles into 12 groups and results were compared to subjective classification. Beluga calls associated with social interactions, travelling, feeding, and interactions with the boat were described. Call type percentages, relative proportions of different whistle contours (shapes), average frequency, and call duration varied with behaviour. Generally, higher percentages of whistles, more broadband pulsed and noisy calls, and shorter calls (<0.49s) were produced during behaviours associated with higher levels of activity and/or apparent arousal. Information on call types, call characteristics, and behavioural context of calls can be used for automated detection and classification methods and in future studies on call meaning and function.

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CHAPTER 1: GENERAL INTRODUCTION

1.1 Animal communication, vocalizations, and contextual use of calls

The study of animal communication is central to the study of animal behaviour and in understanding interactions between individuals and a species' social dynamics. Essentially, communication is the transfer of information from a signaler to a receiver (or receivers); therefore, determining what and how much information is conveyed in a signal is an important area of study. Possible information conveyed includes individual or group identity, emotional state or intent of signaler (what the signaler is going to do next), and important discoveries in the environment such as predators or food (Bradbury and Vehrencamp 1998).

Vocal communication is an important form of communication for many animals and central to understanding vocal communication between animals is the investigation of a species' repertoire and the contexts in which different calls are used. When little is known, descriptions of a species' call types and call characteristics are important as a basis for the study of contextual use and to investigate call meaning and function. Studies describing call types and characteristics are often done by a human observer classifying calls based on aural analysis (listening to calls) and visual inspection of a spectrogram (a visual representation of a call in frequency versus time) (Sjare and Smith 1986a; Seneviratne et al. 2009). To reduce bias and increase reproducibility, more objective methods have also been investigated including: 1) additional observers (Angiel

1997; Deecke et al. 1999), 2) objective classification (categorization based on call properties) (Nowicki and Nelson 1990; Karlsen et al. 2002; Leong et al. 2003), and 3) automated classification (Brown et al. 2006; Deecke and Janik 2006). Studies comparing subjective and objective classification have obtained varying results (Angiel 1997; Nowicki and Nelson 1990; Janik 1999; Karlsen et al. 2002).

After obtaining information on a species' call repertoire, many studies focus on contextual use, meaning, and function of calls important in understanding social interactions. Determining information conveyed by a call (call meaning) can be difficult and complicated, so the context in which calls are emitted is important. Some calls may convey very specific information to the listener while others are apparently more general (reviewed by Seyfarth and Cheney 2003). When a call is emitted in a narrow range and therefore predictable set of circumstances, it can provide very specific information. Predator specific alarm calls are good examples of this. Vervet monkeys, *Cercopithecus aethiops*, emit acoustically different alarm calls when a leopard, snake, or eagle is detected (Seyfarth et al. 1980). The distinction is important because each predator requires different avoidance responses. In contrast to calls that can convey specific information, acoustically similar calls emitted in a wider range of circumstances provide more general information. An example is the whoop call of spotted hyenas, *Crocuta crocuta*. Whoops are loud calls emitted in different contexts to display identity, solicit support of others, or convey information about location (East and Hofer 1991). Information on contextual use and reactions of listeners, usually investigated using

playback experiments, can provide great insight into what information is conveyed by a call and therefore its meaning and to determine if it functions referentially.

In many social animals, acoustic behaviour has been investigated in contexts including different behavioural states (e.g. Rendall 2003), mating and reproduction (e.g. Poole et al. 1988; Manno et al. 2007), in response to predators (e.g. Coss et al. 2007; Greig and Pruett-Jones 2009), and calls can be used for spatial coordination (e.g. Bionski 1991), maintaining contact between individuals or in group cohesion (e.g. Fischer et al. 2001; Ramos- Fernández 2005), and/or to convey emotional state of caller (e.g. Soltis et al. 2002; Rendall 2003). Calls used to maintain contact between individuals, in group cohesion, and in coordination of behaviours may be individually distinct or group specific (Ford 1991; Soltis et al. 2002; McComb et al. 2003; Sayigh et al. 2007; Fernández-Juricic et al. 2009).

Vocal repertoires and behavioural context of calls have been studied in a variety of animal groups, including birds (e.g. Armstrong 1992; Trainer and McDonald 1993; Gammon and Baker 2004; Nicholson et al. 2007; Baker 2009; Seneviratne et al. 2009), terrestrial mammals especially non-humans primates (e.g. Brady 1981; East and Hofer 1981; Rendall et al. 1999; Poole et al. 1988; Robbins 2000; Crockford and Boesch 2003; Leong et al. 2003; Mitchell et al. 2006; Spillmann et al. 2010), and marine mammals (e.g. Sjare and Smith 1986a; 1986b; Ford 1989; Weilgart and Whitehead 1990; Murray et al. 1998; van Parjis et al. 2000; Phillips and Sterling 2001; Karlsen et al. 2002; Díaz López and Shirai 2009; Filatova et al. 2009).

Sound communication in marine mammals has likely evolved as a form of communication over long distances in water, where visual cues are limited and sound transmission is effective (sound waves travel around five times faster in water than in air) with some cetacean sounds travelling tens or even hundreds of kilometres (Tyack and Clark 2000). Also, most whales are social and some migratory; therefore, sound communication especially over long ranges can be extremely important (Tyack and Clark 2000; Tyack and Miller 2002).

Documenting the context in which calls are produced and behaviours associated with call production can be very difficult in whales because the majority of behaviours are underwater and cannot be easily observed at the surface. Therefore, studies have focused on changes in call rates or call types emitted during different behaviours mostly observed at the surface (Sjare and Smith 1986b; Weilgart and Whitehead 1990; dos Santos et al. 2005; Hawkins and Gartside 2010). Call types described in odontocete (toothed whale) species include: 1) whistles, 2) pulsed tones and noisy calls, 3) echolocation clicks, and 4) combined calls. Whistles are tonal sounds that are often narrowband (small frequency range) and usually described by their frequency contour (change in the fundamental frequency over time). Whistles are widely used by odontocetes in communication between conspecifics and have been the focus of most acoustic studies (Ford 1989; Janik and Slater 1998; Bazúa-Durán and Au 2002; Riesch et al. 2006; Azevedo et al. 2010). Whistles have been extensively studied in bottlenose dolphins, *Tursiops truncatus*, where some are thought to be individually distinct and

therefore used to identify individuals, termed 'signature whistles' (Caldwell and Caldwell 1965; Sayigh et al. 2007).

Pulsed and noisy calls have been described in odontocetes and some other animal species but are less studied than whistles. Pulsed and noisy calls are often more broadband (larger frequency range) than whistles. Pulsed calls are made up of a series of pulsed tones and a common measurement is pulse repetition rate (PRR: pulses per second) determined by the harmonic interval, the frequency between harmonics (Watkins 1967). Calls that cannot be separated into harmonic intervals are referred to as noise or noisy calls (Sjare and Smith 1986a). Pulsed and noisy calls do have some communicative properties and may be used in agonistic interactions and longer range communication (Overstrom 1983; Lammers et al. 2003; Mitchell et al. 2006). The most well studied pulsed calls are in killer whales, *Orcinus orca*, where group specific dialects have been described in many geographical areas (Ford 1991; Strager 1995; Filatova et al. 2007).

Combined calls consist of two components: either a call containing both a whistle and noisy or pulsed component or two overlapping calls emitted by one individual. Combined calls have been less studied than both whistles and pulsed or noisy calls but the phenomenon of two calls being emitted simultaneously by one individual has been described in odontocetes such as belugas, *Delphinapterus leucas*, and killer whales, and some bird species (Ford 1989; Murray et al. 1998; Aubin et al. 2000; Karlsen et al. 2002; Filatova et al. 2009; Krakauer et al. 2009). Producing two calls

simultaneously requires two sound producing mechanisms which have been found in both odontocetes and birds (Suthers 1990; Cranford et al. 1996).

1.2 Acoustics studies on beluga whales

Of the whale species for which vocalizations have been studied, beluga whales (*Delphinapterus leucas*; suborder Odontoceti; family Monodontidae) are extremely vocal; they were referred to as “canaries of the sea” by sailors on whaling ships. Beluga whales are highly social and live in an aquatic environment where visual cues are limited and sound travels well. Therefore, studies on vocal communication are extremely important in understanding social structure and ecology of this species. Recordings of beluga calls were first noted by Schevill and Lawrence (1949) and calls were first described and analyzed by Fish and Mowbray (1962). Some beluga acoustic studies, especially early studies, were conducted on captive animals. The controlled settings of aquaria, where underwater behaviours are observable can provide important information on beluga acoustic behaviour but extrapolating to wild populations should be done with caution (Fish and Mowbray 1962; Morgan 1979; Recchia 1994; Vergara and Barrett-Lennard 2008). Beluga vocalizations have also been studied in wild populations in Bristol Bay, Alaska, United States of America (Angiel 1997), the White Sea, Russia (Belikov and Bel’kovich 2006; 2007; 2008), Svalbard, Norway (Karlsen et al. 2002), the St. Lawrence River, Quebec, Canada (Faucher 1988), and the Canadian High Arctic (Sjare and Smith 1986a; 1986b).

Beluga calls have been described as more of a continuum but have been separated into four main call types similar to those described in other odontocetes: 1) whistles, 2) pulsed tones and noisy calls, 3) echolocation clicks, and 4) combined calls (Sjare and Smith 1986a; Karlsen et al. 2002). Beluga calls have been studied in relation to behaviours such as resting, milling, joining a group, travelling, sexual behaviour, social interaction, approaching boats, and alarm response (Sjare and Smith 1986b; Faucher 1988; Karlsen et al. 2002; Belikov and Bel'kovich 2003). However, limited conclusions have been established on the relationships between specific sounds and behavioural contexts so meaning and function of beluga calls are still poorly understood.

1.3 Hudson Bay beluga whales

While acoustic studies have been carried out on beluga populations throughout their circumpolar distribution, they have never been done in Canada's Hudson Bay. Belugas aggregate in river mouths and estuaries in Hudson Bay during the mostly ice-free summer months, and over-winter in Hudson Strait and southwest Davis Strait; however, timing and routes of migration vary among stocks (Figure 1.1; Sergeant 1973; Richard 1993; Kingsley 2000; Richard 2005; Smith 2007; Lewis et al. 2009). Belugas also generally demonstrate high site fidelity to summering ranges often returning to the same rivers each summer (Caron and Smith 1990). Studies have been conducted on Hudson Bay belugas on biology, abundance, distribution, movements, genetics, and



Figure 1.1: Map of eastern Canada.

feeding (Sergeant 1973; Watts and Draper 1986; Idle 1989; de March and Postma 2003; Richard 2005; Lewis et al. 2009; Kelley et al. 2010).

Beluga social structure studies are rare because sex and individuals are difficult to identify in the wild. However, belugas have been observed travelling as individuals or in large groups up to hundreds of animals with average group size around three or four (Cosens and Dueck 1991; Kingsley 2000). Studies have also shown a sexual and/or age segregation of belugas within summer ranges (Smith et al. 1994; Karlsen et al. 2002; Loseto et al. 2006). Smith et al. (1994) found some separation between adult males and females and some evidence of matrilineal groups consisting of nursing females and older female offspring. Karlsen et al. (2002) found only large white belugas that were most likely males in Svalbard, Norway. Loseto et al. (2006) found belugas in the Beaufort Sea segregated based on sex, length (somewhat indicative of age), and reproductive status; females with calves and smaller males segregated from large males and this habitat segregation reflected feeding habits, risk of predation, and reproduction.

Mating in belugas occurs offshore in late winter and during early spring migration (Brodie 1971; Heide-Jørgensen and Tielmann 1994), and females give birth the following year between March and September (Brodie 1971; Sergeant 1973; Heide-Jørgensen and Tielmann 1994). Calving therefore sometimes occurs before belugas arrive in river estuaries or throughout the summer while in estuaries (Brodie 1971; Sergeant 1973; Caron and Smith 1990; Smith et al. 1994).

Based on genetic data three separate beluga stocks have been identified in Hudson Bay: 1) western Hudson Bay where the Churchill River study site for this project

was located, 2) eastern Hudson Bay, and 3) James Bay (Figure 1.2; de March and Postma 2003). The largest aggregations of western Hudson Bay belugas are in the Seal, Nelson, and Churchill Rivers, Manitoba, but their range extends north of these rivers along the Nunavut coast and south to the Ontario border (Figure 1.2; Sergeant 1973; Richard 1993; Richard 2005).

The western Hudson Bay population is estimated at 57,300, making it one of the largest in the world (Richard 2005). In 2004, western Hudson Bay belugas were designated as a species of “special concern” by the Committee on the Status of Endangered Wildlife in Canada (COSEWIC 2004). In the Churchill River, belugas aggregate in the river and estuary during the ice free season from late June until early September with peak numbers from mid-July to mid-August (Hansen et al. 1988; Idle 1989). Different age classes (adults, juveniles, and calves) move in and out of the river generally with the tides but can be observed in the river at any time (Idle 1989).

1.4 Objectives

The relatively large amount of general knowledge about Hudson Bay beluga ecology makes it an ideal population on which to focus acoustic research because it provides a basis for interpretation of call types and call characteristics. The objectives of this study are to: 1) classify Churchill River beluga whale calls based on aural and visual analysis and call characteristics; and 2) describe and compare call types and call characteristics emitted during different beluga behaviours. This is the first description of



Figure 1.2: Map of study area: community of Churchill, Churchill River, Churchill River Estuary, and Hudson Bay.

beluga whale call types, call characteristics, and calls associated with behaviours in Hudson Bay belugas and provides important information needed for future studies on contextual use of calls and call meaning and function. Chapter 2 presents the classification of beluga whale calls from the Churchill River during the summers of 2006-2008 based on sound, call contour, and call characteristics and also the description of call characteristics within call types. Subjective and objective methods were both used and results compared. Chapter 3 presents descriptions and comparisons of call types, whistle contours, and call characteristics in different behavioural states (social interactions, travelling, feeding, and interactions with the boat) of Churchill River beluga whales during the summer of 2007. Chapter 4 summarizes the project including the major findings and conclusions of chapters 2 and 3 and also presents suggestions for future research.

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**CHAPTER 2: Classification of beluga whale, *Delphinapterus leucas*, vocalizations
from the Churchill River, Manitoba, Canada**

2.1 ABSTRACT

Classification of animal vocalizations is often done by a human observer using aural analysis and visual inspection of a spectrogram but more objective methods such as cluster analysis have been utilized to reduce bias and increase reproducibility. Beluga whale, *Delphinapterus leucas*, calls were described from recordings collected in the summers of 2006-2008, in the Churchill River, Manitoba. Calls were classified based on aural and visual analysis, and measured call characteristics. Beluga whale calls (n=706) were separated into 453 whistles (64.2% of total calls), 183 pulsed/noisy calls (25.9%), and 70 combined calls (9.9%). Subjective classification further divided whistles into six main contour types: 1) flat, 2) ascending, 3) descending, 4) hump, 5) dip, and 6) wavy with three to five call types per contour (22 types). Pulsed and noisy calls were divided into 15 types including buzzes, creaks, clicks, clinks, croaks, honks, screeches, squeals, screams, and barks. Combined calls were divided into seven types including whistles with noisy components, honks and creaks with higher whistles, and screeches with lower whistles. Measured parameters varied within each call type but less variation existed in pulsed and noisy call types and some combined call types than in whistles. A more objective hierarchical clustering method was applied to 200 randomly chosen whistles with six call characteristics used as variables; twelve groups were identified

(compared to 22 whistle types identified in the subjective classification). Call characteristics varied less in cluster analysis groups than in subjective whistle types and classification results were similar to the subjective classification of whistle contours. This study provided the first description of beluga calls in Hudson Bay required for further research investigating context-specific calls and call function. Using two methods provides more robust interpretations and an assessment of appropriate methods for future studies.

2.2 INTRODUCTION

Classification of animal vocalizations is often done by a human observer based on aural analysis (listening to the call) and visual inspection of a spectrogram (a visual representation of a call in frequency versus time) (Sjare and Smith 1986a; Armstrong 1992; de Figueiredo and Simão 2009; Seneviratne et al. 2009). This method introduces observer bias and therefore results are difficult to reproduce. Some studies have tried to address this problem using different methods: 1) additional observers (Angiel 1997; Deecke et al. 1999), 2) objective classification systems (categorization based on call properties) such as cluster analysis, multidimensional scaling, and discriminant function analysis (Nowicki and Nelson 1990; Karlsen et al. 2002; Leong et al. 2003; Rendell and Whitehead 2003; Soltis et al. 2005), and 3) automated classification systems such as dynamic time warping that aligns call contours (shapes) of different durations and

analysis software capable of using a neural network (Deecke et al. 1999; Brown et al. 2006; Deecke and Janik 2006).

Call types described in classification of some odontocete (toothed whales) include: 1) whistles, 2) pulsed tones and noisy calls, 3) echolocation clicks, and 4) combined calls (Sjare & Smith 1986a; Ford 1989; van Parijs et al. 2000; Karlsen et al. 2002; Boisseau 2005). Whistles are tonal sounds that are often narrowband (small frequency range) and usually described by frequency contour (change in the fundamental frequency over time or call shape). Whistles are widely used by odontocetes in communication between conspecifics (Ford 1989; Janik and Slater 1998; Riesch et al. 2006). Stereotyped whistles (whistles with little variation in call parameters) and variable whistle types have been described in killer whales, *Orcinus orca* (Thomsen et al. 2001, Riesch et al. 2008), and many other dolphin species (Sayigh et al. 2007; de Figueiredo and Simão 2009; Hickey et al. 2009). Whistles have been extensively studied in bottlenose dolphins, *Tursiops truncatus*, where some are thought to be individually distinct and therefore used to identify individuals, termed 'signature whistles' (Caldwell and Caldwell 1965; Sayigh et al. 2007). Signature whistles have also been proposed in the Costero, *Sotalia guianensis*, and narwhal, *Monodon monoceros*, (Shapiro 2006; de Figueiredo and Simão 2009).

Pulsed and noisy calls are often more broadband (larger frequency range) than whistles. Pulsed calls are made up of a series of pulsed tones and a common measurement is pulse repetition rate (PRR: pulses per second) determined by the harmonic interval, frequency between harmonics (Watkins 1967). Calls that cannot be

separated into harmonic intervals, where PRR cannot be measured, are referred to as noise or noisy calls (Sjare and Smith 1986a). Pulsed and noisy calls have been less studied in most species but the most well studied are the discrete stereotyped pulsed calls of killer whales in which group specific dialects have been described in many geographical areas (Ford 1991; Strager 1995; Filatova et al. 2007).

Combined calls consist of two components: either a call containing both a whistle and noisy or pulsed component or two overlapping calls emitted by one individual. Combined calls have been less studied than whistles and pulsed or noisy calls but the phenomenon of two calls being emitted by one individual, requiring two sound producing mechanisms (Suthers 1990; Cranford et al. 1996), has been described in odontocete species such as belugas, *Delphinaterus leucas*, and killer whales, and some bird species (Ford 1989; Murray et al. 1998; Aubin et al. 2000; Karlsen et al. 2002, Filatova et al. 2009; Krakauer et al. 2009).

Beluga whales are a small odontocete species that are very social and extremely vocal and were referred to as “canaries of the sea” by sailors on whaling ships. Recordings of beluga calls were first noted by Schevill and Lawrence (1949) and calls were first described and analyzed by Fish and Mowbray (1962). Beluga vocalizations have been studied in captive animals held in aquaria (Recchia 1994; Vergara and Barrett-Lennard 2008) and in wild populations in Bristol Bay, Alaska (Angiel 1997), the White Sea, Russia (Belikov and Bel’kovich 2006; 2007; 2008), Svalbard, Norway (Karlsen et al. 2002), the St. Lawrence River, Quebec (Faucher 1988), and the Canadian High Arctic (Sjare and Smith 1986a; 1986b). Beluga calls have been described as more of a

continuum but similar to other odontocetes have been separated into four main types: 1) whistles, 2) pulsed tones and noisy calls, 3) echolocation clicks, and 4) combined calls.

Beluga whales have a circumpolar distribution in Arctic and sub-Arctic waters. In Hudson Bay, Canada, groups of belugas aggregate in the summer in river mouths and estuaries, with telemetry results indicating that most Hudson Bay beluga winter in Hudson Strait and southwest Davis Strait (Richard et al. 1990; Smith 2007; Lewis et al. 2009). Three stocks have been identified in Hudson Bay: 1) western Hudson Bay where the Churchill River study site for this study was located, 2) eastern Hudson Bay, and 3) James Bay (Figure 2.1; de March and Postma 2003).

This study provides the first description of beluga calls in Hudson Bay. The purpose was to classify calls based on aural and visual analysis, and measured call characteristics from recordings collected in the summers of 2006-2008 in the Churchill River, Manitoba. Before studies on context-specific calls and call function can be conducted on a species in a particular geographic area, descriptions of call types and call characteristics need to be documented. In this study, calls were subjectively classified and then a more objective hierarchical clustering method was applied to a random subset of whistles to compare results. Using two methods not only provides for more robust interpretations but also the opportunity to assess independent approaches to determine which methods to use in future studies. Information on call types and call characteristics also provide baseline data for future studies on beluga calls including contextual use and call function.

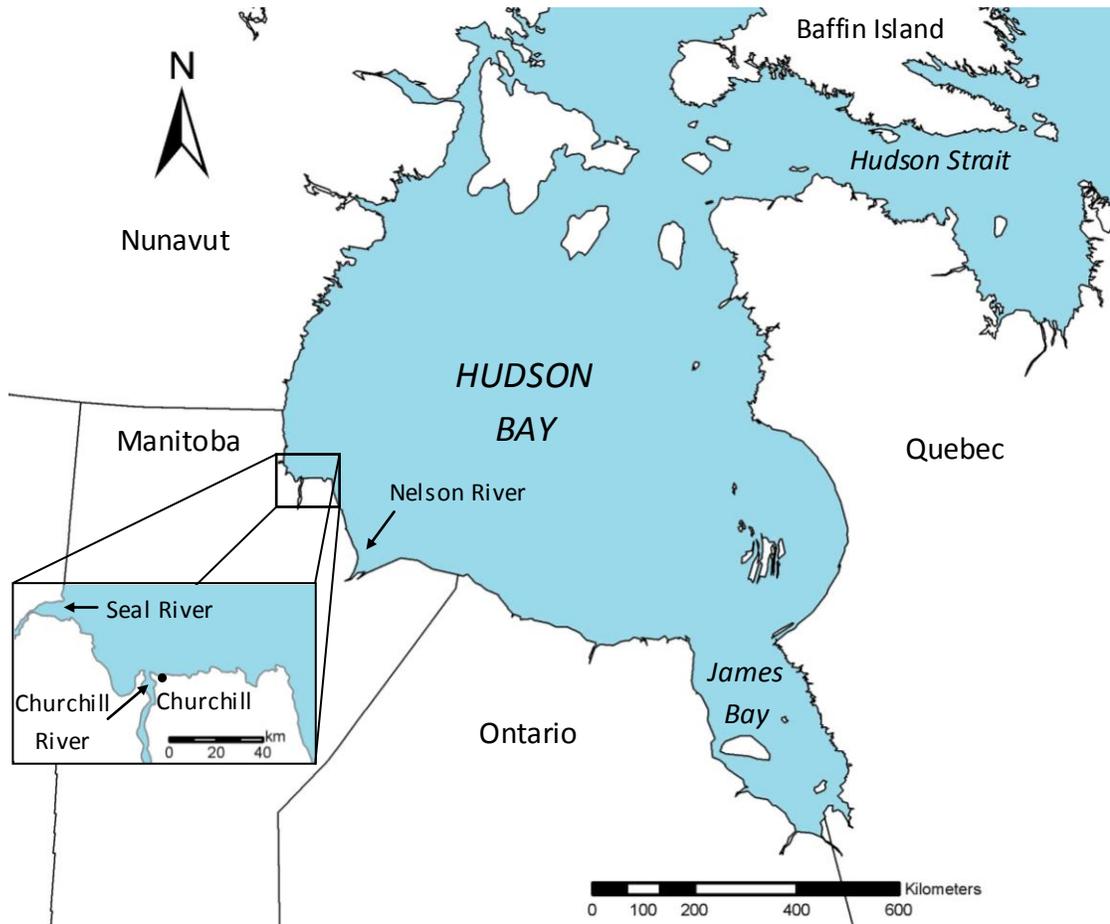


Figure 2.1: Map of study area: community of Churchill, Churchill River, Churchill River Estuary, and Hudson Bay.

2.3 METHODS

2.3.1 Study area

Data were collected in the Churchill River and the Churchill River Estuary which opens into Hudson Bay (58° 45'N; 94° 4'W) near the town of Churchill, Manitoba (Figure 2.1) during July and August 2006-2008 (11 July - 18 August, 2006, 9-24 July, 2007, and 7-19 August, 2008). Belugas aggregate in this area during the ice free season from late June until early September, with peak numbers from mid-July to mid-August (Hansen et al. 1988; Idle 1989). Belugas in the Churchill River are part of the western Hudson Bay stock, estimated at 57,300 whales, one of the largest beluga populations in the world (Richard 2005). Different age classes (adults, juveniles, and calves) move in and out of the river generally with the tides but can be observed at any time (Idle 1989; personal observation).

2.3.2 Data collection

Sound recordings were collected using a portable hydrophone system from a small boat, usually a 4.2 meter Zodiac and sometimes a 4.8 meter aluminum motor boat. The engine was turned off during recording sessions to reduce background noise. Belugas were generally seen in small groups (5-10) but also in larger groups (up to ~50). Recordings were collected when whales were within 50m, but sometimes closer than 20m when whales approached the boat. A High Tech, Inc. hydrophone (Gulfport,

Mississippi, USA, model HTI-96-MIN; sensitivity: -165 dB, flat frequency response from 5 Hz to 30 KHz \pm 1.0 dB) and a Marantz PMD 660 digital recorder (16 Hz to 22 kHz -0.5 dB, 44.1 KHz sampling rate) were used to collect recordings with the hydrophone lowered to a depth of 5-10 meters. Forty-four hours total were recorded: 20.5 hours in 2006, 17 hours in 2007, and 6.5 hours in 2008. Additional information including number of belugas and the presence of juveniles (determined by the presence of gray individuals) and calves (also determined by their gray colour and small size) were noted during recordings. Beluga behaviours were also noted during recordings for behavioural context analysis (Chapter 3).

2.3.3 Analysis

Because of recording equipment limitations, detailed analysis of echolocation was not possible. The recording system was limited to frequencies below 22 kHz but beluga broadband clicks can have a frequency spectrum of 100 Hz to 120 kHz and peak frequencies at 40 kHz and above (Gurevich and Evans 1976; Au et al. 1985). All calls (excluding echolocation clicks) were extracted from 10 minute recording segments; twenty-four 10 minute recordings equalling four hours were used. In 2006, one 10 minute recording was used from each of five days in July and four days in August. In 2007 and 2008, one 10 minute recording was used from each day recordings were collected (eight days in July 2007 and seven days in August 2008). Selection of segments spread throughout the study period provided a representation of the beluga call

repertoire throughout the summer and during different behaviour states (Chapter 3).

This was also an attempt to reduce the chance of pseudo-replication. Satellite telemetry data show belugas in the Canadian High Arctic generally move between rivers or bays throughout the summer (Richard et al. 2001). Also, some belugas tagged in the Nelson River, Manitoba (just south of the Churchill River) moved north and others south during the summer towards different rivers in western and southern Hudson Bay (Smith 2007).

First, by simultaneously listening and visually scrolling through spectrograms in Adobe® Audition® 2.0 (FFT size of 256) all calls except echolocation clicks were isolated from the 10 minute recording segments. Each call was then graded qualitatively on a scale of 1-5 based on sound quality (the amount of background noise or overlapping calls) (modified from Faucher 1988; Deecke 2003): 1 = very high signal-to-noise-ratio (call was clear: no background noise or overlapping calls), 2 = high signal-to-noise-ratio (call was relatively clear: minor background noise or slightly overlapping calls), 3 = moderate signal-to-noise-ratio (call was less clear: relatively faint with some background noise or overlap), 4 = low signal-to-noise-ratio (call was not clear: relatively faint with background noise or overlapping calls), and 5 = very low signal-to-noise-ratio (call was not clear: either faint and/or too much background noise or overlap to measure call properties). Lower quality recordings (graded 4 and 5) were not used in further analysis.

Beluga calls (n=706) were extracted and separated into three main categories based on previous descriptions: 1) whistles, 2) pulsed or noisy calls, and 3) combined calls. For subjective classification, calls were further classified based aural and visual

analysis (including call contour), and when possible PRR similar to Sjare & Smith (1986a) and Karlsen et al. (2002).

Call properties were obtained visually or using Raven 1.3 (Cornell Lab of Ornithology, Bioacoustics Research Group, Cornell University, Ithaca, New York) functions viewed in a Hann window with an FFT size of 512 and a 50% overlap. Measurements obtained from the fundamental frequency of each whistle were based on Sjare and Smith (1986a) and Baron et al. (2008) and included: 1) starting frequency, 2) ending frequency, 3) minimum frequency, 4) maximum frequency, 5) frequency bandwidth (range), 6) duration, 7) number of inflection points (change in slope from positive to negative or negative to positive), 8) number of steps (zero slope between two positive or two negative slopes), and 9) if the call was found in sequence (yes = call repeated at least twice/no = single call). Measurements for each pulsed and noisy call were based on Sjare and Smith (1986a) and included: 1) minimum frequency, 2) maximum frequency, 3) frequency bandwidth, 4) duration, 5) PRR (where applicable), and 6) in sequence (yes/no). If PRR could not be determined the call was considered a noisy call (Sjare and Smith 1986a). For combined calls, the measurements above were taken for each component and duration of the entire call (either combined duration of the two components or the longer duration of the two calls).

2.3.4 Cluster analysis

For a more objective classification, a random subset of 200 whistles was placed into statistical categories using measurement variables entered into a cluster analysis (SYN-TAX 2000; Department of Plant Taxonomy and Ecology, L. Eötvös University, Budapest, Hungary). Different variable/measurement combinations were run using different hierarchical clustering methods (data not shown) but the method in which measurements were less variable and that best represented whistle contours described was the Unweighted Pair Group Method with Arithmetic Mean (UPGMA) or average linkage with a Chord distance matrix (data shown). Cluster variables included: starting frequency, ending frequency, difference between starting and ending frequency to represent overall contour trend of the whistle (zero = flat, negative = increasing, positive = decreasing), frequency bandwidth, number of inflection points, and number of steps. Note that pulsed, noisy, and combined calls were not included in this cluster analysis because most parameters could not be measured.

2.4 RESULTS

2.4.1 Subjective classification

2.4.1.1 Whistles

Whistles constituted the majority of calls analyzed (64.2%) and were classified based on contour and frequency modulation according to methods described by Sjare

and Smith (1986a) and Karlsen et al. (2002). Six main contour types were identified: 1) flat, 2) ascending, 3) descending, 4) hump, 5) dip, and 6) wavy. Each contour type had three to five subtypes for a total of 22 whistle call types; call parameters were measured (Table 2.1). See Figure 2.2 for representative spectrograms of each whistle call type.

Contour type flat – W1a, W1b, and W1c

Flat whistles were the second most common contour type (15.9% of all calls analyzed, 24.7% of whistles) and separated into three call types (Table 2.1). Call type W1a and W1b whistles were both simple with unmodulated frequency (Figure 2.2) and had similar frequency measurements (Table 2.1). Unlike W1a whistles, W1b whistles were segmented and had a longer mean duration. The majority of W1a and W1b whistles were within 1.0-5.0 kHz (91.5% and 81.2%, respectively) but ranged up to 8.2 kHz. Call type W1c whistles were generally flat but had some frequency modulation in at least a portion of the call (Figure 2.2) with 0-17 inflection points (mean = 3.2 ± 2.8). W1c was the second most common whistle call type (7.9% of total calls, 12.4% of whistles) and the majority were within 1.0-5.0 kHz (85.7%) but ranged up to 12.6 kHz.

Contour type ascending – W2a, W2b, and W2c

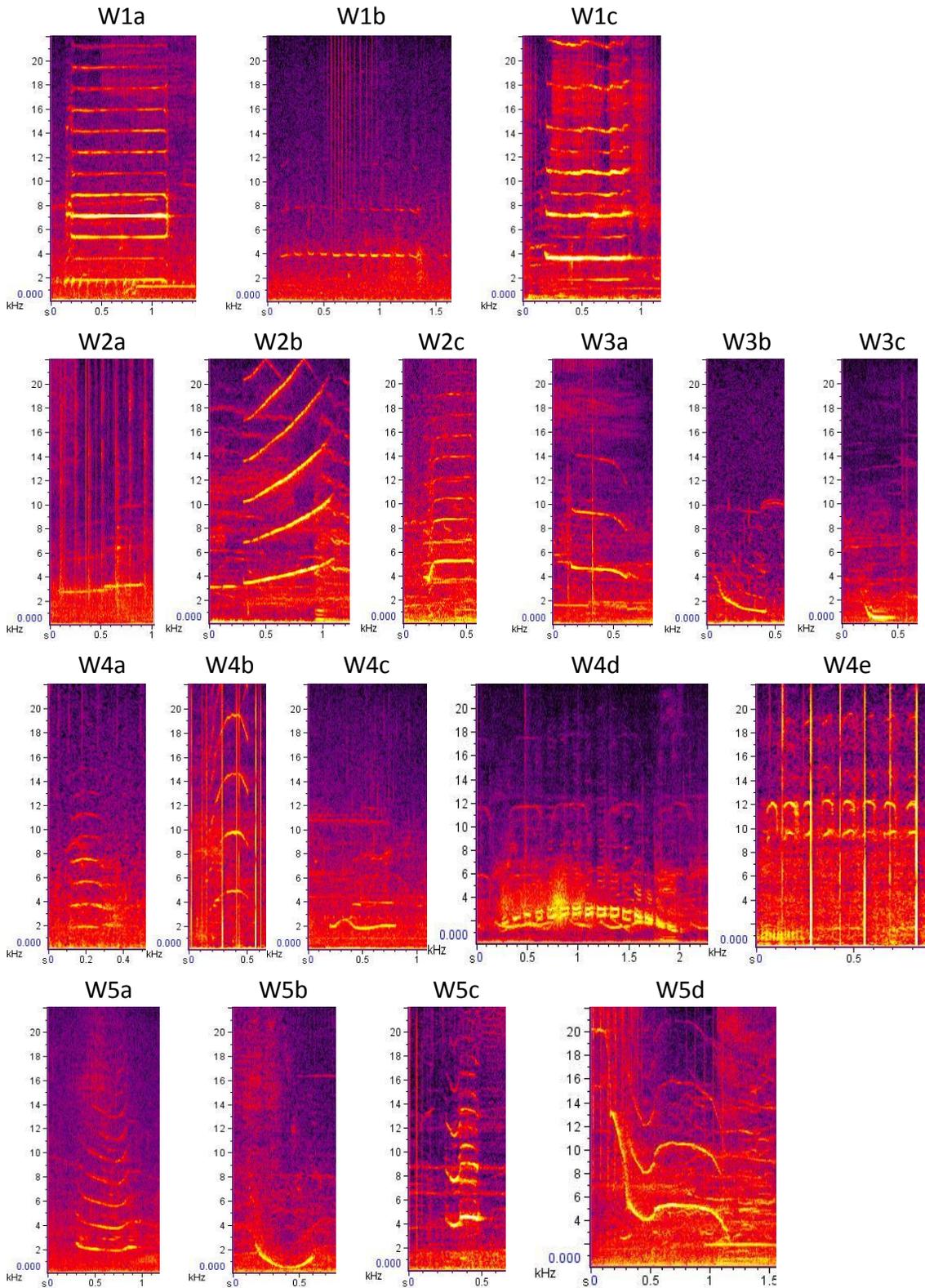
Ascending whistles were the most common contour type (20.2% of all calls analyzed, 31.6% of whistles) and separated into three call types (Table 2.1). Like flat whistles, these were relatively simple, although some contained complex features such as inflection points and steps. Call types W2a and W2b whistles were similar in that both

Table 2.1: Descriptive statistics of whistles (mean \pm standard deviation) emitted by belugas in the Churchill River, Manitoba.

Call Type (#)	Call contour	n	% of total calls	Frequency (kHz)				Band-width	Duration (s)	Inflection Points	Steps	% found in sequence
				Start	End	Minimum	Maximum					
W1a	flat	40	5.7	2.5 \pm 2.0	2.5 \pm 2.0	2.3 \pm 2.0	2.7 \pm 2.0	N/A	0.78 \pm 0.47	0	0	12.5
W1b	flat segmented	16	2.3	2.6 \pm 1.6	2.8 \pm 1.7	2.4 \pm 1.6	3.1 \pm 1.7	N/A	1.15 \pm 0.60	0	0	6.3
W1c	mostly flat	56	7.9	3.1 \pm 2.3	3.3 \pm 2.2	3.0 \pm 2.3	3.6 \pm 2.3	0.6 \pm 0.3	0.56 \pm 0.32	3.2 \pm 2.8 (0-17)	0.1 \pm 0.3 (0-2)	26.8
W2a	slightly ascending	40	5.7	3.0 \pm 2.2	3.6 \pm 2.3	2.9 \pm 2.2	3.7 \pm 2.3	0.8 \pm 0.3	0.59 \pm 0.70	0.1 \pm 0.2 (0-1)	0.1 \pm 0.4 (0-2)	17.9
W2b	ascending	30	4.2	6.1 \pm 4.2	9.7 \pm 5.7	6.0 \pm 4.2	10.0 \pm 5.8	4.0 \pm 2.3	0.62 \pm 0.60	0.4 \pm 0.8 (0-3)	0.6 \pm 1.4 (0-6)	23.3
W2c	ascending then flat	73	10.3	3.1 \pm 3.1	4.3 \pm 3.6	3.1 \pm 3.1	4.5 \pm 3.6	1.3 \pm 0.9	0.61 \pm 0.44	0.4 \pm 1.0 (0-6)	0.1 \pm 0.4 (0-2)	20.5
W3a	slightly descending	38	5.4	3.8 \pm 2.3	3.1 \pm 2.4	3.1 \pm 2.4	4.0 \pm 2.4	0.9 \pm 0.4	0.64 \pm 0.35	0.3 \pm 0.8 (0-4)	0.0 \pm 0.16 (0-1)	23.7
W3b	descending	12	1.7	6.4 \pm 4.9	3.7 \pm 4.5	3.7 \pm 4.4	6.4 \pm 4.9	2.7 \pm 1.1	0.65 \pm 0.47	0.5 \pm 1.7 (0-6)	0.1 \pm 0.3 (0-1)	50.0
W3c	descending then flat	12	1.7	3.9 \pm 4.0	2.8 \pm 3.9	2.7 \pm 3.7	4.0 \pm 4.0	1.3 \pm 0.8	0.52 \pm 0.27	0.2 \pm 0.6 (0-2)	0.1 \pm 0.3 (0-1)	16.6
W4a	shallow hump	20	2.8	2.3 \pm 1.2	2.5 \pm 1.3	2.2 \pm 1.2	3.2 \pm 1.3	1.0 \pm 0.4	0.38 \pm 0.31	1.0 \pm 0.0	0	15.0
W4b	hump	18	2.5	3.4 \pm 4.0	3.8 \pm 4.1	3.1 \pm 3.8	5.7 \pm 4.1	2.6 \pm 0.9	0.58 \pm 0.38	1.3 \pm 0.6 (1-3)	0.5 \pm 0.6 (0-2)	17.0
W4c	hump then flat	12	1.7	1.7 \pm 1.2	1.6 \pm 1.4	1.3 \pm 1.3	2.3 \pm 1.5	1.0 \pm 0.5	0.82 \pm 0.35	1.0 \pm 0.0	0.1 \pm 0.3 (0-1)	7.7

Table 2.1 cont.

Call Type (#)	Call contour	n	% of total calls	Frequency (kHz)				Band-width	Duration (s)	Inflection Points	Steps	% found in sequence
				Start	End	Minimum	Maximum					
W4d	hump segmented	7	1.0	1.4±0.4	1.3±0.6	1.0±0.2	2.9±0.5	1.9±0.5	2.20 ±1.34	1.6±1.0 (1-3)	0	0.0
W4e	hump chirps	3	0.4	6.6±2.5	6.7±2.1	6.6±2.5	7.4±2.5	0.9±0.2	1.32 ±0.97	12.3 ±8.4 (7-22)	0	100.0
W5a	shallow dip	16	2.3	2.7±1.4	2.7±1.6	1.8±1.5	2.8±1.5	1.0±0.2	0.41 ±0.44	1.0±0.0	0	31.0
W5b	dip	6	0.8	4.8±4.7	4.7±5.8	2.8±5.1	5.3±5.5	2.5±0.5	0.48 ±0.21	2.0±1.5 (1-4)	0.2±0.4 (0-1)	50.0
W5c	dip then flat	4	0.6	5.1±2.2	5.8±1.8	4.0±1.9	6.1±2.1	2.1±1.6	0.31 ±0.09	1.5±0.6 (1-2)	0.5±1.0 (0-2)	50.0
W5d	dip then hump	5	0.7	7.5±4.3	4.4±4.5	4.2±4.5	7.8±4.1	3.6±1.6	0.68 ±0.34	2.2±0.4 (2-3)	0	0.0
W6a	shallow waves	16	2.3	3.8±2.8	4.3±2.8	3.7±2.8	4.8±3.0	1.1±0.4	1.18 ±0.88	22.0 ±21.5 (4-71)	0.2±0.5 (0-2)	32.0
W6b	deep waves	8	1.1	7.9±5.5	9.1±5.7	6.0±3.8	11.2 ±5.5	5.1±3.8	1.28 ±0.40	12.1 ±8.4 (7-32)	0.1±0.4 (0-1)	25.0
W6c	variable waves	18	2.5	4.6±2.7	5.0±3.3	4.3±2.8	5.8±3.2	1.5±1.1	0.63 ±0.44	8.4±4.0 (4-16)	0.2±0.4 (0-1)	27.7
W6d	steep waves	3	0.4	2.2±0.3	1.8±0.8	1.2±0.3	2.6±0.1	1.4±0.3	2.00 ±0.71	17.3 ±3.8 (13-20)	0	0.0



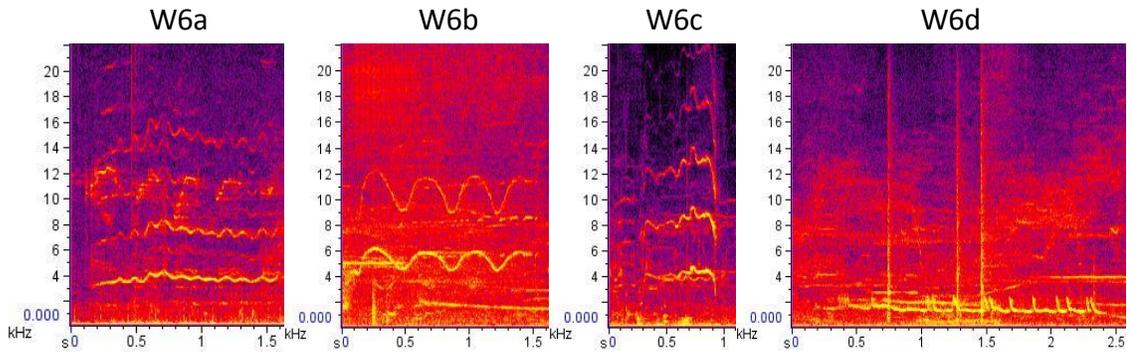


Figure 2.2: Representative spectrograms (frequency in kHz versus time in secs) of whistle call types emitted by belugas in the Churchill River, Manitoba.

were ascending but W2b whistles were steeper (frequency bandwidths >1.5 kHz and up to 8.4 kHz) and had higher mean frequency measurements than W2a whistles (Table 2.1). Also, 50.0% of W2b whistles had the majority (>60%) of their frequency range within 1.0-5.0 kHz with 33.0% of whistles >10.0 kHz and ranged up to 22.0 kHz (the upper limit of the recording system). In contrast, 82.5% of W2a whistles had the majority of their frequency range within 1.0-5.0 kHz and only 2.5% over 10.0 kHz. Call type W2c whistles were ascending at the beginning then flat (Figure 2.2) and were the most common whistles (10.3% of total calls analyzed, 16.1% of whistles). W2c whistle frequency measurements were more similar to W2a whistles than W2b whistles (Table 2.1) and 84.9% of W2c whistles had the majority of their frequency range within 1.0-5.0kHz and 5.5% over 10.0 kHz.

Contour type descending – W3a, W3b, and W3c

Descending whistles were less common than ascending whistles (8.8% of all calls analyzed, 13.7% of whistles) and separated into three call types (Table 2.1). Call types were similar in descriptions to ascending contour call types except whistle trend was descending not ascending. Call types W3a and W3b whistles were both descending but W3b calls were steeper (frequency bandwidth >1.5 kHz and up to 5.2 kHz). Call type W3a whistles were more common than the other two call types of this contour. Call type W3a and W3b whistles varied considerably in measured parameters (Table 2.1). However, W3b whistles were emitted over a larger frequency range; 66.0% of W3b whistles had the majority of their frequency range within 1.0-5.0 kHz and 25.0% over

10.0 kHz (up to 18.0 kHz) compared to 81.6% of W3a whistles between 1.0-5.0 kHz and only 2.6% over 10.0 kHz. Also, W3b whistles were found in sequence 50.0% of the time compared to only 23.7% in W3a whistles. Call type W3c whistles were descending at the beginning then flat (Figure 2.2) and had frequency measurements similar to W3a but with higher degree of variation (higher standard deviations) (Table 2.1). W3c whistles had the same percentage as W3b whistles (66.0%) with the majority of their frequency range within 1.0-5.0 kHz and also, 25.0% over 10.0 kHz (up to 13.9 kHz).

Contour type hump – W4a, W4b, W4c, W4d, and W4e

Hump whistles were as common as descending whistles (8.5% of all calls analyzed, 13.2% of whistles) and separated into five call types (Table 2.1). Call type W4a and W4b whistles had similar contours, frequency measures, and durations but W4b whistles had larger humps with frequency bandwidths >1.5 kHz and ranged up to 4.1 kHz (Table 2.1). Frequency measurements varied considerably in call types W4a and W4b but 95.0% of W4a whistles were 1.0-5.0 kHz and none were >10.0 kHz, whereas 72.2% of W4b whistles were 1.0-5.0 kHz and 5.6% were >10.0 kHz.

Call type W4c whistles were described as ascending then descending (hump) then flat (Figure 2.2). Again, measured parameters varied considerably within the call type (high standard deviations) (Table 2.1) but only one whistle was >5.0 kHz. Call type W4d whistles had a hump contour but consisted of segments (Figure 2.2). W4d whistles were more stereotyped with less variation in call measurements (Table 2.1) and all whistles were <5.0 kHz. Call type W4d had the highest mean duration of any whistle call

type (Table 2.1); all whistles were >1.50s and the longest was 5.21s. Call type W4e whistles were similar in shape to W4a whistles but differed in that humps were repeated (eight to 22 times) and had a distinct ‘chirping’ sound (Figure 2.2). W4e whistles were only emitted three times (0.4% of total calls, 0.7% of whistles) but exhibited little variation in call properties and were relatively high frequency (4.0-10.0kHz) (Table 2.1).

Contour type dip – W5a, W5b, W5c, and W5d

Dip whistles were the least common whistles (4.4% of all calls analyzed, 6.8% of whistles) and separated into four call types (Table 2.1). Three of the four call types described were similar to hump contour call types but no segmented dips similar to call type W4d were found. Call type W5a and W5b whistles had similar contours but W5b whistles were larger dips with frequency bandwidths >1.5 kHz and up to 3.3 kHz. Call types W5a and W5b had considerable variation in frequency measures (Table 2.1); however, most W4a whistles (93.4%) had the majority of their frequency range between 1.0-5.0 kHz and none were >10.0kHz, whereas 83.3% of W5b whistles were between 1.0-5.0 kHz and 16.7% over 10.0kHz.

Call type W5c whistles were described as descending then ascending (dip) then flat (Figure 2.2). W5c whistles were only emitted four times (0.6% of total calls, 0.9% of whistles), three of which had the majority of their frequency range within 1.0-5.0 kHz. Call type W5d whistles had a dip then hump contour and were only emitted five times (0.7% of total calls, 1.1% of whistles). Most W5d whistles had relatively high mean

frequency bandwidth; four of five whistles had a bandwidth >2.0 kHz and up to 5.4 kHz. W5d whistles also had relatively high mean frequency measurements (Table 2.1) and all but one whistle was >5.0 kHz.

Contour type wavy – W6a, W6b, W6c, and W6d

Wavy whistles were relatively uncommon (6.3% of all calls analyzed, 10.0% of whistles) and the most complex whistles; wavy whistles had the highest mean number of inflection points and contained 4-71 inflection points (Table 2.1). Wavy whistles were separated into four call types based on wave shape (Table 2.1). Call types W6a and W6b both contained whistles with uniform waves but W6b whistles contained larger waves (Figure 2.2). Call type W6b whistles therefore had a higher mean frequency bandwidth (Table 2.1) and ranged from 1.6-13.0 kHz. W6a whistles had a lower mean frequency bandwidth and ranged from 0.4-1.7kHz. W6b whistles were also emitted at relatively higher frequencies (higher mean frequency measurements) (Table 2.1); only 25.0% of W6b whistles had the majority of their frequency range within 1.0-5.0 kHz and 62.5% were >10.0 kHz. In contrast, 75.0% of W6a whistles were 1.0-5.0 kHz and only 6.3% above 10.0 kHz. W6c whistles which consisted of variable sized waves had frequency measurements similar to W6a whistles (Table 2.1; Figure 2.2). Mean frequency measures of call type W6c whistles were similar to those of W6a (Table 2.1). Also, 66.7% of W6c whistles had the majority of their frequency range within 1.0-5.0 kHz and only 5.6% above 10.0 kHz (similar percentages to W6a). W6c whistles had a lower mean number of inflection points and a shorter mean duration than other wavy call types

(Table 2.1). Call type W6d whistles consisted of steep and shallow waves (Figure 2.2). W6d whistles were only emitted three times (0.4% of total calls, 0.7% of whistles) but were stereotyped with little variation in frequency measurements (Table 2.1). All three W6d whistles were 1.0-3.0 kHz and had 13-20 inflection points.

2.4.1.2 Pulsed and noisy calls

Pulsed and noisy calls constituted about a quarter of the calls analyzed (25.9%) and were classified based on aural and visual analysis and PRR where it could be measured. Calls in which the PRR could not be measured were classified as noisy. Fifteen pulsed and noisy call types were identified (Table 2.2). See Figure 2.3 for representative spectrograms. Pulse repetition rates could be measured for ten of the call types resulting in five noisy call types. Because of their nature, fewer call parameters were measured for pulsed and noisy calls than for whistles (Table 2.2).

'Buzzes' (P1a = flat buzz, P1b = flat buzz clicks, and P1c = thick wavy buzz) were the most common pulsed or noisy calls and P1b was the most common call type (4.2% of all calls analyzed, 16.4% of pulsed/noisy calls) (Table 2.2). 'Buzz' subtypes sounded similar and had similar frequency measurements but were separated because of differences in contour and/or PRR (Table 2.2; Figure 2.3). P1a calls had a similar contour to P1b calls (flat) but PRR could not be measured. P1c calls had a wavy contour which differed from the flat contour of P1a and P1b calls and P1c calls had higher PRR than P1b calls (Figure 2.3; Table 2.2).

Table 2.2: Descriptive statistics of pulsed and noisy calls (mean \pm standard deviation) emitted by belugas in the Churchill River, Manitoba.

Call Type (#)	Call contour	n	% of total calls	Frequency (kHz)			Duration (s)	PRR (pulses/s)	% found in sequence
				Minimum	Maximum	Frequency Bandwidth			
P1a	flat buzz	20	2.8	6.0 \pm 2.0	7.5 \pm 2.5	1.5 \pm 1.1	1.01 \pm 0.55	N/A	20
P1b	flat buzz clicks	30	4.2	6.1 \pm 2.0	7.7 \pm 2.9	1.6 \pm 1.2	0.86 \pm 0.52	71 \pm 18	33
P1c	thick wavy buzz	9	1.3	4.9 \pm 0.6	9.5 \pm 0.8	4.6 \pm 1.1	0.63 \pm 0.32	246 \pm 8	22
P2	thick creak	12	1.7	2.8 \pm 2.1	5.3 \pm 2.5	2.5 \pm 1.1	1.16 \pm 0.36	207 \pm 57	17
P3	slightly descending curly	7	1.0	1.1 \pm 0.6	2.0 \pm 0.8	0.9 \pm 0.4	0.97 \pm 0.42	73 \pm 22	29
P4	clicks of restricted frequency	8	1.1	0.4 \pm 0.2	1.7 \pm 0.8	1.3 \pm 0.6	2.21 \pm 1.16	34 \pm 13	13
P5	clinks	9	1.3	3.2 \pm 2.1	4.4 \pm 2.3	1.3 \pm 0.8	1.09 \pm 0.64	48 \pm 8	33
P6	croaks segmented	4	0.6	0.2 \pm 0.2	1.5 \pm 0.6	1.3 \pm 0.4	0.46 \pm 0.30	41 \pm 4	25
P7	honk	29	4.1	0.3 \pm 0.1	0.7 \pm 0.2	0.3 \pm 0.1	0.27 \pm 0.12	482 \pm 149	55
P8	slightly ascending hollow honk	8	1.1	0.1 \pm 0.1	0.7 \pm 0.3	0.5 \pm 0.3	1.23 \pm 0.38	300 \pm 84	13
P9	thick flat screech	2	0.3	4.6 \pm 1.1	9.6 \pm 4.9	5.0 \pm 3.7	0.28 \pm 0.02	87 \pm 3	0
P10	thick hump screech	16	2.3	1.1 \pm 0.4	2.3 \pm 0.7	1.2 \pm 0.6	0.71 \pm 0.40	N/A	25
P11	slightly ascending squeal	13	1.8	2.4 \pm 2.3	4.7 \pm 2.8	2.2 \pm 1.7	0.57 \pm 0.37	N/A	38
P12	thick flat scream	7	1.0	0.6 \pm 0.4	1.6 \pm 0.4	0.9 \pm 0.5	1.14 \pm 0.47	N/A	14
P13	thick bark	9	1.3	0.4 \pm 0.2	1.5 \pm 0.3	1.1 \pm 0.3	0.99 \pm 0.52	N/A	11

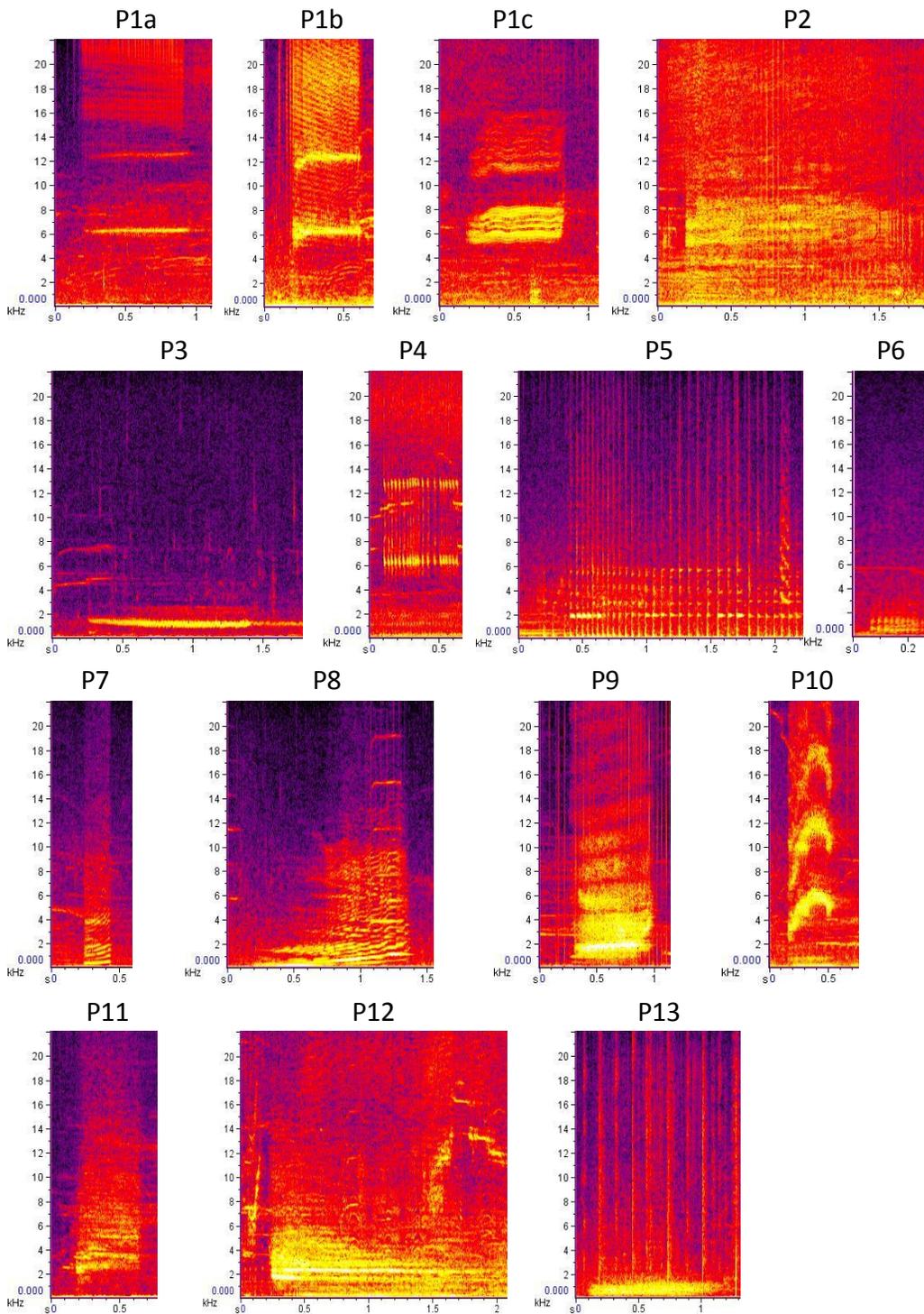


Figure 2.3: Representative spectrograms (frequency in kHz versus time in secs) of pulsed and noisy call types emitted by belugas in the Churchill River, Manitoba.

Most pulsed and noisy call measurements varied less, especially PRR, than whistle call measurements described above (Table 2.1; 2.2). P4 calls had the lowest mean PRR of 34 ± 13 (mean \pm standard deviation). P5 and P6 calls also had relatively low mean PRR, 48 ± 8 and 41 ± 4 , respectively. P7 calls (honk) had the highest mean PRR of 482 ± 149 and were the second most common pulsed or noisy calls (4.1% of all calls, 15.8% of pulsed and noisy calls). P8 calls also had relatively high mean PRR of 300 ± 84 . Duration of pulsed and noisy calls was variable within most call types; mean durations ranged from 0.27s (P7) to 2.21s (P4) (Table 2.2).

2.4.1.3 Combined calls

Combined calls constituted only 9.9% of calls analyzed and were classified based on contour, aural and visual analysis, and call characteristics of each component. Seven call types were described and call parameters measured (Table 2.3): C1 = whistle with noisy component at end, C2 = whistle with noisy component at beginning, C3 = whistle with noisy component in middle, C4 = low honk with higher whistle, C5 = thick creak with higher whistle, C6 = wavy honk with higher component, and C7 = ascending then flat thick screech with lower flat whistle. See Figure 2.4 for representative spectrograms.

Three combined call types (C1, C2, and C3) consisted of a whistle and noisy component forming one call, observed both visually from the spectrogram and audibly from the recording. Frequency parameters and durations (combined durations of components) were variable within each call type (Table 2.3). Most whistle components

Table 2.3: Descriptive statistics of combined calls (mean \pm standard deviation) emitted by belugas in the Churchill River, Manitoba.

Call Type (#)	n	% of calls	Whistle component					Pulsed or Noisy Component					Whole call												
			Frequency (kHz)					Frequency (kHz)					PRR (pulses /sec)	Dur (s)	% in sequ										
			Start	End	Min	Max	Band-width	Dur (s)	Infl. Pts	Steps	Min	Max				Band-width	Dur (s)								
C1	19	2.7	3.0 \pm 1.8	3.0 \pm 1.9	2.7 \pm 1.8	3.3 \pm 1.8	0.6 \pm 0.3	0.33 \pm 0.22	0.4 \pm 0.8 (0-3)	0.1 \pm 0.2 (0-1)	2.3 \pm 1.4	4.1 \pm 2.8	1.8 \pm 1.6	0.31 \pm 0.25	N/A	0.64 \pm 0.28	21								
C2	10	1.4	3.1 \pm 3.3	4.1 \pm 4.3	2.9 \pm 3.2	4.2 \pm 4.2	1.3 \pm 1.4	0.51 \pm 0.29	0.3 \pm 0.7 (0-2)	0	2.6 \pm 3.3	4.2 \pm 4.3	1.6 \pm 1.2	0.54 \pm 0.37	N/A	1.05 \pm 0.48	20								
C3	3	0.4	5.3 \pm 4.3	6.4 \pm 6.3	5.2 \pm 4.4	6.5 \pm 6.2	1.4 \pm 1.8	0.09 \pm 0.02	0	0	5.3 \pm 5.8	7.8 \pm 7.6	2.5 \pm 1.9	0.13 \pm 0.05	N/A	0.83 \pm 0.51	33								
C4	13	1.8	6.7 \pm 6.9	7.5 \pm 7.8	6.5 \pm 6.7	7.5 \pm 7.8	1.0 \pm 1.2	0.24 \pm 0.13	0	0	7.3 \pm 1.9	7.6 \pm 1.9	7.2 \pm 1.9	7.9 \pm 2.0	0.7 \pm 0.3	0.22 \pm 0.11	0.8 \pm 1.2 (0-4)	0.2 \pm 0.4 (0-1)	0.3 \pm 0.2	0.6 \pm 0.2	0.3 \pm 0.1	0.25 \pm 0.12	449 \pm 213	0.47 \pm 0.21	31
C5	7	1.0	6.9 \pm 1.0	6.7 \pm 1.1	6.6 \pm 0.6	7.5 \pm 0.5	0.9 \pm 0.4	0.41 \pm 0.16	0.2 \pm 0.4 (0-1)	0.2 \pm 0.4 (0-1)	1.5 \pm 1.4	3.0 \pm 2.5	1.5 \pm 1.5	1.16 \pm 0.41	183 \pm 23	1.57 \pm 0.44	29								
C6	15	2.1	10.5 \pm 3.0	10.5 \pm \pm 3.2	10.2 \pm \pm 3.1	11.2 \pm \pm 3.2	0.9 \pm 0.4	0.16 \pm 0.03	0.4 \pm 0.5 (0-1)	0	0.2 \pm 0.2	0.5 \pm 0.2	0.3 \pm 0.1	0.84 \pm 0.42	376 \pm 102	0.99 \pm 0.42	60								
C7	4	0.6	1.1 \pm 0.3	1.2 \pm 0.3	1.0 \pm 0.3	1.5 \pm 0.3	0.5 \pm 0.2	0.70 \pm 0.24	0	0	3.4 \pm 2.5	8.2 \pm 2.8	4.9 \pm 3.2	0.78 \pm 0.27	N/A	1.47 \pm 0.51	0								

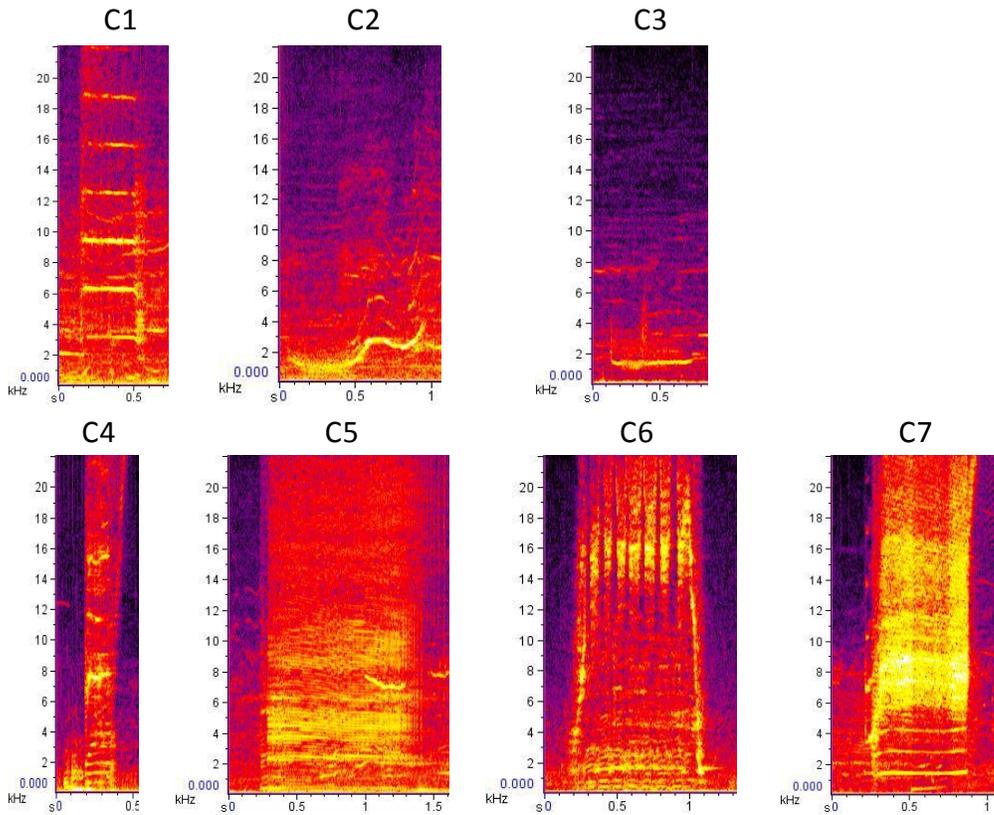


Figure 2.4: Representative spectrograms (frequency in kHz versus time in secs) of combined call types emitted by belugas in the Churchill River, Manitoba.

in C1 were simple (unmodulated or slightly ascending) evident in the low mean frequency bandwidth of 0.6 ± 0.3 (Table 2.3; Figure 2.4). Call type C1 was the most common combined call type (2.7% of all calls analyzed, 26.8% of combined calls). C3 calls had a noisy component in the middle and whistle components before and after (Figure 2.4).

The other four combined call types (C4, C5, C6, and C7) contained two calls emitted simultaneously by one individual but both components were not necessarily the same duration (Figure 2.4). All four call types were discrete categories with little variation in most frequency parameters and duration measures (Table 2.3). Call types C4, C5, and C6 consisted of a low pulsed call and higher whistle, whereas call type C7 consisted of a higher noisy component and a lower flat whistle (Figure 2.4). Call type C6 had a distinct 'laughing' sound and was the second most common combined call type (2.1% of total calls, 21.1% of combined calls). Pulse repetition rates differed in the C4, C5, and C6 pulsed calls but could not be measured in the C7 noisy calls (Table 2.3).

2.4.2 Cluster analysis

UPGMA Chord cluster tree analysis divided whistles into two main clusters (termed A and B). Cluster A was further divided into four clusters and B into eight (Figure 2.5). Whistle call types described in subjective classification for each branch are presented in Figure 2.6 and call characteristics in Table 2.4. Cluster A included 40 whistles whereas cluster B had 160. Division between A and B appeared to be mostly

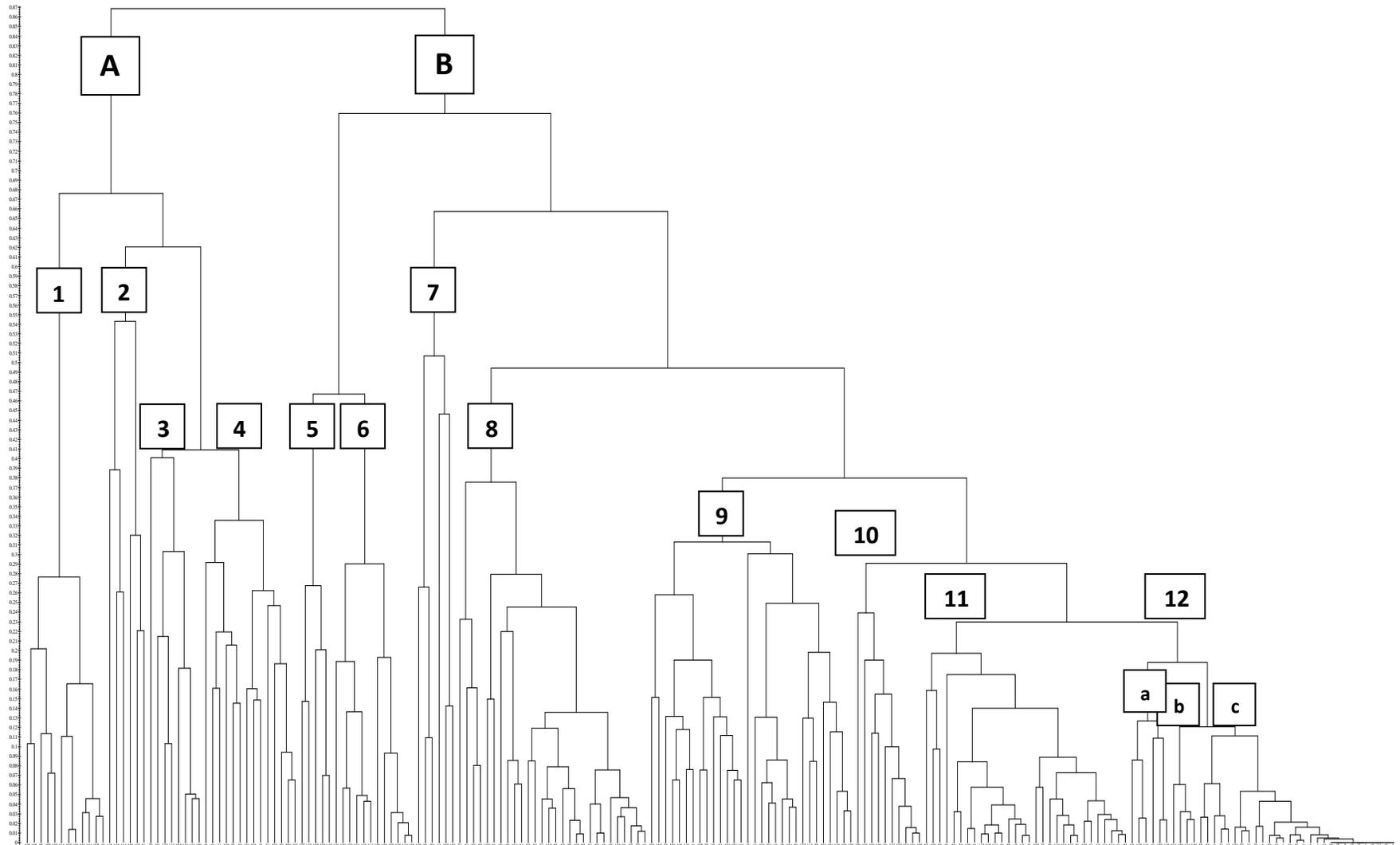
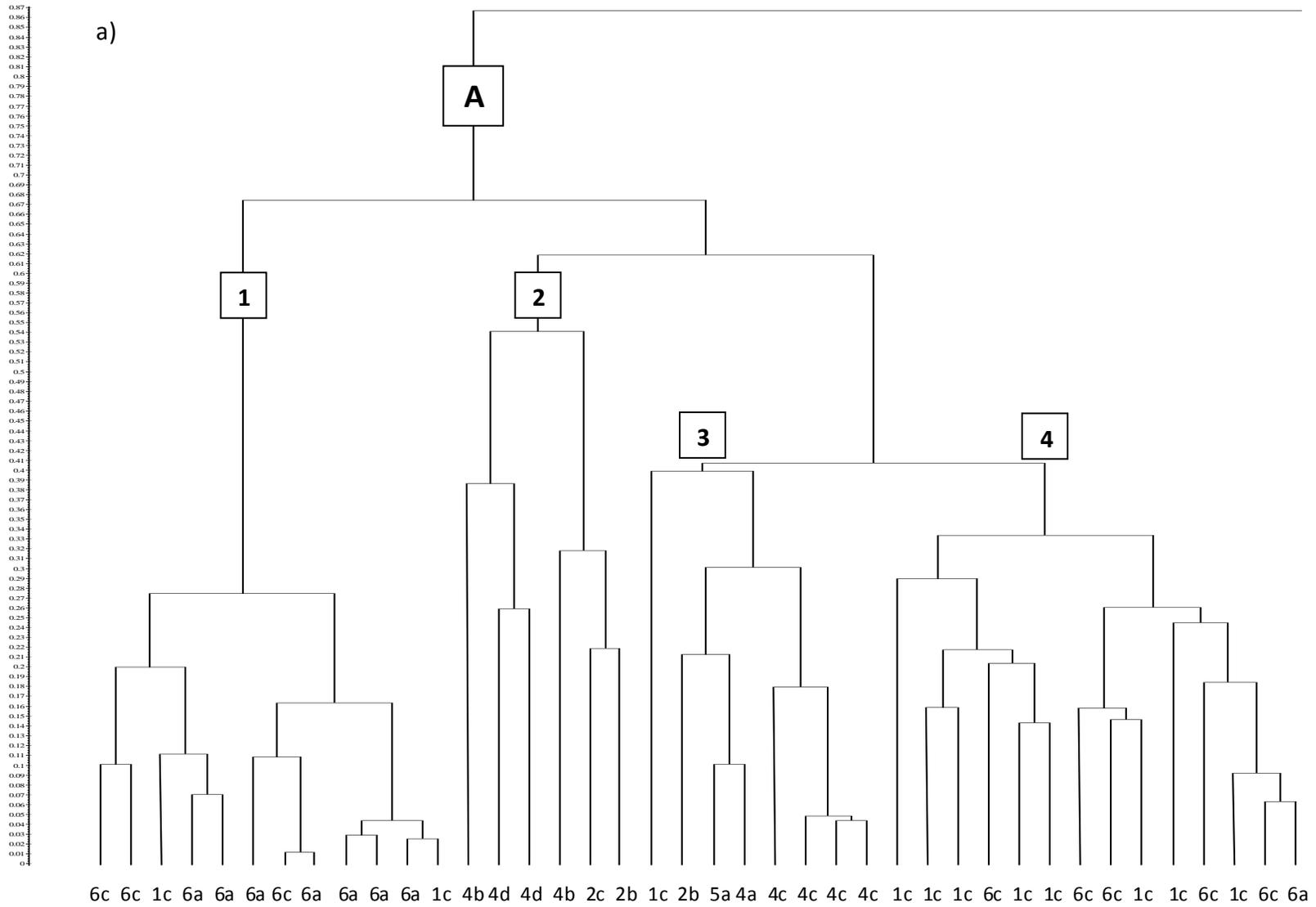
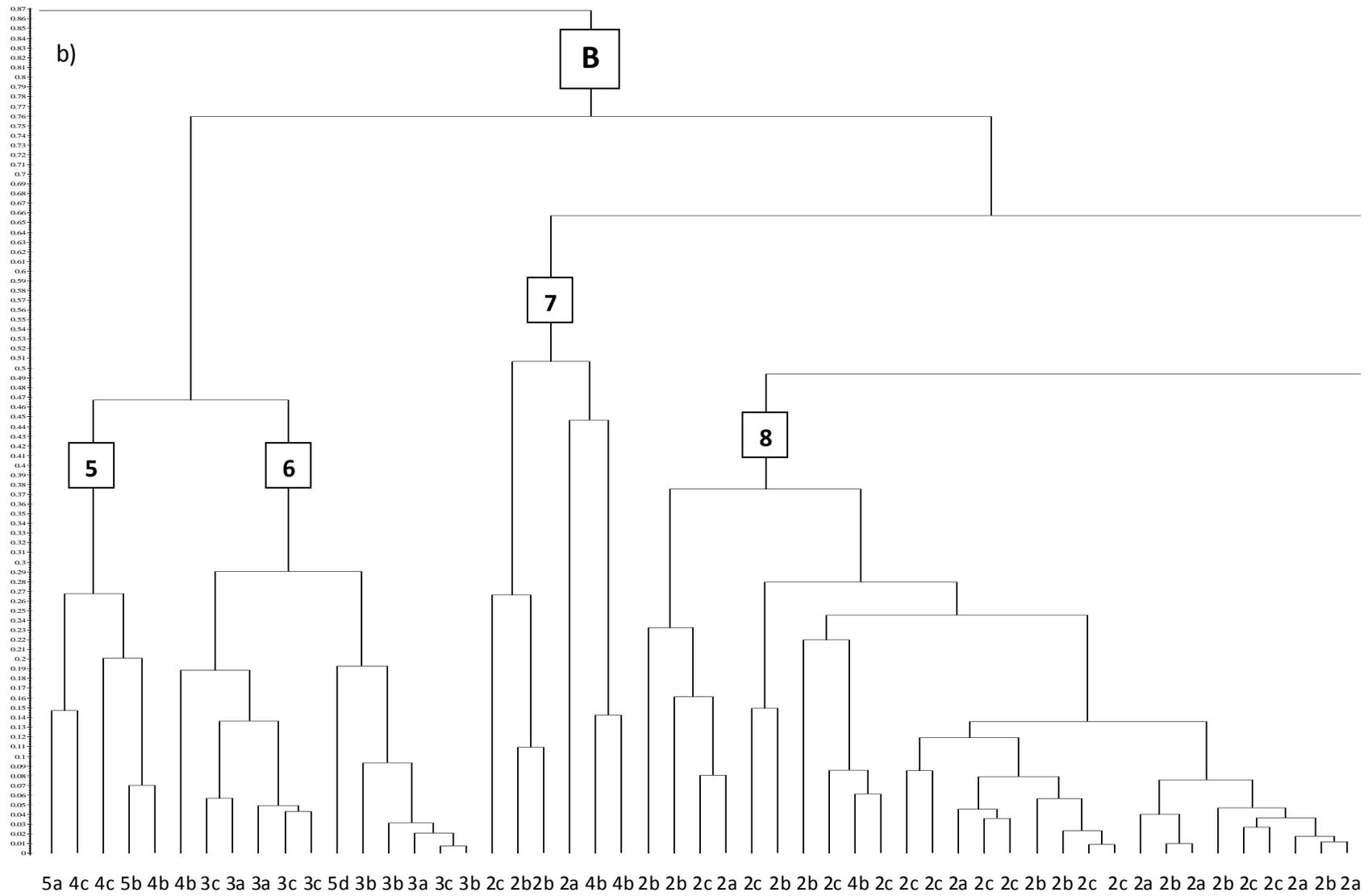
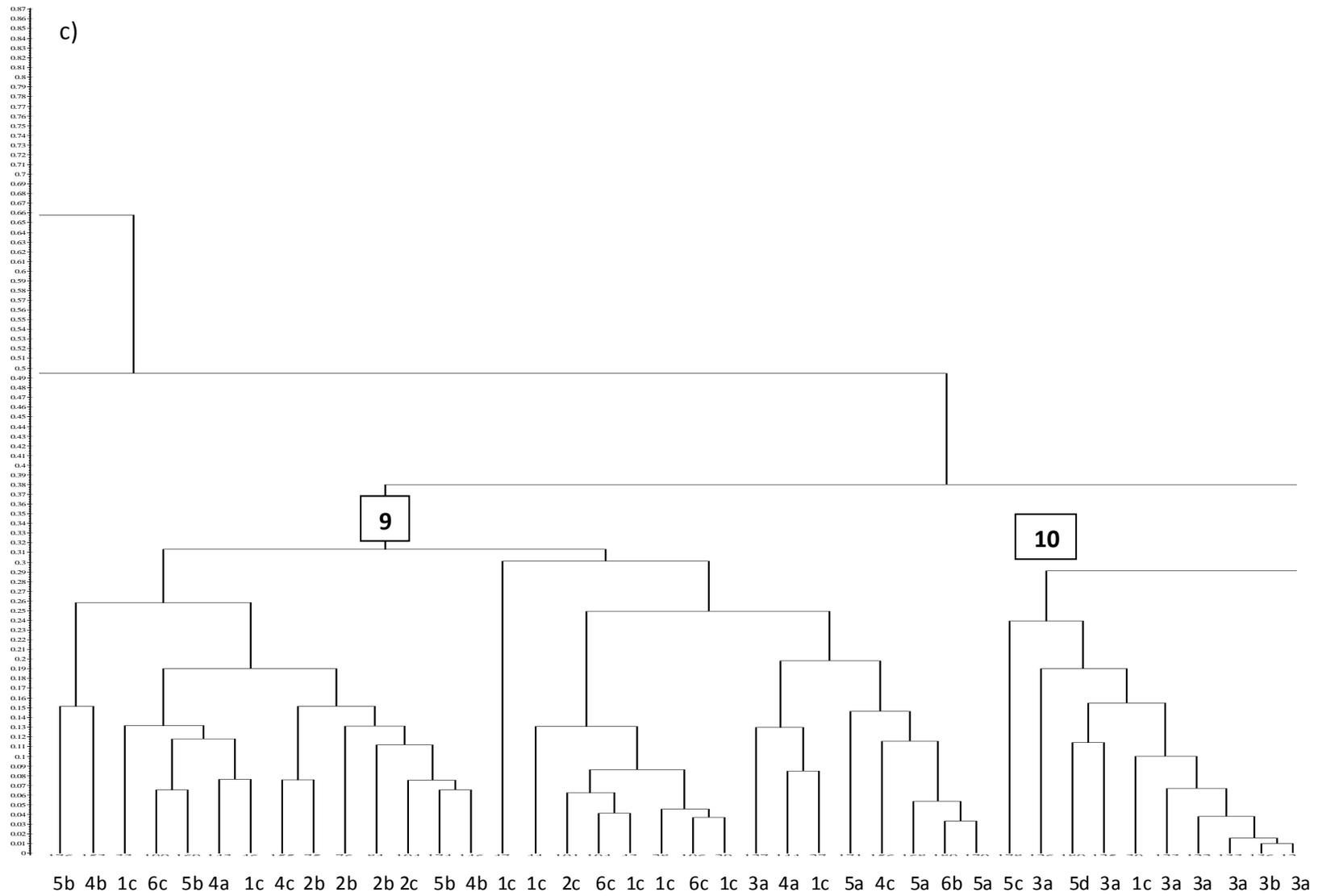


Figure 2.5: UPGMA, Chord cluster tree using starting frequency, ending frequency, difference between starting and ending frequency, frequency bandwidth, number of inflection points, and number of steps as variables.







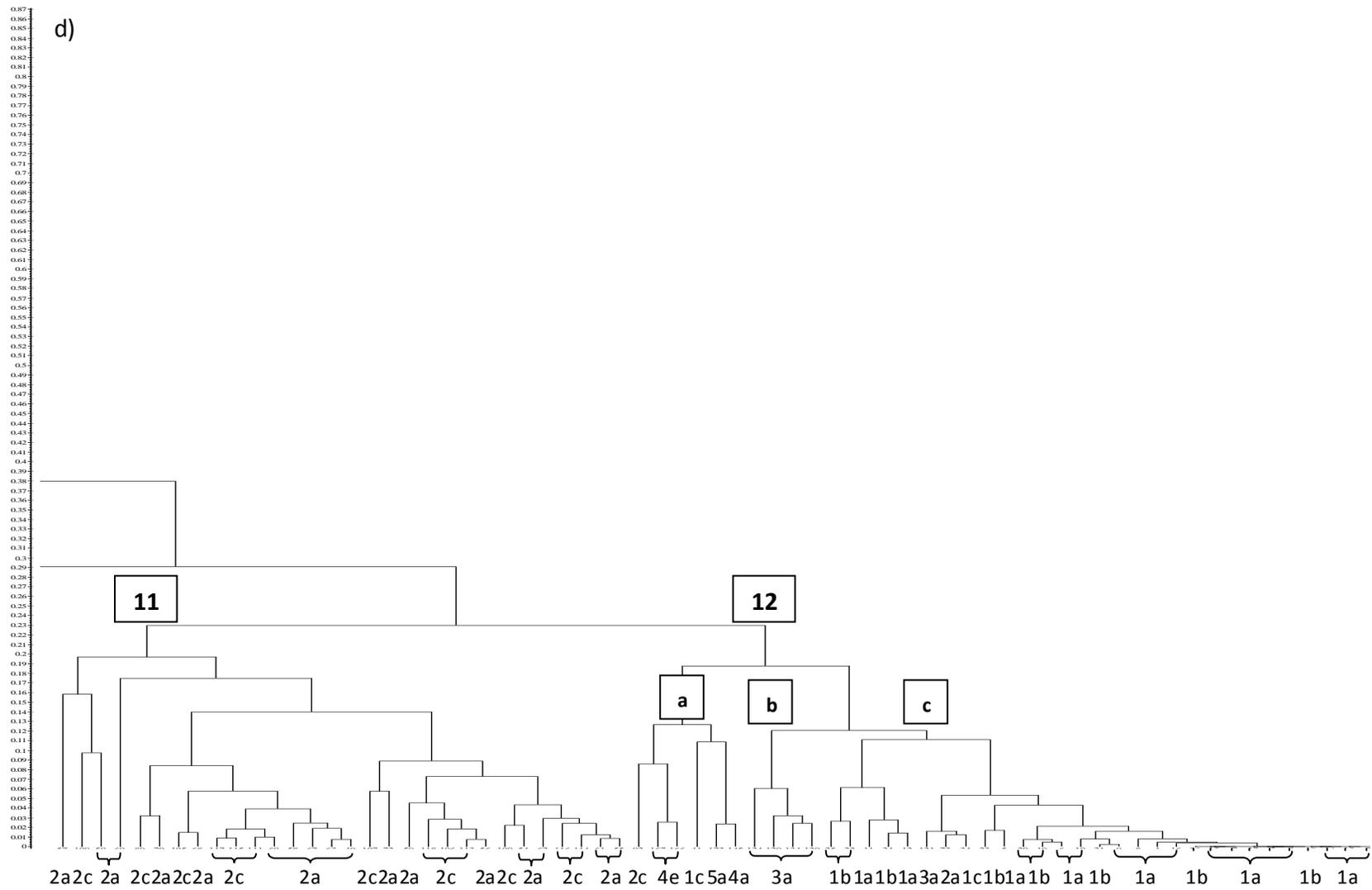


Figure 2.6: Subjective call types grouped in UPGMA, Chord cluster tree: a) cluster A, groups A1-A4, b) cluster B, groups B5-B8, c) cluster B, groups B9 and B10, d) cluster B, groups B11 and B12.

Table 2.4: Descriptive statistics of whistles in cluster analysis groups (mean \pm SD) emitted by belugas in the Churchill River, Manitoba.

Group #	Dominant call type(s)	n	% of calls	Start Freq (kHz)	End Freq (kHz)	Min Freq (kHz)	Max Freq (kHz)	Band-width	Duration (s)	Inflection Points	Steps
A1	W6a	12	6.0	2.7 \pm 2.2	3.0 \pm 2.3	2.5 \pm 2.2	3.6 \pm 2.3	1.1 \pm 0.6	1.19 \pm 0.98	24.9 \pm 23.6 (4-71)	0.2 \pm 0.6 (0-2)
A2	W2c,W4b,W4d	6	3.0	0.9 \pm 0.5	2.0 \pm 1.2	0.9 \pm 0.4	3.2 \pm 0.8	2.3 \pm 0.6	1.08 \pm 0.67	2.0 \pm 0.9 (1-3)	0.2 \pm 0.4 (0-1)
A3	W4c	8	4.0	1.3 \pm 0.7	1.0 \pm 0.8	2.0 \pm 1.5	2.0 \pm 1.5	1.0 \pm 0.7	0.59 \pm 0.18	1.5 \pm 1.1 (1-4)	0.1 \pm 0.4 (0-1)
A4	W1c,W6d	14	7.0	3.3 \pm 2.2	3.6 \pm 2.5	3.1 \pm 2.2	4.0 \pm 2.6	0.9 \pm 0.5	0.64 \pm 0.45	4.5 \pm 2.3 (2-10)	0.1 \pm 0.4 (0-1)
TOTAL (Group A)		40	20.0	2.3 \pm 2.1	2.8 \pm 2.2	2.2 \pm 2.0	3.4 \pm 2.2	1.2 \pm 0.7	0.86 \pm 0.69	9.7 \pm 16.2 (1-71)	0.2 \pm 0.4 (0-2)
B5	W4b,W4c,W5b	6	3.0	3.1 \pm 2.0	2.0 \pm 1.1	1.7 \pm 1.3	3.9 \pm 2.3	2.2 \pm 1.1	0.68 \pm 0.62	1.0 \pm 0.0	0
B6	W3a,W3b,W3c	11	5.5	2.9 \pm 2.1	1.0 \pm 0.9	0.9 \pm 0.9	3.0 \pm 2.2	2.0 \pm 1.5	0.59 \pm 0.29	0.2 \pm 0.6 (0-2)	0
B7	W2b,W4b	6	3.0	1.8 \pm 0.5	3.2 \pm 1.4	1.7 \pm 0.3	4.0 \pm 1.0	2.3 \pm 0.9	0.81 \pm 0.49	0.3 \pm 0.5 (0-1)	2.2 \pm 1.5 (1-4)
B8	W2a,W2b,W2c	28	14.0	3.3 \pm 3.5	5.6 \pm 5.3	3.3 \pm 3.4	5.9 \pm 5.5	2.6 \pm 2.3	0.47 \pm 0.30	0.1 \pm 0.4 (0-1)	0.1 \pm 0.4 (0-2)
B9	W1c,many	30	15.0	5.1 \pm 4.1	5.8 \pm 5.0	4.4 \pm 3.4	6.1 \pm 4.9	1.7 \pm 1.9	0.63 \pm 0.46	2.2 \pm 2.0 (1-9)	0.2 \pm 0.5 (0-2)
B10	W3a	10	5.0	6.2 \pm 4.0	5.1 \pm 3.5	5.0 \pm 3.4	5.2 \pm 4.4	1.3 \pm 0.6	0.57 \pm 0.29	0.5 \pm 0.9 (0-2)	0.3 \pm 0.7 (0-2)
B11	W2a,W2c	30	15.0	4.5 \pm 4.0	5.3 \pm 4.7	4.5 \pm 4.0	5.4 \pm 4.7	1.0 \pm 0.8	0.65 \pm 0.78	0	0.1 \pm 0.3 (0-1)
B12a	W4e	6	3.0	7.0 \pm 2.8	7.1 \pm 2.9	6.8 \pm 2.9	7.6 \pm 2.9	0.8 \pm 0.1	0.50 \pm 0.70	1.5 \pm 0.8 (1-3)	0
B12b	W3a	4	2.0	6.1 \pm 1.8	5.6 \pm 1.9	5.5 \pm 1.8	6.3 \pm 2.1	0.8 \pm 0.4	0.59 \pm 0.17	0	0
B12c	W1a,W1b	29	14.5	2.9 \pm 2.5	2.9 \pm 2.5	2.7 \pm 2.5	3.1 \pm 2.6	0.0 \pm 0.1	0.90 \pm 0.61	0	0
TOTAL (Group B)		160	80.0	4.1 \pm 3.5	4.6 \pm 4.3	3.6 \pm 3.3	5.1 \pm 4.3	1.4 \pm 1.6	0.65 \pm 0.55	0.6 \pm 1.2 (0-9)	0.2 \pm 0.6 (0-4)

due to complexity of the whistles based on the amount of frequency modulation defined by the number of inflection points (Table 2.4). All whistles in cluster A had at least one inflection point, eight whistles (20.0%) had one, five (12.5%) had two, and the remainder (27 or 67.5%) had more than two inflection points (nine had ten or more and five had 20 or more). In contrast, the majority of whistles in cluster B (108 or 67.5%) had no inflection points, 33 (20.6%) had one, 11 (6.9%) had two, only eight (5.0%) had more than two, and none had ten or more. This A-B division also appeared to be based partially on absolute frequency since cluster A whistles were generally emitted at lower frequencies (Table 2.4). A large majority (80.0%) of cluster A whistles were <4.0 kHz with no whistles >10.0 kHz, whereas fewer cluster B whistles (60.6%) were <4.0 kHz and 10.0% of those whistles were >10.0 kHz.

Group A1 (n=12)

Group A1 was characterized by whistles with the greatest number of inflection points; it had the highest mean (24.9 ± 23.6) and inflection points ranged from 4-71 (Table 2.4). Ten of 12 whistles (83.3%) were classified as wavy contour type defined in the subjective classification: seven were classified as W6a (small uniform waves) and three as W6c (variable waves). Two other whistles were classified as flat contour types (W1c, mostly flat) but contained inflection points in at least a portion of the whistle (Figure 2.6a; Figure 2.2). Ten of 12 whistles were 1.0-4.0 kHz and none were >10.0 kHz. Group A1 had the highest mean duration (Table 2.4) and contained whistles up to 3.57s.

Group A2 (n=6)

Group A2 was a small group with fewer inflection points than groups A1 and A4 (mean = 2.0 ± 0.9 , range 1-3) (Table 2.4). Four of the six whistles (66.7%) were classified as hump contour type: two of which were classified as W4b (hump), and two as W4d (hump segmented). The other two whistles were classified as ascending contour types (Figure 2.6a; W2c, ascending then flat). Group A2 had the highest mean frequency bandwidth in cluster A (Table 2.4). Mean frequency measurements were similar to other groups in cluster A and all whistles were <5.0 kHz which may explain, in part, why they were grouped in cluster A (relatively low frequency is a defining characteristic). As with group A1, group A2 had a relatively high duration (Table 2.4) and contained some of the longer whistles with durations up to 2.02s and four of six were approximately 1.00s.

Group A3 (n=8)

Group A3 was also a small group with fewer inflection points than groups A1 and A4 (mean = 1.5 ± 1.1 , range 1-4) (Table 2.4). Five of the eight whistles (63.0%) were classified as whistle call type W4c (hump then flat) and the remaining three whistles were one each of W1c (mostly flat), W4a (shallow hump), and W5b (dip) call types (Figure 2.6a). Little variation existed in start and end frequencies (Table 2.4) and all whistles had the majority of their frequency range <5.0 kHz. Again, this appears to be the defining characteristic that clustered group A3 whistles into cluster A.

Group A4 (n=14)

Group A4 had similar characteristics to group A1 with a relatively high mean number of inflection points (4.5 ± 2.3 , range 2-10) and similar frequency measurements (Table 2.4). All but one whistle was classified as either W1c (mostly flat; eight whistles) or W6c (variable waves; five whistles). The remaining whistle was classified as W6a (small uniform waves, Figure 2.6a). W6c and W1c whistles had similar call properties (i.e. contain inflection points) but W6c whistles generally had higher frequency bandwidths and were emitted at higher frequencies than W1c whistles (Table 2.1).

Group B5 (n=5)

Group B5 was a small group with four of six whistles classified as hump contour types: two were classified as W4b (hump) and two as W4c (hump then flat). The other two were classified as W5b (dip) whistles (Figure 2.6b). All whistles in this group were characterized by having one inflection point and similar frequency measurements (Table 2.4); all but one whistle was 1.0-4.0 kHz and frequency bandwidths were 1.0-2.5 kHz.

Group B6 (n=12)

Group B6 had similar call characteristics to group B5 (Table 2.4) but in group B6 all but one whistle was classified as a decreasing contour type: three were classified as W3a (slightly descending), three as W3b (descending), and four as W3c (descending then flat) (Figure 2.6b). Little variation existed in the start and end frequencies (Table 2.4) and all whistles except two were <4.0 kHz.

Group B7 (n=6)

Group B7 was a small group with four of six whistles classified as ascending contour type: one was classified as W2a (slightly ascending), two as W2b (ascending), and one as W2c (ascending then flat) (Figure 2.6b). Many whistles in the cluster analysis did not contain any steps but all whistles in group B7 contained at least one (range 1-4). Frequency measurements had little variation (Table 2.4); all whistles in this group were 1.0-5.0 kHz and all but one had a frequency bandwidth between 1.0-3.0 kHz.

Group B8 (n=28)

Group B8 was a relatively large group with all but one whistle classified as ascending contour type: six were classified as W2a (slightly ascending), ten as W2b (ascending), and 11 as W2c (ascending then flat) (Figure 2.6b). All whistles in this group had a general ascending trend (starting frequency was lower than ending frequency resulting in a negative difference); however, the amount whistles ascended varied with the difference between starting and ending frequency ranging from -0.3 to -7.7 kHz. Frequency measurements within the group varied considerably (Table 2.4) and group B8 had the lowest mean duration (0.47 ± 0.30) with 23 of the 28 whistles (82.0%) shorter than 0.60s.

Group B9 (n=30)

Group B9 was another large group and was the most variable group in terms of subjective whistle call types represented (all contour types were represented and 11

whistle call types included) (Figure 2.6c). However, 20 of 30 whistles (66.7%) had an ascending trend (starting frequency lower than ending frequency). Group B9 had relatively high mean number of inflection points (Table 2.4); all whistles had at least one inflection point and contained all whistles in cluster B with more than two inflection points (six whistles). Frequency measurements varied considerably (Table 2.4); eighteen of 30 whistles (60.0%) were 1.0- 5.0kHz and four (13.3%) over 10.0 kHz.

Group B10 (n=10)

Seven of B10 whistles were classified as descending contour types: six were classified as W3a (slightly descending) and one as W3b (descending) (Figure 2.6c). All whistles had at least a slightly descending trend (starting frequency higher than ending frequency). Frequency parameters varied within the group (Table 2.4) but whistles had relatively high frequencies with only two whistles <3.0 kHz and two >10.0 kHz. Group B10 and subsequent groups contained lower mean frequency bandwidths than the above groups (Table 2.4); seven of ten whistles (70.0%) in group B10 had a bandwidth <1.0 kHz.

Group B11 (n=30)

Group B11 was a relatively large group but all whistles were classified as the ascending contour type and only two subjective whistle call types represented. Seventeen whistles were classified as W2a (slightly ascending) and 13 as W2c (ascending then flat) (Figure 2.6d). Frequency measurements varied (Table 2.4) but whistles were

similar in contour (no whistles contained inflection points and only three had one step, the rest had none). Group B11 had a relatively low mean frequency bandwidth (Table 2.4) and 23 of 30 whistles (76.7%) had bandwidths <1.0 kHz. Group B11 whistles can be described as simple whistles (none contained inflection points and few contained steps) with ascending contours.

Group B12 (n=39)

Group B12 was the largest group and whistles were simple whistles defined by small frequency bandwidths and low numbers of inflection points. Group B12 whistles had a low mean frequency bandwidth (Table 2.4) with all but one whistle having a frequency bandwidth <1.0 kHz and the majority (33 or 84.6%) with no inflection points. Group 12 was dominated by flat contour whistles (28 of the 39 or 71.8%): 17 were classified as W1a (flat whistles), nine as W1b (flat segmented whistles), and two as W1c (mostly flat whistles). Three subgroups were identified within the cluster analysis (Figure 2.6d).

Subgroup B12a contained six whistles with a mix of the subjective whistle call types found in group 12 (Figure 2.6d). All whistles in subgroup B12a had at least one inflection point and subgroup B12a contained all the whistles in group B12 that contained inflection points. Whistles had relatively high mean frequency measurements (Table 2.4); four of the six whistles were >6.5 kHz and ranged up to 11.0 kHz.

Subgroup B12b contained four whistles, all classified as W3a (slightly ascending) and none had inflection points. The starting and ending frequency of all whistles

differed by about -0.5 kHz. Similar to subgroup B12a, mean frequency measurements were relatively high and ranged from 4.3-9.4 kHz.

Subgroup B12c contained 29 whistles and all but two whistles were flat contour types classified as W1a or W1b (W1b whistles were segmented). The other two whistles in this subgroup were classified as W2a (slightly ascending) and W3a (slightly descending). Subgroup B12c had the lowest mean frequency bandwidth of all the groups. Also, compared to the other two subgroups, B12c had lower mean frequency measurements (Table 2.4); the majority (23 of 29 or 79.3%) of whistles were 1.0-4.2 kHz.

2.5 DISCUSSION

2.5.1 Subjective classification

Determining biologically significant categories in a species' vocal repertoire is a difficult task, and particularly difficult in beluga because little investigation has been done on which call properties are perceived as important to them. The common method used to classify animal vocalizations is a human observer subjectively classifying calls into categories using aural and visual analysis of spectrograms. Detailed comparisons between studies can be difficult because of the subjectivity and because of the information often presented. For example, good representative spectrograms of call types are not always given; therefore, descriptions by the authors and some measurements are sometimes the only information provided. Also, sound descriptions

given by authors are subjective; calls described as 'screams' in two studies may differ in acoustic structure.

Similar to other beluga populations, calls described in this study form a graded continuum (Sjare and Smith 1986a; Karlsen et al. 2002); however, general trends in contour, sound, and some call measurements permitted classification of whistle, pulsed/noisy calls, and combined calls into different contour and call types. Beluga calls were classified into three main types similar to other beluga studies: 1) whistles (64.2% of total calls analyzed), 2) pulsed/noisy (25.9%), and 3) combined calls (9.9%). Proportions of the three main call types were similar to those found in other beluga populations in their summer ranges. In Svalbard, Norway, Karlsen et al. (2002) classified 62.6% of calls as whistles, 31.4% as pulsed/noisy calls, and 6.1% as combined calls. In Cunningham Inlet, Nunavut, 64.9% of calls were classified as whistles and 35.1% as pulsed/noisy calls, but no combined calls were described (Sjare and Smith 1986a). In Bristol Bay, Alaska, 57.2% of calls were classified as whistles, 42.1% as pulsed/noisy calls, and 0.7% combined (only one call type) (Angiel 1997). Faucher (1988) classified more than 50% of calls in St. Lawrence belugas as pulsed and noisy calls and did not describe any combined calls. The reason for the higher percentages of pulsed and noisy calls in St. Lawrence belugas compared to other studies is not known but could be due to differences in acoustic environment, behaviour states of belugas between areas, and/or distribution of the whales resulting in different call types being used for either shorter or longer range communication. Call type usage may vary in different behavioural contexts (Weilgart and Whitehead 1990; Thomsen et al. 2001) and in different beluga

distributions because pulsed and noisy calls are more suited to longer range communication than whistles especially compared to higher frequency whistles (Watkins et al. 1997; Janik 2000; Miller 2006).

2.5.1.1 Whistles

Whistles represented 64% of total calls analyzed suggesting that they are an important form of communication for beluga. Whistles are generally thought to be used in shorter range communication between conspecifics with proposed functions including group cohesion, group identification, and individual identification (Janik and Slater 1998; Riesch et al. 2006; Sayigh et al. 2007). Beluga whistles classified here do not form discrete categories as demonstrated by the variation (high standard deviations) within the subjective call types described. Similar variation and graded categories have been found in other beluga whistle classification (Sjare and Smith 1986a; Faucher 1988; Karlsen et al. 2002). Subjective classification focuses on call contour resulting in considerable variation in frequency parameters; however, contour is regarded as important in classifying calls and is most likely biologically significant. For example, in playback experiments to bottlenose dolphins, *Tursiops truncatus*, Ralston and Herman (1995) and Harley (2008) found dolphins discriminated calls based on contour rather than acoustic parameters.

Contour is also considered important because call parameters (frequency and duration) can be affected by the context in which the call is emitted and other variables.

Variation in frequency parameters has been found in signature whistles emitted by the same individual in different contexts (Janik et al. 1994). Call frequencies can be altered in response to background noise such as wind, boat noise, and other biological noises or to reduce detection by prey (Lesage et al. 1999; Foote and Nystuen 2008). For example, mean frequency of beluga calls in the St. Lawrence increased when boats were close (Lesage et al. 1999). Call duration may also increase in response to boat noise (Foote et al. 2004).

The six main whistle contour types described in Churchill River belugas were also produced by belugas in other locations. Sjare and Smith (1986a) and Faucher (1988) described a seventh contour type 'trills' not found in this study or by Karlsen et al. (2002) and Belikov and Bel'kovich (2007). It is possible, however that similar whistles to 'trills' were recorded but placed into a different category. In this study, call type W4e whistles ('chirps') were similar in sound description but did not appear to be similar in contour to 'trills'. Proportions of whistle contours found in this study were also similar to other studies with ascending and flat whistles being the most common but proportions of the less common whistle contour types differed among studies (Sjare and Smith 1986a; Karlsen et al. 2002; Hickey et al. 2009).

Further classification into whistle call types varied between beluga call studies. Twenty-two whistle call types were described in this study compared to 16 described by both Sjare and Smith (1986a) and Faucher (1988), 12 by Angiel (1997), ten by Karlsen et al. (2002), and 28 by Belikov and Bel'kovich (2006; 2007). Some whistle types found in other studies were not found in Churchill River belugas, and some call types found in

this study were not described in the other studies. Call types described by Sjare and Smith (1986a) and Faucher (1988) appear to be further divided in this study leading to a higher number whistle call types. For example, W2a and W2b (slightly ascending and ascending) whistles would likely be classified as one call type (CT2a, ascending) by Sjare and Smith (1986a) and Faucher (1988) and similarly W3a and W3b (slightly descending and descending) would be classified as one (CT3a, descending).

Frequency measurements varied within call types but similar to belugas in other areas (Sjare and Smith 1986a; Belikov 2006), the majority of whistles were emitted at relatively low frequencies (<5.0 kHz) although higher frequency whistles up to 22.0 kHz (the upper limit of the recording system) were also found. Belikov and Bel'kovich (2006) separated higher frequency whistles from lower frequency whistles recorded from White Sea beluga but noted that higher frequency whistles (>5.0 kHz) were rare. Low frequency whistles were also found in this study, 6.0% of whistles had a minimum frequency <0.5 kHz. Low frequency calls are common in baleen whales (Berchok et al. 2006; Baumgartner et al. 2008) but have also been recorded in belugas and bottlenose dolphins (Karlsen et al. 2002; van der Woude 2009).

2.5.1.2 Pulsed and noisy calls

In acoustic studies, pulsed and noisy calls have been less studied than whistles and information given in publications is variable. Researchers often provide less detailed information on classification because pulsed and noisy calls do not have a clear contour

where many frequency parameters can be measured. Pulsed and noisy calls are often described and classified based on sound and grouped into large categories with highly variable PRR (Sjare and Smith 1986a; Faucher 1988), making comparisons among studies difficult. However, some comparisons can be made with previous studies that included descriptions, some measurements, and representative spectrograms and at least some of the pulsed and noisy calls found in Churchill River belugas appear similar to calls in other areas (Angiel 1997; Sjare and Smith 1986a; Karlsen et al. 2002; Belikov and Bel'kovich 2008).

Echolocation clicks can be described by PRR and frequency properties but because of recording equipment limitations, detailed analysis was not possible. However, clicks similar in sound to echolocation clicks but with a smaller frequency bandwidth and within the limitations of the recording equipment were recorded (P4). Similar clicks with restricted frequency range were described by Sjare and Smith (1986a) and Faucher (1988). Both studies only provided average PRR, frequency measurements, and durations for three groups of pulsed calls and one group of noisy calls so further comparisons on call type and characteristic similarities were difficult. Call type 16 described by Angiel (1997) has a similar description to clicks of restricted frequency but had a much wider range of PRR (47 to 250 pulses/second) than found in this study. In contrast to echolocation clicks used primarily for navigation and prey detection (Akamatsu et al. 2005; Rutenko and Vishnyakov 2006; Au et al. 2009), narrowband clicks appear to have at least some communicative function (Watkins and Schevill 1971; Sjare and Smith 1986b).

Comparisons with pulsed calls described by Karlsen et al. (2002) were difficult given the information presented; however, calls such as 'creaks' and 'screams' were described similar to some calls described here. Belikov and Bel'kovich (2008) classified pulsed and noisy calls into three main categories: 1) pulsed tones with high repetition rates further classified into five types, 2) pulsed tones with low repetition rates further classified into seven types, and 3) noisy calls further classified into four types.

Classification was primarily based on frequency and time characteristics and PRR rather than sound so comparisons are difficult but two prominent call types recorded in the White Sea (low pulse repetition rate 1, IPT1, and low pulse repetition rate 2, IPT2) were not found in this study or in other beluga populations (Belikov and Bel'kovich 2008).

Angiel (1997) separated beluga pulsed calls into 11 categories. Call type 24 described by Angiel (1997) as a 'trumpet' sound corresponded well to P7 ('honk') described in this study. Both call types had similar PRR and appeared similar in representative spectrograms. Call type 25 described by Angiel (1997) as a 'creaking' sound corresponds to P2 ('creak') described in this study; both call types have a broad frequency bandwidth (frequency range) and similar PRR. Call type 26 may be similar to P1b (flat buzz clicks) or P1c (wavy buzz) as it was described as a 'buzzing' sound with some frequency modulation; also, frequency bandwidths and PRR of call types 26, P1b, and P1c were all similar (Angiel 1997).

Noisy calls are not well studied but have been described in other beluga populations (Sjare and Smith 1986a; Karlsen et al. 2002; Belikov and Bel'kovich 2008) and also in other animals (Mitchell et al. 2006). Both Sjare and Smith (1986a) and

Karlsen et al. (2002) grouped noisy calls into one large group but Belikov and Bel'kovich (2008) described four noisy call types. Two of the call types (Noisy call 2 and Noisy call 3) described by Belikov and Bel'kovich (2008) appeared to correspond to noisy call types described here (P13, thick bark, and P11, slightly ascending squeal, respectively); however, comparisons are difficult based on the information given and the nature of noisy calls having few measureable characteristics.

Pulsed and noisy calls have communicative properties in some animals but their function in belugas is largely unknown (Overstrom 1983; Lammers et al. 2003; Mitchell et al. 2006). Killer whales primarily use discrete pulsed calls in group identification (Ford 1989). Pulsed and noisy call types described in this study were generally more discrete than whistles with at least some call types having little variation in call measurements especially PRR. Therefore, it is possible that discrete beluga pulsed and noisy calls have important communicative function and may contain individual or group specific information and may be used as contact calls.

2.5.1.3 Combined calls

Two main types of combined calls were described in this study: 1) one call containing both a tonal and noisy component, and 2) two calls overlapping emitted by one individual. For the latter, calls were only included if the signal strength of both calls was similar and if two calls were emitted together in the same way on more than three

occasions on different days. This reduced the chance that the two calls were emitted by two individuals not one but this possibility cannot be discounted completely.

Karlsen et al. (2002) separated combined calls into six categories, most of which fell into the category in which one call contains both a whistle and pulsed or noisy component. The description of call type D by Karlsen et al. (2002) corresponded to C1 (whistle with noisy component at end) and call type C corresponds to C2 (whistle with noisy component at beginning). However, both call types in Karlsen et al. (2002) were higher frequency and slightly shorter duration than call types described here. Angiel (1997) also described a similar call type to C1. Similar calls to the second most common combined call type in this study, C6 (wavy honk with higher component) which had a very distinct 'laughing' sound, were not described in other beluga populations.

Some combined calls described in this study appeared to be variations on pulsed or noisy calls. C1, C2, and C3 were whistles with the addition of a noisy component. Also, pulsed or noisy components of C4 (honk with higher whistle), C5 (thick creak with high whistle), and C7 (ascending then flat screech with lower flat whistle) were similar to pulsed or noisy calls described but with the addition of a whistle. For example, the pulsed call in C4 and P7 sound similar (both were described as honks) and had similar PRR, minimum and maximum frequencies, frequency bandwidths, and durations. But C4 contained a higher frequency whistle of similar duration to the honk component. In C7, the noisy call sounds similar to P9 (both were described as 'screeches') but differed somewhat in contour, frequency parameters, and duration and C7 also contained a lower flat whistle. C7 calls were only emitted four times (0.6% of total calls) but with

little variation and was the only combined call where the pulsed component was emitted at a higher frequency than the whistle component.

Combined call type C5 also appeared to be a variation of a pulsed call. It had a very distinct 'creaking' sound similar to P2. Both had similar PRR and frequency measurements with almost identical durations. C5 calls also contained higher shorter whistles, most of which were flat. C5 calls appeared very similar to a contact call emitted between a captive beluga mother and her calf, recorded and described by Vergara and Barrett-Lennard (2008). When C5 calls were recorded in the Churchill River often at least one mother and calf pair was observed; therefore, it is possible that C5 calls serve as a contact call between mothers and calves in the Churchill River as well. However, additional research is required to confirm this. Of note, the mother of the captive beluga calf recorded at the Vancouver aquarium was a wild beluga captured from the Churchill River in 1990 (Vergara and Barrett-Lennard 2008).

The phenomenon of two calls being emitted simultaneously by one individual has been found in odontocetes and birds (Ford 1989; Murray et al. 1998; Aubin et al. 2000; Karlsen et al. 2002, Filatova et al. 2009; Krakauer et al. 2009) but their function is not completely known. In penguins, two-voice calls are thought to be used to recognise individuals (Aubin et al. 2000). Proposed functions for killer whales are based on the idea that two calls can provide more information about the individual calling and increase the chance a call is recognized (Miller 2002; Filatova et al. 2009). More specifically, (Miller 2002) proposed a function based on the mixed-directionality of the call; the lower frequency component is omnidirectional (transmitted in all directions)

and the higher frequency component is highly directional. The higher component can therefore provide information on the direction of movement of the caller and indicate its orientation to the listener; this can be used to synchronize movements or maintain contact between individuals (Miller 2002). As discussed above, pulsed call type P2 and combined call type C5 sound similar and had similar call properties; both may serve as contact calls between individuals (specifically mother and calves) and the higher whistle in C5 may relay information about orientation of the caller to the listener (mother to calf or vice versa).

2.5.2 Cluster analysis

Most objective classification methods or automated classification systems have been generally confined to whistles where the contour can adequately describe the call and measurements can be made. Hierarchical clustering was used in this study to group whistles more objectively than the above subjective classification. Studies comparing subjective and objective classification have obtained varying results (Angiel 1997; Nowicki and Nelson 1990; Deecke et al. 1999; Janik 1999; Karlsen et al. 2002). The two methods often do not agree in part because subjective classification generally focuses on call contour while at least some characteristics used in more objective methods represent absolute frequencies and not call contour. Automated classification systems have had more success with stereotyped calls because by definition calls within each

stereotyped call type have similar call properties with little variation (Deecke and Janik 2006).

Some disagreement existed between the subjective categories and the hierarchical clustering in this study and clustered groups' measurements varied less than the subjective groups'. Cluster analysis may however, miss some important features and subtle differences in call contours not readily captured in measurements but which human observers would see or hear. For example, W2a whistles (slightly ascending) and W2c whistles (ascending then flat) emitted at the same frequency would have almost identical measured characteristics but different contours; therefore, they would likely be separated by a human observer but grouped together in more objective methods. This was evident in the UPGMA cluster analysis; in group B11 all calls were classified as either W2a or W2c (17 and 13, respectively). In the subjective classification, W2a and W2c whistles were classified as different call types because contour and sound differed. Cluster analysis is confined to using measurements that may not adequately describe all call types and results are affected by which parameters are used.

Hierarchical clustering represented the larger contour whistle types (flat, ascending, descending, hump, dip, and wavy) adequately by placing the majority of whistles (78.5%) into a cluster with whistles of the same subjective contour types described here. Clusters A and B separated complex whistles from more simple whistles; cluster A contained whistles with more inflection points and consisted of most of the W6, wavy, whistles (85.0%).

Some differences between subjective and objective call classification in this study have logical explanations and are important to consider in future studies. More inflection points in some W1c (mostly flat) whistles resulted in clustering with wavy calls. Even though W1c whistles generally had a flat call contour (low frequency bandwidth) and were subjectively classified as such, other call properties were similar to some wavy calls. W1c whistles were most similar to W6a whistles (small waves) because frequency bandwidths of W6a whistles were relatively small compared to other wavy whistles. Therefore, some W1c whistles may be more closely related to W6a than the subjective classification implies. These results provide further evidence that a continuum exists within beluga vocalizations.

Hierarchical cluster analyses may, however, have some application to graded vocalizations by classifying sounds on different levels based on relatedness. The general trend from most to least similar appeared to be represented well in the cluster analysis. Cluster B contained ascending and flat whistles (simple whistles) clustered together and were furthest from the most complex, wavy whistles (cluster A). Cluster B also contained hump and dip whistles (similar and intermediate in complexity) clustered together. Some of the disagreement with subjective categories can be explained by the use of starting and ending frequency as variables which adds absolute frequency measures not taken into account in subjective classification. Belikov and Bel'kovich (2006; 2007) noted that White Sea belugas show a bimodal distribution of whistles with a band around 5 kHz where no whistles were emitted. Therefore, absolute frequency may be important in some beluga populations. While a bimodal distribution was not

observed in this study, it highlights the importance of considering absolute frequency measures in classification.

Statistical measures have the advantage of being objective and repeatable making it possible to compare results between studies and geographic areas. Objective methods can also handle large datasets more efficiently than human observers. However, the lack of a standard set of measurements used in objective analyses still makes it difficult to compare among studies. Also, objective classification may not always be the most meaningful since only call properties are considered with no information on how calls are received (Deecke et al. 1999). Without knowing how belugas perceive calls it is difficult to determine which call properties are biologically important. Playback experiments have been used in some species to obtain information on call perception to determine which call properties are important (Ralston and Herman 1995; Rendall et al. 1999; Soltis et al. 2002; marine mammal review by Deecke 2006). More research on beluga call perception is required to determine which call properties should be included in a standard set of measurements. Knowledge of which characteristics are perceived as important to belugas will allow for more biologically relevant call classification and improved comparisons among studies.

2.5.3 Conclusions

In summary, calls produced by Churchill River belugas appear to be similar to calls recorded in other areas, although some different calls were also described. The

more objective approach using hierarchical clustering showed similarities in call classification to the subjective approach but also revealed some important differences. Information on call types can be used to improve automated classification and detection of beluga calls. More detailed investigation of beluga calls within categories and additional research on call perception will also aid in categorizing whistles into more discrete categories based on acoustic properties that are biologically relevant.

This study provided the first description of beluga calls and call characteristics in Hudson Bay required as baseline understanding for future research investigating context-specific calls and call function. For example, proportion of the whistle contours emitted during different behavioural contexts has been studied in some odontocete species (Sjare and Smith 1986b; Weilgart and Whitehead 1990; dos Santos et al. 2005; Azevedo et al. 2010; Hawkins and Gartside 2010) and can be investigated further in belugas (see Chapter 3). Descriptions of call types can also be used to direct future studies on context of specific calls. For example, as mentioned previously call type C5 is similar to a contact call used by a captive beluga mother to its calf (Vergara and Barrett-Lennard 2008) but more detailed contextual observations need to be done to confirm C5 has a similar function in wild Churchill River belugas.

Beluga acoustic studies in the Hudson Bay region are particularly important because of predicted ecosystem changes. First, reduction of sea ice in Hudson Bay will increase marine vessel traffic, creating a noisier environment. Animals sometimes alter frequency and/or duration of calls in response to increased background noise potentially affecting their communication success (Lesage et al. 1999; Miller et al. 2000;

Foote et al. 2004; Nemeth and Brumm 2009). Second, a recent increase in killer whale sightings in Hudson Bay (Higdon and Ferguson 2009) may also have an effect on belugas. Killer whales are a predator of belugas and can have an effect on the acoustic behaviour of their prey (Campbell et al. 1988; Morisaka and Connor 2007). Beluga call types and call characteristics described in this study can be used in future studies monitoring effects of increased noise and killer whale sightings.

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**CHAPTER 3: Beluga whale, *Delphinapterus leucas*, vocalizations
produced during different behaviours in the Churchill River, Manitoba, Canada**

3.1 ABSTRACT

Documenting the context in which animal calls are produced can be very difficult but is important in determining what information is conveyed in calls and understanding social interactions. Beluga whales, *Delphinapterus leucas*, are a small odontocete (toothed whale) species that are very social and extremely vocal. The purpose of this study was to describe beluga call types and call characteristics associated with different behaviours in the Churchill River, Manitoba from recordings collected from 9-27 July, 2007. Beluga calls (n=265) were analyzed: 67 during social interactions, 60 during travelling, 67 during feeding, and 71 during interactions with the boat. Percentages of call types (whistle and pulsed/noisy calls) differed among behaviours ($\chi^2 = 9.36$, $df = 3$, $p = 0.02$). The highest percentage of whistles was produced during feeding and the highest percentage of pulsed/noisy calls during travelling. The relative proportions of whistle contour types (flat, ascending, descending, hump, dip, and wavy) and some call characteristics including average whistle frequency (Kruskal-Wallis = 12.616, $df = 3$, $p = 0.006$) and call duration (Kruskal-Wallis = 18.363, $df = 3$, $p = 0.0004$) also varied with behaviour. Generally, higher percentages of whistles, more broadband pulsed and noisy calls, and shorter calls (<0.49s) were produced during behaviours associated with higher

levels of activity and/or apparent arousal (social interactions, feeding, and interactions with the boat) versus calls produced during travelling. More whistles were emitted at higher frequencies (≥ 5.0 kHz) during feeding and interactions with the boat and more complex whistles (defined by number of inflection points) were produced during social interactions and feeding. Associations between calls and behaviour in belugas were found and information obtained here establishes a basis for studying the information content and function of specific beluga calls.

3.2 INTRODUCTION

Vocal communication is an important form of communication for many animals so investigating vocalizations is important in studying social dynamics and interactions between individuals. Central to understanding vocal communication between animals is the investigation of a species' repertoire and the contexts in which calls are used (e.g. Ford 1991; Armstrong 1992; reviewed by Seyfarth and Cheney 2003). In social terrestrial and aquatic animals, acoustic behaviour has been investigated in contexts such as response to predators (e.g. Coss et al. 2007; Greig and Pruett-Jones 2009), spatial coordination (e.g. Bionski 1991), maintaining contact between individuals (e.g. Fischer et al. 2001; Ramos- Fernández 2005), behavioural states (e.g. Rendall 2003), mating and reproduction (e.g. Poole et al. 1988; Manno et al. 2007), and emotional state of caller (e.g. Soltis et al. 2002; Rendall 2003). In animals that communicate over long distances or live in environments where visual cues are limited, call types and properties, and contextual use have been the focus of studies (Weilgart 1985; Poole et al. 1988; Ford

1989; McComb et al. 2003; Mitchell et al. 2006). Call usage, types, and structure including frequency measurements and duration can vary with context suggesting that call characteristics are important features in determining call meaning and function (Rendall et al. 1999; Soltis et al. 2002; Rendall 2003; Bazúa-Durán and Au 2004; Mitchell et al. 2006).

Documenting the context in which calls are produced and behaviours associated with call production can be very difficult especially in whales where the majority of behaviours are underwater, and therefore cannot be easily observed at the surface. Few behavioural context studies on whale calls compare specific call parameters, such as frequency measurements and duration, but rather focus on comparing call rates (number of calls per individual) or call types between behaviours observed at the surface (Sjare and Smith 1986a; Weilgart and Whitehead 1990; dos Santos et al. 2005; Hawkins and Gartside 2010). Call types described in odontocete (toothed whale) species include: 1) whistles, 2) pulsed tones and noisy calls, 3) echolocation clicks, and 4) combined calls (Sjare & Smith 1986a; Ford 1989; van Parijs et al. 2000; Karlsen et al. 2002; Boisseau 2005).

Whistles are tonal sounds widely used in communication between conspecifics and their structure is more suited to shorter range communication (Ford 1989; Janik 2000a; Thomsen et al. 2002; Riesch et al. 2006). Possible functions include use as individual signatures and/or contact calls, coordination of movements, or to provide information on the motivational state of the caller (Caldwell and Caldwell 1965; Weilgart and Whitehead 1990; Thomsen et al. 2001; Thomsen et al. 2002; Riesch et al.

2006; Sayigh et al. 2007; Hawkins and Gartside 2010). Pulsed calls are made up of a series of pulsed tones and pulsed and noisy calls are often more broadband (larger frequency range) than whistles. The functional significance of pulsed and noisy calls is not well understood but it has been suggested that they have communicative functions especially in agonistic interactions and longer range communication (Overstrom 1983; Lammers et al. 2003; Mitchell et al. 2006). Combined calls include two components: either one call that contains both a whistle and noisy or pulsed component or two calls overlapping emitted by one individual. Combined calls have been described in some odontocete species such as belugas, *Delphinapterus leucas*, and killer whales, *Orcinus orca*, and some birds (Aubin et al. 2000; Karlsen et al. 2002; Filatova et al. 2009; Krakauer et al. 2009), but their function is poorly understood.

Beluga whales have a circumpolar distribution in Arctic and sub-Arctic waters and are a small odontocete species that are very social and extremely vocal. Beluga vocal repertoires have been studied in some geographic areas (Sjare & Smith 1986a; Faucher 1988; Angiel 1997; Karlsen et al. 2002; Belikov and Bel'kovich 2007). Calls have been described as more of a continuum but similar to other odontocetes can be separated into four main types: 1) whistles, 2) pulsed tones and noisy calls, 3) echolocation clicks, and 4) combined calls (Sjare & Smith 1986a; Karlsen et al. 2002; Belikov and Bel'kovich 2007; 2008).

Beluga calls have also been studied in relation to behaviours such as social interactions, resting, milling, joining of groups, travelling, sexual behaviour, interactions with boats, alarm response, and disturbance by humans (Sjare and Smith 1986a;

Faucher 1988; Karlsen et al. 2002; Belikov and Bel'kovich 2003). Differences in levels of activity and apparent arousal as well as degree of coordination among individuals associated with behaviours can affect acoustic behaviour and call structure (Sjare and Smith 1986a; Weilgart and Whitehead 1990; Fichtel and Hammerschmidt 2002; Rendall 2003; Soltis et al. 2005; Schehka and Zimmermann 2009). Behaviours such as feeding and social interactions are highly active (Karlsen et al. 2002; Weilgart and Whitehead 1990; Hawkins and Gartside 2010) while interactive behaviours (social, sexual, and with boats) may be associated with high arousal levels (Ford 1989; Sjare and Smith 1986a; Hawkins and Gartside 2009a). Some behaviours, including feeding, social interactions, and travelling, also require at least some degree of coordination among individuals (Weilgart and Whitehead 1990; Similä and Ugarte 1993; Quick and Janik 2008; Hawkins and Gartside 2009a). Behaviours such as resting and milling are associated with relatively low activity (slow swimming), low arousal levels (little to no interactions), and often a low degree of coordination among individuals (Sjare and Smith 1986a; Weilgart and Whitehead 1990; Karlsen et al. 2002; Hawkins and Gartside 2010). Limited conclusions, however, have been established on the relationships between specific beluga sounds and behaviours. Therefore, meaning and function of beluga calls are still poorly understood.

In Hudson Bay, groups of belugas aggregate in the summer in river mouths and estuaries with telemetry results indicating that most Hudson Bay belugas winter in Hudson Strait and southwest Davis Strait (Richard et al. 1990; Smith 2007; Lewis et al. 2009). Three stocks have been identified in Hudson Bay: 1) western Hudson Bay where

the Churchill River, Manitoba, study site for this study is located, 2) eastern Hudson Bay, and 3) James Bay (de March and Postma 2003). The purpose of this study was to compare calls produced in association with different beluga behaviours observed in the Churchill River, Manitoba, from recordings collected in July 2007. Call types and characteristics produced during social interactions, travelling, feeding, and interactions with the boat were compared. This was the first description of calls in relation to behaviours in Hudson Bay belugas and established a basis for studying more specific call meaning and function.

3.3 METHODS

3.3.1 Study area

Data were collected from 9-24 July, 2007 in the Churchill River and Churchill River Estuary which opens into Hudson Bay (58° 45'N; 94° 4'W) near the town of Churchill, Manitoba (Figure 3.1). Belugas aggregate in this area during the ice free season from late June until early September with peak numbers from mid-July to mid-August (Hansen et al. 1988; Idle 1989). Belugas in this area are part of the western Hudson Bay stock, estimated at 57,300 whales, making it one of the largest beluga populations in the world (Richard 2005). Different age classes (adults, juveniles, and calves) of belugas move in and out of the river generally with the tides but can be observed in the river at any time (Idle 1989; personal observation).

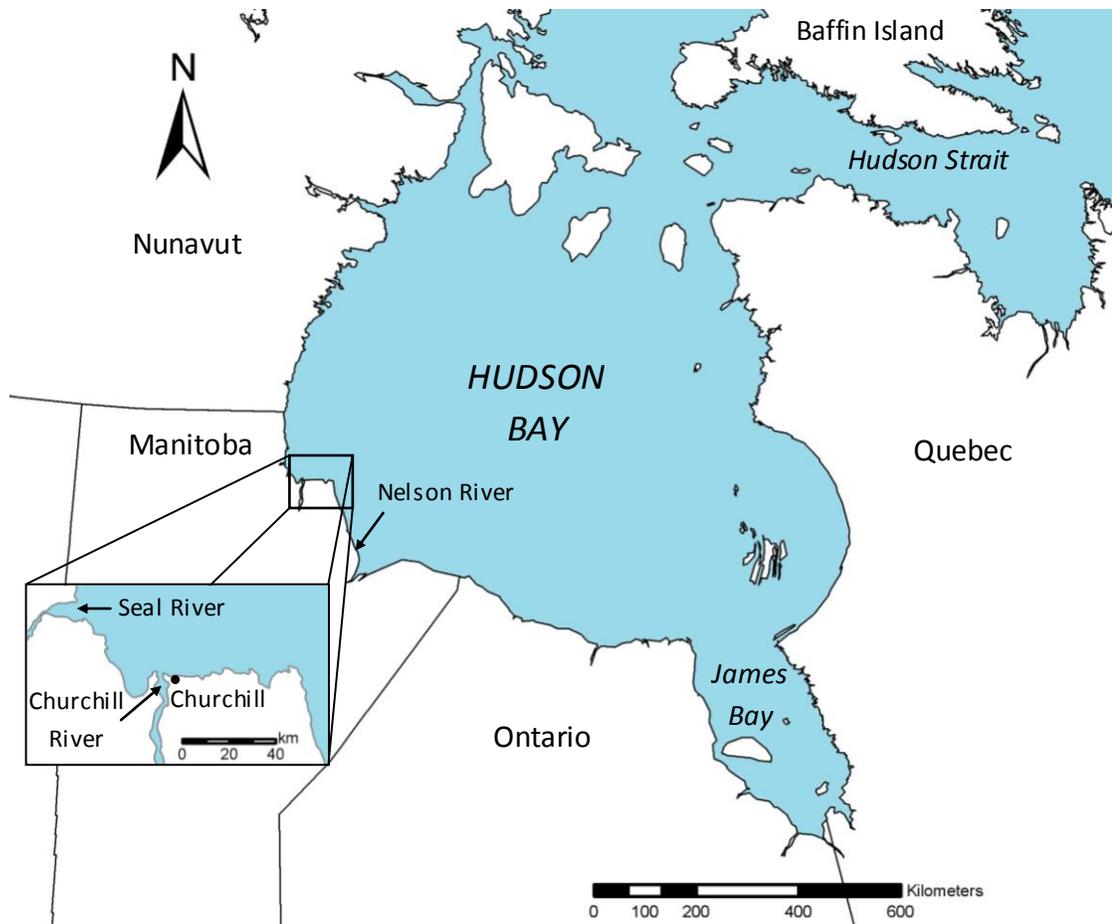


Figure 3.1: Map of study area: community of Churchill, Churchill River, Churchill River Estuary, and Hudson Bay.

3.3.2 Data collection

3.3.2.1 Sound recordings

Sound recordings were collected using a portable hydrophone system from a small boat, usually a 4.2 meter Zodiac and sometimes a 4.8 meter aluminum motor boat. To reduce background noise, the engine was turned off during recording sessions. Belugas were generally seen in small groups (5-10) but sometimes in larger groups (up to ~50). Recordings were collected when whales were within 50m, but sometimes closer than 20m when whales approached the boat. Recordings were collected using a High Tech, Inc. hydrophone (Gulfport, Mississippi, USA, model HTI-96-MIN; sensitivity: -165 dB, flat frequency response from 5 Hz to 30 KHz \pm 1.0 dB) and a Marantz PMD 660 digital recorder (16 Hz to 22 kHz -0.5 dB, 44.1 KHz sampling rate). The hydrophone was lowered down the side of the boat to a depth of 5-10 meters and beluga behaviours, approximate number of beluga in the area and within 20m of the boat, and number of juveniles and calves (determined by grey colouration and size) were noted during recordings.

3.3.2.2 Behaviours

Seven beluga behaviours were observed: social interactions, travelling, feeding, interactions with the boat, milling, and resting. Social interactions referred to two or more belugas in body contact including touching flukes or flippers or rolling together

and were sometimes accompanied by splashing (Sjare and Smith 1986a; Faucher 1988). Whales were considered travelling when swimming in a consistent direction at regular surfacing intervals often coordinated between group members. Feeding was indicated when whales in an area were engaged in non-directed swimming (whales facing different directions when surfacing) and mostly shallow dives (indicated by short dives <1.0 min). Capelin, *Mallotus villosus*, or parts of capelin, an important part of Hudson Bay beluga diet (Kelley et al. 2010), were often visible at the surface and Arctic terns, *Sterna paradisaea*, were often seen diving into the water to take fish. Similar beluga feeding behaviour was described by Watts and Draper (1986). Interactions with the boat were defined as whales that changed direction to approach the boat within 15m, often passing under the boat. Belugas interacting with the boat for a sustained period engaged in behaviours such as blowing bubbles, biting the hydrophone, and/or turning upside down underneath the boat facing up towards the boat. Similar interactions with the boat were described by Faucher (1988) and Hawkins and Gartside (2009b). Milling was defined as whales swimming and orienting in different directions with little to no directed or coordinated movements (Faucher 1988; Karlsen et al. 2002). Finally, resting was defined as whales bobbing at or near the surface with little to no directed movement (Sjare and Smith 1986a).

3.3.3 Analysis

Recordings analysed were limited to segments in which the majority (>60%) of whales within acoustic range were involved in one of the behaviours described above.

While milling and resting were observed on occasion, whales were rarely engaged in either behaviour. Whales were also never observed resting over a long period of time (>30 min) as was observed by Sjare and Smith (1986a) in Cunningham Inlet beluga.

Milling and resting were therefore not included in further analysis.

Calls for feeding belugas were extracted from two 10-minute segments, one from each of July 10 and 16. Calls for interactions with the boat were extracted from 9, 3, and 10-minute segments from July 10, 12, and 18, respectively. Calls for travelling were extracted from three 10-minute segments, one from each of July 12, 14, and 19. Calls for social interactions were extracted from two 10-minute segments, one from each of July 16 and 18.

First, by simultaneously listening and visually scrolling through spectrograms in Adobe® Audition® 2.0 (FFT size of 256) all calls except echolocation clicks were isolated from recording segments. Because of recording equipment limitations, detailed analysis of echolocation was not possible; the recording system was limited to frequencies below 22 kHz but beluga broadband clicks can have a frequency spectrum of 100 Hz to 120 kHz and peak frequencies at 40 kHz and above (Gurevich and Evans 1976; Au et al. 1985). Each extracted call was then graded qualitatively on a scale of 1-5 based on sound quality (the amount of background noise or overlapping calls) (modified from Faucher 1988; Deecke 2003): 1 = very high signal-to-noise-ratio (call was clear: no background noise or overlapping calls), 2 = high signal-to-noise-ratio (call was relatively clear: minor background noise or slightly overlapping calls), 3 = moderate signal-to-noise-ratio (call was less clear: relatively faint with some background noise or overlap),

4 = low signal-to-noise-ratio (call was not clear: relatively faint with background noise or overlapping calls), and 5 = very low signal-to-noise-ratio (call was not clear: either faint and/or too much background noise or overlap to measure call properties). Lower quality recordings (graded 4 and 5) were not used in further analysis.

Beluga calls (n=265) were extracted: 67 during social interactions, 60 during travelling, 67 during feeding, and 71 during interactions with the boat. Calls were first separated into three main types based on previous descriptions: 1) whistles, 2) pulsed/noisy calls, and 3) combined calls. Chi-square analysis tested for differences in the proportion of call types within each behaviour (combined calls were excluded from the test due to low sample sizes).

Whistles were then further classified into six whistle contour types: W1 = flat, W2 = ascending, W3 = descending, W4 = hump, W5 = dip, and W6 = wavy (see Figure 2.2). A frequency distribution compared relative proportions of whistle contour between behaviours. Call type W1, W2, and W3 whistles can be described as simple contour types containing few or no inflection points (changes in slope from positive to negative or negative to positive) and call type W4, W5, and W6 whistles can be described as more complex having at least one but often more inflection points (Chapter 2; Weilgart and Whitehead 1990). A frequency distribution also compared percentages of simple and complex whistle contours between behaviours.

Call properties were obtained visually or using Raven 1.3 functions viewed in a Hann window with an FFT size of 512 and a 50% overlap (Cornell Lab of Ornithology, Bioacoustics Research Group, Cornell University, Ithaca, New York). Measurements

obtained from the fundamental frequency for each whistle were based on Sjare and Smith (1986b) and Baron et al. (2008) and included: 1) starting frequency, 2) ending frequency, 3) minimum frequency, 4) maximum frequency, 5) frequency bandwidth (range), 6) duration, and 7) number of inflection points.

Because average frequency (average of low and high frequency) distribution did not fit the assumption of normality, a non-parametric Kruskal-Wallis test was conducted to compare average frequency between behaviours. The Kruskal-Wallis test was performed in MYSTAT® version 12.02 (a student version of SYSTAT®). A frequency distribution compared percentages of average whistle frequency produced during different behaviours in ranges defined as: very low frequencies (<1.0 kHz), low frequencies (1.0-4.9 kHz), intermediate frequencies (5.0-9.9 kHz), and relatively high frequencies (≥ 10.0 kHz).

Distribution of call durations also did not fit the assumption of normality so a Kruskal-Wallis test was conducted in MYSTAT® to compare call durations among behaviours. A frequency distribution also compared percentages of calls produced during behaviours in ranges defined as: <0.20s, 0.20 to 0.49s, 0.50 to 0.99s, 1.00 to 1.49s, 1.50 to 1.99s, and ≥ 2.00 s.

Because of the small sample size, pulsed and noisy calls were separated only into calls where the pulse repetition rate (PRR) could be measured (pulsed) and could not (noise or noisy) (Sjare and Smith 1986b). PRR was determined by harmonic interval and measured in pulses per second (Watkins 1967). Measurements for each pulsed and noisy call were also obtained visually or using Raven 1.3 functions based on

characteristics described by Sjare and Smith (1986b): 1) minimum frequency, 2) maximum frequency, 3) frequency bandwidth, 4) duration, and 5) PRR (where applicable). Combined calls were not further classified and no measurements were taken due to the small sample size.

3.4 RESULTS

3.4.1 Call Types

Whistles were the dominant call type in all behaviours, followed by pulsed/noisy calls then combined calls, which were uncommon (Table 3.1). Percentages of whistles and pulsed/noisy calls differed among behaviours ($\chi^2 = 9.36$, $df = 3$, $p = 0.02$). Whistle percentage was highest during feeding, then interactions with the boat, social interactions, and finally, travelling (Table 3.1). Pulsed/noisy calls percentage was highest during travelling, then interactions with the boat, social interactions, and finally, feeding (Table 3.1). Combined calls were uncommon but percentage was highest during social interactions, then travelling, and finally, interactions with the boat with none produced during feeding (Table 3.1).

3.4.2 Whistles

Contour types

Relative proportions of whistle contour types varied between behaviours (Figure 3.2). Ascending whistles (W2) were the most common contour type during social

Table 3.1: Number and percentage of whistles, pulsed/noisy calls, and combined calls emitted by beluga during four behavioural states in the Churchill River, Manitoba.

Call Type	Social interactions	Travelling	Feeding	Interactions with the boat
whistles	49 (73.1%)	38 (63.3%)	57 (85.1%)	52 (73.2%)
pulsed/noisy	14 (20.9%)	19 (31.7%)	10 (14.9%)	16 (22.5%)
combined	4 (6.0%)	3 (5.0%)	0 (0%)	3 (4.2%)
TOTAL	67 (100%)	60 (100%)	67 (100%)	71 (100%)

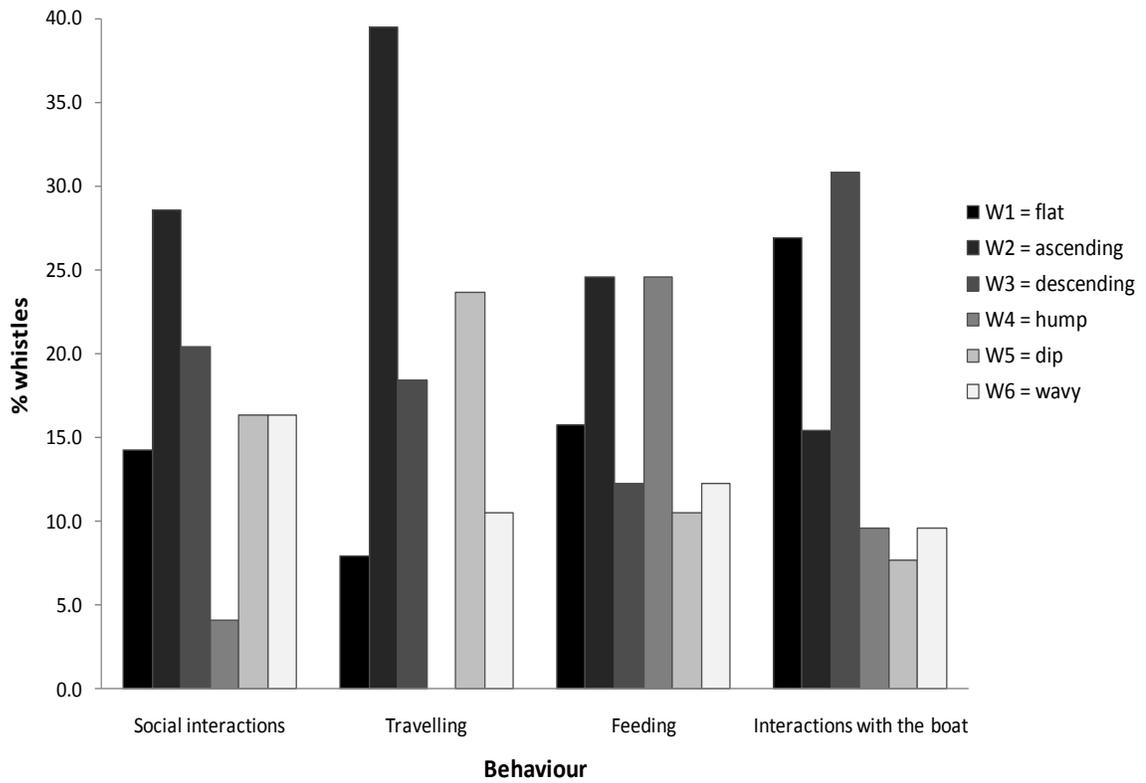


Figure 3.2: Percentages of whistle contour types (W1,W2,W3,W4,W5, and W6) emitted by belugas in the Churchill River, Manitoba during four different behaviours.

interactions and travelling and the second most common during feeding. Hump whistles (W4) were the most common contour type during feeding but the least common during social interactions and travelling; during the latter no hump whistles were found (Figure 3.2). Descending whistles (W3) were the most common contour type during interactions with the boat and the second most common during social interactions. Along with W2 and W3 whistles, social interactions were also associated with relatively high percentages of flat (W1) and wavy (W6) whistles (Figure 3.2). W1 whistles were the second most common contour type during interactions with the boat and dip whistles (W5) were the second most common contour type during travelling and the least common during feeding and interactions with the boat (Figure 3.2).

Social interactions, travelling, and interactions with the boat were associated with comparable percentages of simple (W1, W2, and W3) and complex whistles (W4, W5, and W6) with the majority of whistles being simple (Figure 3.3; 63.3%, 65.8%, and 73.1%, respectively). During feeding, simple and complex whistles were produced in similar percentages (Figure 3.3).

Call parameters

Whistles produced during interactions with the boat had the highest mean start, end, minimum, and maximum frequencies, followed by feeding but all behaviours had whistles with similar mean frequency bandwidths (1.3-1.8) (Table 3.2). High mean durations were found in whistles produced during travelling and interactions with the

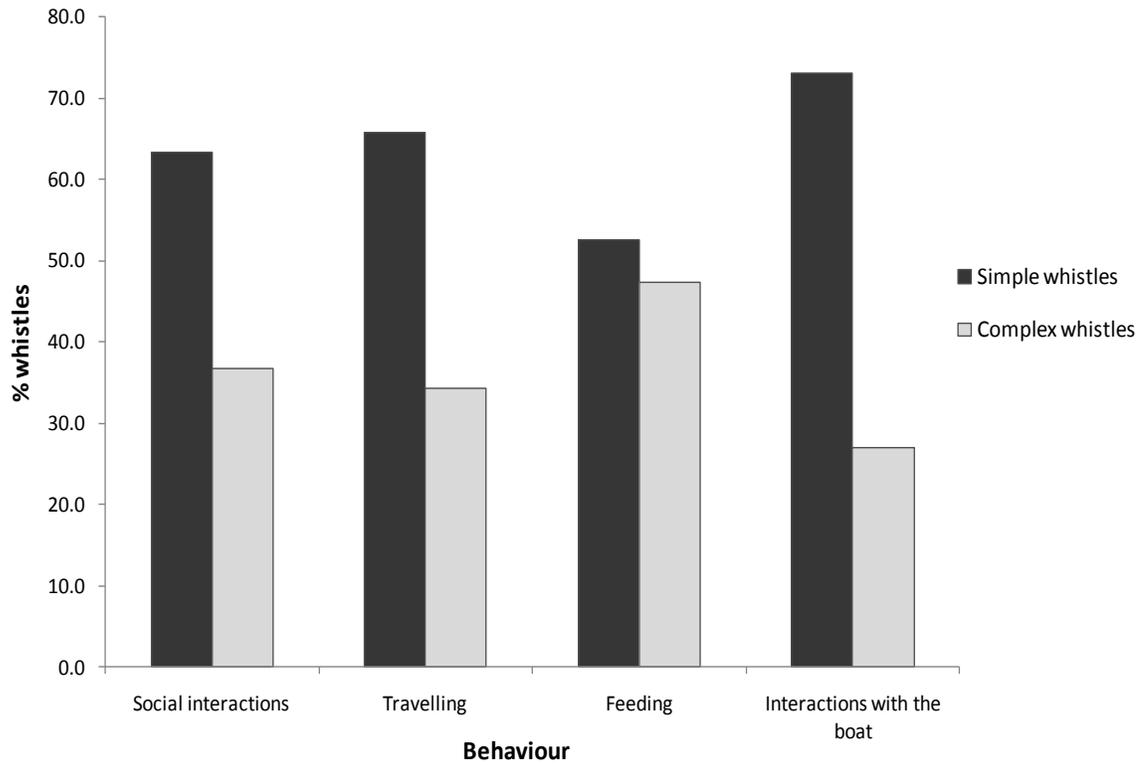


Figure 3.3: Percentages of simple whistle contour types (W1 = flat, W2 = ascending, W3 = descending) and complex contour types (W4 = hump, W5 = dip, W6 = wavy) emitted by belugas in the Churchill River, Manitoba during four different behaviours.

Table 3.2: Descriptive statistics of whistles (mean \pm standard deviation) emitted by beluga during four behavioural states in the Churchill River, Manitoba.

Call measurements	Social interactions (n=49)	Travelling (n=38)	Feeding (n=57)	Interactions with the boat (n=52)
Start frequency (kHz)	3.8 \pm 3.2	4.1 \pm 3.6	4.8 \pm 3.2	5.9 \pm 4.3
Min frequency (kHz)	4.4 \pm 4.1	4.6 \pm 4.8	5.1 \pm 3.1	5.8 \pm 4.6
Max frequency (kHz)	3.2 \pm 3.3	3.4 \pm 3.5	4.4 \pm 2.9	5.1 \pm 4.2
High frequency (kHz)	5.0 \pm 4.1	5.1 \pm 4.7	5.7 \pm 3.1	6.6 \pm 4.7
Freq Bandwidth (kHz)	1.8 \pm 1.5	1.7 \pm 1.6	1.3 \pm 1.0	1.4 \pm 1.3
Duration (sec)	0.58 \pm 0.38	0.75 \pm 0.46	0.60 \pm 0.58	0.76 \pm 0.55
# of inflection points	3.0 \pm 5.9	1.8 \pm 3.0	3.0 \pm 7.6	1.3 \pm 3.9

boat and whistles produced during social interactions and feeding had the highest mean number of inflection points (Table 3.2).

Distribution of average whistle frequency differed among behaviours (Figure 3.4; Kruskal-Wallis = 12.616, $df = 3$, $p = 0.006$). A relatively high percentage of whistles produced during all behaviours were 1.0-4.9 kHz (46.2 to 65.8%) with the vast majority of whistles during social interactions and travelling <4.9 kHz (79.6% and 73.7%, respectively) (Figure 3.4). During feeding and interactions with the boat, about half of the whistles were ≥ 5.0 kHz (42.1% and 51.9%, respectively) and a relatively high number were 5.0-9.9 kHz (36.8% and 32.7%, respectively). The highest percentage of whistles ≥ 10.0 kHz were produced during interactions with the boat (19.2%) (Figure 3.4).

3.4.3 Call duration

Call duration varied among behaviours (Figure 3.5; Kruskal-Wallis = 18.363, $df = 3$, $p = 0.0004$). A relatively high percentage of calls were 0.20-0.49s during social interactions (39.7%), feeding (46.3%), and interactions with the boat (36.8%) and a relatively high percentage of calls were 0.50-0.99s during travelling (47.4%) (Figure 3.5). The majority of calls during all behaviours were <1.00s (71.9-86.6%). All behaviours were also associated with a relatively small percentage of very short (<0.20s) and long calls (≥ 1.50 s) (Figure 3.5).

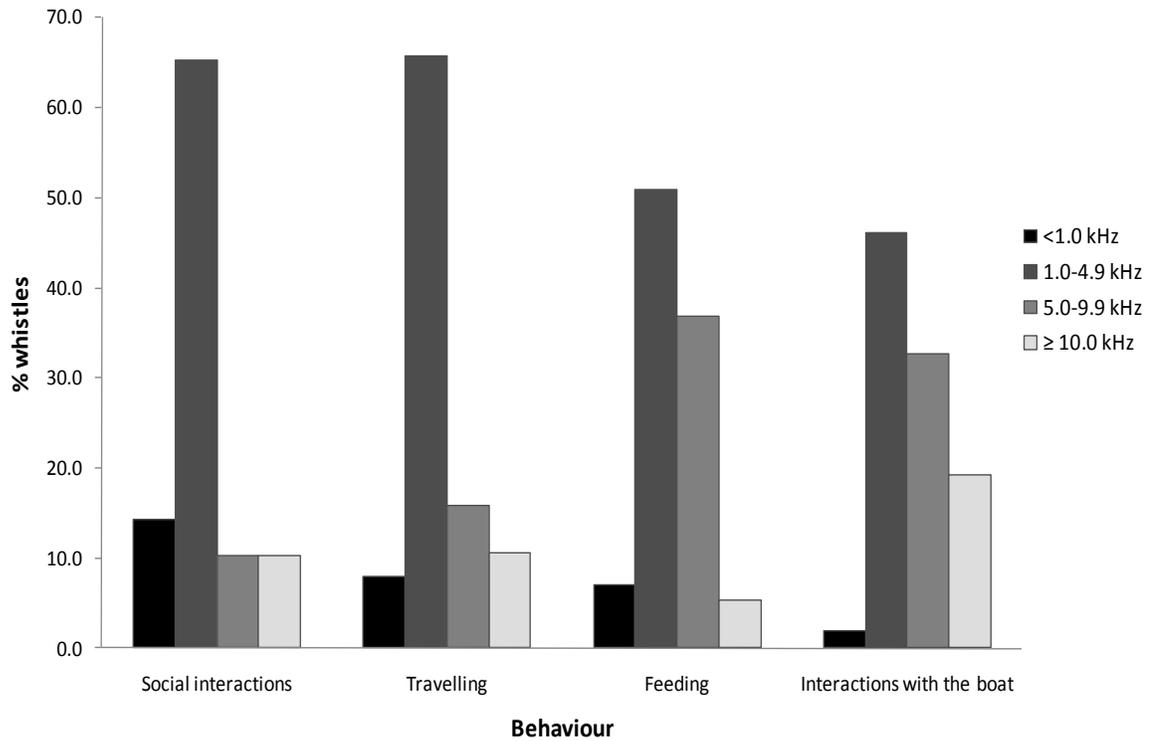


Figure 3.4: Percentages of whistles emitted by belugas in the Churchill River, Manitoba during four behavioural states in frequency ranges defined as: very low frequency = <1.0kHz, low frequency = 1.0-4.9 kHz, intermediate frequency = 5.0-9.9 kHz, and relatively high frequency = ≥10.0 kHz.

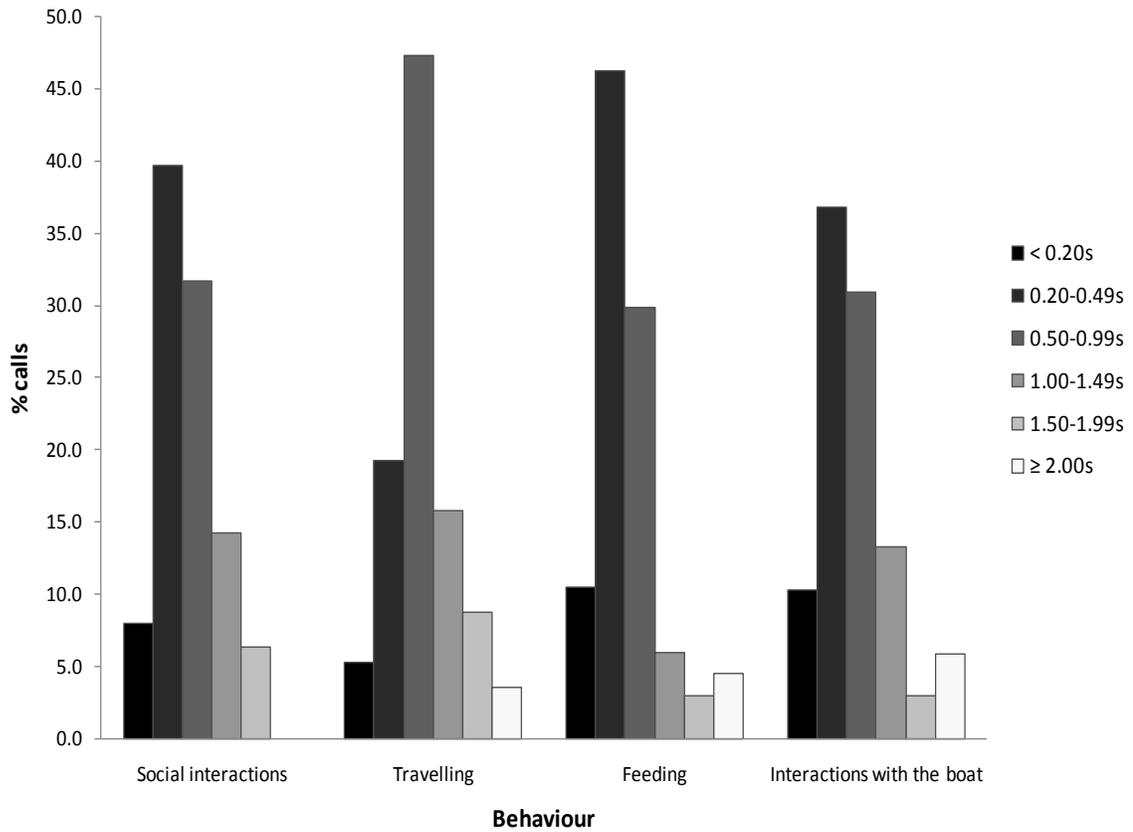


Figure 3.5: Percentages of call durations emitted by belugas in the Churchill River, Manitoba during four different behavioural states in duration ranges defined as: <0.20s, 0.20-0.50s, 0.50-1.00s, 1.00-1.50s, 1.50-2.00s, and ≥2.00s.

3.4.4 Pulsed and noisy calls

Pulsed calls produced during social interactions and pulsed and noisy calls produced during interactions with the boat were relatively broadband (high mean frequency bandwidths) compared to calls produced during travelling and feeding (Table 3.3). Pulsed and noisy calls produced during travelling were more narrowband (lower mean frequency bandwidth) and had lower mean frequency measurements compared to calls associated with other behaviours (Table 3.3). Pulsed and noisy calls produced during feeding and noisy calls produced during social interactions were moderately broadband (intermediate mean frequency bandwidths to calls produced during social and boat interactions, and travelling) (Table 3.3). The lowest mean PRR (62 ± 35) was measured in pulsed calls produced during social interactions, followed by feeding, travelling, and finally, interactions with the boat, but PRR also varied considerably in the latter three (Table 3.3). Pulsed and noisy calls produced during social interactions and travelling had higher mean durations than those produced during feeding and interactions with the boat.

3.5 DISCUSSION

3.5.1 Call Types

Many studies on call context have investigated call rates in different behavioural states (Sjare and Smith 1986a; Weilgart and Whitehead 1990; Belikov and Bel'kovich

Table 3.3: Descriptive statistics of pulsed and noisy calls (mean \pm standard deviation) emitted by beluga during four behavioural states in the Churchill River, Manitoba.

Behaviour	Call type	n	Min freq (kHz)	Max freq (kHz)	Freq Bandwidth (kHz)	Duration (sec)	PRR (pulses/sec)
Social interactions	pulsed	8	2.9 \pm 2.4	13.0 \pm 7.7	10.2 \pm 9.7	1.01 \pm 0.46	62 \pm 25
	noisy	6	5.7 \pm 3.6	9.8 \pm 3.8	4.0 \pm 2.0	0.74 \pm 0.55	N/A
Travelling	pulsed	10	2.6 \pm 2.6	4.2 \pm 3.7	1.6 \pm 1.3	0.94 \pm 0.55	226 \pm 132
	noisy	9	1.8 \pm 3.3	3.3 \pm 3.6	1.5 \pm 0.4	1.16 \pm 0.41	N/A
Feeding	pulsed	8	6.9 \pm 2.3	10.5 \pm 2.0	3.6 \pm 1.9	0.71 \pm 0.35	187 \pm 221
	noisy	2	5.5 \pm 1.0	8.5 \pm 0.5	3.0 \pm 1.6	0.45 \pm 0.13	N/A
Interactions with the boat	pulsed	10	2.9 \pm 3.2	10.8 \pm 8.7	7.9 \pm 8.2	0.59 \pm 0.45	340 \pm 222
	noisy	6	4.5 \pm 5.3	10.2 \pm 7.1	6.9 \pm 6.2	0.54 \pm 0.36	N/A

2003; dos Santos et al. 2005; Hawkins and Gartside 2010). Due to the large number of belugas and sometimes poor water visibility, accurate estimates of individuals were extremely difficult and prevented analysis of call rates. Therefore, this study focused on percentages of call types (whistles, pulsed/noisy calls, and combined calls), whistle contours (flat, ascending, descending, hump, dip, and wavy), and measured call characteristics (in particular frequency and duration) associated with different behaviours. Belugas were highly vocal in all behaviours (social interactions, travelling, feeding, and interactions with the boat). Some studies on odontocetes found whales were largely silent while travelling (van Parjis and Corkeron 2001; Karlsen et al. 2002). Karlsen et al. (2002) hypothesized that the relative silence in travelling belugas in Norway was to reduce predator detection by killer whales. Killer whale sightings near Churchill have increased in recent years but are still relatively rare (Higdon and Ferguson 2009); therefore, belugas would generally not be expected to reduce calling in this area to avoid detection by predators.

Similar to other odontocete studies, the dominant call type here in all behaviours was whistles, the focus of most studies on behavioural context of calls (Sjare and Smith 1986a; Faucher 1988; Weilgart and Whitehead 1990; dos Santos et al. 2005; Hawkins and Gartside 2010). Call rates, especially whistle rates, generally increase during more active and higher arousal behaviours such as social interactions and feeding (Sjare and Smith 1986a; Faucher 1988; van Parjis and Corkeron 2001; Jones and Sayigh 2002; Belikov and Bel'kovich 2003; Bazúa-Durán and Au 2004; Cook et al. 2004; dos Santos et al. 2005; Simon et al. 2007; Quick and Janik 2008; Díaz López and Shirai 2009). Even

though call rates could not be obtained in this study, higher percentages of whistles were produced during behaviours associated with higher levels of activity and/or apparent arousal (feeding, social interactions, and interactions with the boat). This supports the hypothesis that whistling is important in beluga communication during close-range social interactions.

The high percentage of whistles found during feeding was consistent with some other studies on odontocetes (van Parjis and Corkeron 2001; Acevedo-Gutiérrez and Stienessen 2004). Acevedo-Gutiérrez and Stienessen (2004) found that bottlenose dolphins, *Tursiops truncatus*, increased whistling rate during feeding and hypothesized that this was to attract other dolphins to join and assist in cooperative feeding. While some odontocete species engage in cooperative feeding (van Opzeeland et al. 2005; Benoit-Bird and Au 2009), it is not clear if belugas do. Beluga feeding behaviour observed and described in this study was also observed in the Churchill River by Watts and Draper (1986), however little is known about feeding strategies in belugas. The higher percentage of whistles in Churchill River belugas produced during feeding may be used to convey information to other whales about the food source, to maintain contact between individuals, or to coordinate movements (Hauser and Marler 1993; van Opzeeland et al. 2005), but it is unclear whether an increase in conspecifics would increase foraging success.

A relatively high percentage of whistles were also found during interactions with the boat similar to findings in Indo-Pacific bottlenose dolphins, *Tursiops aduncus*, interacting with boats (Hawkins and Gartside 2009a). Belugas approached the boat and

engaged in investigative behaviours including biting the hydrophone, swimming under the boat (sometimes upside down), and blowing bubbles. Whistles may be used to communicate with others about the objects being investigated, potentially those from a group that the individual left to approach the boat.

The highest percentage of pulsed and noisy calls was found during travelling. Specific pulsed and noisy calls have been related to some behavioural contexts (Sjare and Smith 1986a; Jacobs et al. 1993; van Parjis et al. 2000; Lammers et al. 2003) but their function is poorly understood. However, pulsed and noisy call structure is more suitable for longer range communication (Watkins et al. 1997; Miller 2006; Mitchell et al. 2006) so the higher percentage found during travelling may indicate that travelling belugas were communicating with individuals further away. More research is required on pulsed and noisy calls in travelling belugas in the Churchill River to determine their function.

3.5.2 Whistles

Contour types

Percentages of the six whistle contours identified in this study differed among behaviours. Whistle contour types also varied in other beluga populations and toothed whale species (Sjare and Smith 1986a; Weilgart and Whitehead 1990; dos Santos et al. 2005; Hawkins and Gartside 2009b; Hawkins and Gartside 2010). This suggests that whales use certain whistle contour types to communicate specific information about the activity they are engaged in or about themselves.

W2 (ascending) whistles were most common during all behaviours except interactions with the boat. Cunningham Inlet belugas emitted a high rate of ascending whistles during social interactions (Sjare and Smith 1986a) and ascending whistles were highly associated with social behaviour and travelling in Indo-Pacific bottlenose dolphins (Hawkins and Gartside 2010). These results suggest that ascending whistles are important in interactions between conspecifics during social interactions and possibly to coordinate movements during travelling, social interactions, and feeding (three behaviours requiring some coordination between individuals). W3 (descending) whistles were also relatively common during social interactions. Based on motivation-structure rules, Morton (1977) explained that ascending sounds indicate lower hostility and more amicable interactions while descending sounds indicate increasing hostility; this may indicate the presence of both hostile and amicable social interactions among Churchill River belugas during recordings.

W4 (hump) whistles were most common during feeding and relatively uncommon in all other behaviours. W5 (dip) whistles were common during travelling but relatively uncommon in all other behaviours and W1 (flat) whistles were relatively uncommon during travelling. An increased number of hump whistles during feeding/surface active behaviour and low number of flat whistles during travelling were also found in North Atlantic pilot whales, *Globicephala mela* (Weilgart and Whitehead 1990). High percentages of some contours in one behaviour compared to others and similarities among studies suggest that contour may be an important feature in

information content of calls and may contain context-specific information about the behaviour or the caller.

The majority of whistles produced during social interactions, travelling, and interactions with the boat were classified as simple whistles (W1, W2, or W3). However, during feeding the percentages of whistles classified as simple and complex (W4, W5, or W6) were similar. Other studies have generally found more complex whistles are emitted during behaviours associated with higher levels of activity and/or apparent arousal and more simple whistles are emitted during travelling and more restful behaviours involving slow swimming speeds and low degree of movement coordination (Taruski 1976; Weilgart and Whitehead 1990; Azevedo et al. 2010). While complex whistles produced by belugas during feeding, a relatively active behaviour, fit with previous findings, whistles recorded in the context of social and boat interactions did not. Interactions with the boat sometimes involved relatively slow swimming speeds and were therefore often not generally a high active behaviour. Interactions with the boat also did not involve interactions with conspecifics where motivation of the caller may elicit complex calls (Morton 1977); these factors could have contributed to a lower than expected number of complex whistles during interactions with the boat.

Social interactions were also associated with a lower than expected percentage of complex whistles, however whistles with complex structures were produced. Social interactions had the highest percentage of wavy whistles (W6) and social interactions and feeding were associated with a higher mean number of inflection points (an indication of whistle complexity) than whistles produced during travelling and

interactions with the boat. Feeding and social interactions were also associated with a more even distribution of contours compared to travelling and a lesser extent to interactions with the boat. These results support previous findings on bottlenose dolphins, *Tursiops truncatus*, and Indo-Pacific bottlenose dolphins that more diverse whistle types are associated with behaviours involving higher levels of activity and/or apparent arousal, such as feeding and interactions (dos Santos et al. 2005; Hawkins and Gartside 2009a). Morton (1977) examined the relationship between physical structure of calls and the motivation of the caller, explaining that more complex calls can potentially convey more information. Therefore, in accordance with the results of this study, more complex whistles and a higher diversity of whistle contours would be expected during behaviours such as feeding and social interactions, which involve more complex coordination of movements and where information on the motivation of the caller may be more important (i.e. in agonistic or amicable social interactions).

Call Parameters

Average whistle frequency varied between behaviours. Whistles of 1.0-4.9 kHz were the most common during all behaviours, although about half of the whistles produced during feeding and interactions with the boat were ≥ 5.0 kHz. Higher frequency calls are generally emitted in behaviours associated with higher levels of activity and/or arousal (Ford 1989; Rendall 2003; Azevedo et al. 2010). Atlantic spotted dolphins, *Stenella frontalis*, emitted whistles with higher frequency parameters during more active behaviours such as fast movements, prey pursuit, and physical contact than

during travelling (Azevedo et al. 2010). The highest percentages of whistles emitted at 5.0-9.9 kHz and ≥ 10.0 kHz occurred during interactions with the boat when belugas were generally closer to the boat compared to other behaviours. Higher frequency calls are more directional and therefore have a shorter detection range (Janik 2000a). This combined with higher apparent arousal levels during investigative interactions with the boat may have contributed to the higher percentages of whistles ≥ 5.0 kHz. Because of the close proximity of belugas to the boat (and therefore the hydrophone) during interactions with the boat and because of the directionality and shorter detection range of higher frequency calls, higher frequency calls were more readily recordable compared to during other behaviours. This may have contributed in part to the higher percentage of whistles ≥ 5.0 kHz. The directionality of higher frequency whistles may have also contributed to a relatively high percentage of whistles ≥ 5.0 kHz during feeding to maintain contact or coordinate movements between individuals also feeding close by.

During social interactions and travelling the majority of whistles were < 4.9 kHz. Higher frequency whistles may be expected during social interactions, a relatively active behaviour associated with higher apparent arousal, based on other odontocete studies. However, the lower frequency of whistles compared to other studies may have been due to the absence of very active and/or higher arousal behaviours such as breaching, tail slapping, or sexual behaviour observed during social interactions in other toothed whale studies (Ford 1989; Thomsen et al. 2002; Belikov and Bel'kovich 2003; dos Santos et al. 2005).

3.5.3 Call Duration

The majority of calls (whistles, pulsed, and noisy) in behaviours associated with higher levels of activity and/or apparent arousal (all except travelling) were <0.49s. Ford (1989) found calls emitted by killer whales during higher social arousal were generally shorter. However, duration is not often discussed in marine mammal studies on contextual use of calls because changes in duration may reflect other variables such as boat noise or other background noise (Lesage et al. 1999; Foote et al. 2004), in addition to changes in context.

3.5.4 Pulsed and noisy calls

Pulsed and noisy calls produced during beluga social and boat interactions were generally more broadband (higher mean frequency bandwidths) compared to calls produced during feeding, which in turn were generally more broadband than calls produced when travelling. Therefore, calls emitted during behaviours associated with higher levels of activity and/or apparent arousal were generally more broadband (larger frequency range). Calls produced during social interactions had the lowest mean PRR, followed by feeding, travelling, and finally, interactions with the boat; however, very little is known about the function of PRR in behavioural or social contexts. Some studies have researched click activity used for echolocation (low PRR) and generally report an increase in clicks during feeding most likely used for prey detection (Jones and Sayigh

2002; Nowacek 2005; Simon et al. 2007) but few studies discuss PRR of other pulsed and noisy calls in relationship to behaviours.

Because whistles are more commonly studied in social and behavioural contexts, the functional significance of pulsed and noisy calls is less well understood. Some studies have recorded and/or associated pulsed or noisy calls to behaviours, indicating that pulsed and noisy calls have important social functions in communication (Sjare and Smith 1986a; Jacobs et al. 1993; Herzing 1996; van Parjis et al. 2000; Díaz López and Shirai 2009). Differing PRR between calls produced during different behaviours in this study suggests that PRR may be an important feature to consider in future studies on the contextual use of pulsed calls. Further research with larger sample sizes would be necessary to reveal stronger differences between pulsed and noisy call measurements associated with behaviours and to investigate relationships between specific call types or call structure and behaviour.

3.5.5 Other variables affecting acoustic behaviour

Acoustic behaviour and call structure can be influenced by many factors, including: group size and composition (e.g. Quick and Janik 2008; Hawkins and Gartside 2010); emotional state or motivation of caller (e.g. Morton 1977; Rendall 2003; Soltis et al. 2005); morphological features such as body size or physical condition (e.g. Fitch and Hauser 1995; Fitch 1997; Pfefferle and Fischer 2006); individual or sex differences (e.g. Caldwell and Caldwell 1965; Sayigh et al. 1995; Rogers et al. 2006; Kennedy et al. 2009); geographic location (e.g. Stafford et al. 2001; Jones and Sayigh 2002; Shieh and Liang

2007); and habitat or environmental variables (e.g. Taruski 1976; Faucher 1988; Nowacek 2005; Maruska and Mensinger 2009). Recording segments analyzed in this study were collected over 16 days; some segments analysed for behavioural context of calls were collected on the same day, while others were not. Implicit in analyses comparing call types between behaviours was the assumption that vocal expression of a given behaviour did not vary among days, or among different whales recorded. Because individuals could not be identified, it was not possible to record the same individuals or groups of whales engaged in different behaviours over the study duration; however, all recordings were collected in the river or estuary (within 1 km of the river) at high tide during similar environmental conditions (e.g. Beaufort level [wind speed and wave height] and water temperature). Therefore, location and environmental variables changed little between different recording segments, and impacts on call expression during the studied behaviours were likely minimal. While effects of some variables, such as individual or group differences, cannot be ruled out, recordings were collected from many individuals/groups reducing effects of potential call biases introduced by factors such as sex, body size, and individual or group-specific calls.

3.5.6 Conclusions

This was the first study to describe and compare calls and call characteristics in Hudson Bay belugas produced during different behaviours. In summary, acoustic behaviour varied among social interactions, travelling, feeding, and interactions with the boat in Churchill River beluga. Whistles were the dominant call type produced during all

behaviours, suggesting an important role in communication between conspecifics. Call types, whistle contours, and some call characteristics varied with behaviour. Relative proportions of whistle contours varied with behaviour but further study is required to make conclusions about the function of specific contours. Generally, higher percentages of whistles, more broadband pulsed and noisy calls, and higher percentages of shorter calls (<0.49s) were produced during behaviours associated with higher levels of activity and/or apparent arousal. Higher frequency whistles (≥ 5.0 kHz) were found during feeding and interactions with the boat, and more complex whistles with more inflection points were found during feeding and social interactions. Relationships between more and less active behaviours or those associated with high and low arousal levels may have been more evident if calls during milling and resting (behaviours associated with low levels of activity and apparent arousal with little coordination) could have been recorded and analyzed for comparison.

In future research relating beluga calls to behaviour, it would be valuable to identify the individual or group emitting the calls either using localization methods or targeting groups separated from other belugas. Although difficult in the Churchill River, the latter would allow for more detailed study of behaviour while collecting recordings. Accurate group size estimates could be obtained and used to calculate call rates for comparison between behaviours and to determine group size effect on call rates (Cook et al. 2004; dos Santos et al. 2005; Quick and Janik 2008; Díaz López and Shirai 2009).

To better understand the function or meaning of calls, future research should investigate specific call types and contextual use. Calls with very context-specific

meanings can provide very specific information (reviewed by Seyfarth and Cheney 2003). Some examples include bray feeding calls in bottlenose dolphins (Janik 2000b), grunts and other food-related calls in rhesus macaques, *Macaca mulatta* (Hauser and Marler 1993), predator-specific alarm calls in some primates (Seyfarth et al. 1980; Coss et al. 2007), and baboon, *Papio cynocephalus ursine*, mother-infant contact calls (Fischer et al. 2001).

Information on behavioural context of calls and communication between conspecifics are important aspects of study to understand meaning and function of calls, and especially important in a social species like belugas. Information gained from this study associated some call types, whistle contour types, and call characteristics with certain behaviours. This provides a basis for additional, more in-depth research on context-specific calls and call meaning and function which can then be used to infer beluga behaviour in recordings from autonomous recording devices collected without behavioural observations.

3.6 REFERENCES

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CHAPTER 4: DISCUSSION

4.1 Classification

Beluga whale, *Delphinapterus leucas*, calls were classified and call characteristics described from recordings collected in the summers of 2006-2008 in the Churchill River and Churchill River Estuary, Manitoba where belugas aggregate during the summer (Hansen et al. 1988; Idle 1989). Calls were classified based on aural and visual analysis, and measured call characteristics. Beluga calls (n=706) were separated into 453 whistles (64.2% of total calls), 183 pulsed or noisy calls (25.9%), and 70 combined calls (9.9%). Proportions of the three main call types were similar to those found in other beluga populations within their summer range but combined calls have only been described in some (Sjare and Smith 1986a; Karlsen et al. 2002).

Subjective classification further divided whistles into six main contour types (flat, ascending, descending, hump, dip, and wavy) comprising 22 call types. The most common whistle contour type was W2 (ascending; 20.2% of total calls), followed by W1 (flat; 15.9%) and the most common whistle call type was W2c (ascending then flat; 10.3%), followed by W1a (flat; 5.7%) and W2a (slightly ascending; 5.7%). Pulsed and noisy calls have been less studied than whistles and classification information provided is often less detailed. Pulsed and noisy calls in this study were divided into 15 types including buzzes, creaks, clicks, clinks, croaks, honks, screeches, squeals, screams, and barks. The most common pulsed or noisy calls were buzzes followed by honks.

Combined calls were divided into seven types including whistles with noisy components, honks and creaks with higher whistles, and screeches with lower whistles. The most common combined calls were whistles with noisy components at the end (C1; 2.7% of total calls), followed by wavy honks with higher components (C6; 2.1%). Some combined calls described in this study appear to be variations on pulsed or noisy calls. The added higher frequency whistle may function to convey additional information such as location or orientation to receiver (Miller 2002; Filatova et al. 2009). Measured parameters varied less in pulsed and noisy and some combined call types than in whistles. Similar whistle contours, and some pulsed, noisy and combined calls were described in other beluga populations but some were not (Sjare and Smith 1986a; Angiel 1997; Faucher 1988; Karlsen et al. 2002; Belikov and Bel'kovich 2006; 2007; 2008).

A more objective UPGMA Chord distance hierarchical clustering method was applied to 200 randomly chosen whistles. Six call characteristics (starting and ending frequency, difference between them, frequency bandwidth, number of inflection points, and number of steps) were used as variables and 12 groups were identified. The first separation by cluster analysis into two large groups appeared to be mostly due to number of inflection points and to a lesser extent to absolute frequencies (start and end frequencies); one group had a higher mean number of inflection points and consisted of most W6 (wavy) whistles used in analysis (85.0%) and also had lower frequency measurements. Separation into the 12 smaller groups appeared to be due to a combination of the variables but in particular start and end frequencies and frequency bandwidth.

Results of the cluster analysis were comparable to the subjective classification of whistle contours (W1, W2, W2, W3, W4, W5, and W6) but differed in the whistle type classification. Clustered group measurements varied less than subjective call types; however, cluster analysis may miss some important features and subtle differences in call contours not readily captured in measurements but which human observers would see or hear.

4.2 Calls and behaviour

Beluga call types and call characteristics (including frequency measurements and duration) were described during different behaviours in the Churchill River, Manitoba from recordings collected from 9-27 July, 2007. Beluga calls (n=265) were extracted: 67 during social interactions, 60 during travelling, 67 during feeding, and 71 interactions with the boat. Belugas were highly vocal in all behaviours and the dominant call type in all behaviours was whistles, similar to other odontocete studies (Sjare and Smith 1986b; Faucher 1988; Weilgart and Whitehead 1990). Whistle and pulsed/noisy call percentages differed within behaviours ($\chi^2 = 9.36$, $df = 3$, $p = 0.02$). The highest percentage of whistles was produced during feeding (85.1%) and the highest percentage of pulsed and noisy calls was produced during travelling (31.7%). Combined calls were uncommon in all behaviours (0-6.0%).

Relative proportions of whistle contour types (W1 = flat, W2 = ascending, W3 = descending, W4 = hump, W5 = dip, W6 = wavy) and some call characteristics varied with behaviour. W2 whistles were the most common contour type produced during social

interactions and travelling and the second most common during feeding. W4 whistles were the most common contour type during feeding but the least common during social interactions and travelling.

Average whistle frequency (Kruskal-Wallis = 12.616, $df = 3$, $p = 0.006$) and call duration (Kruskal-Wallis = 18.363, $df = 3$, $p = 0.0004$) also varied with behaviour. A relatively high percentage of whistles produced during all behaviours were 1.0-4.9 kHz (46.2 to 65.8%) but about half of the whistles produced during feeding and interactions with the boat were ≥ 5.0 kHz (42.1% and 51.9%, respectively). For duration, a relatively high percentage of calls were 0.20-0.49s during social interactions (39.7%), feeding (46.3%), and interactions with the boat (36.8%) and a relatively high percentage of calls were 0.50-0.99s during travelling (47.4%).

Pulsed calls produced during social interactions and pulsed and noisy calls produced during interactions with the boat were more broadband (high mean frequency bandwidths) than calls produced during travelling and feeding. The lowest mean PRR (62 ± 35) was measured in pulsed calls produced during socializing. Generally, higher percentages of whistles, more broadband pulsed and noisy calls, and shorter calls (<0.49 s) were produced during behaviours associated with high levels of activity or apparent arousal (social interactions, feeding, and interactions with the boat) compared to travelling. Also, more complex whistles (higher mean number of inflection points) were found during feeding and social interactions. Complex calls can contain more information than simple calls (Morton 1977) and therefore more complex calls might be expected during behaviours involving more complex coordination of movements and

where motivation of the caller may be more important (i.e. in agonistic or friendly social interactions) such as feeding and social interactions.

4.3 Conclusions and future research

This was the first description and classification of calls in Hudson Bay beluga whales and is required as baseline understanding for future research investigating context-specific calls and call meaning and function. Knowledge of beluga calls can also be used to improve automated detection and classification of calls. Studies comparing subjective and objective classification have obtained varying results (Angiel 1997; Nowicki and Nelson 1990; Deecke et al. 1999; Janik 1999; Karlsen et al. 2002) in part because subjective classification generally focuses on call contour, whereas at least some measurements used in more objective methods are based on absolute frequencies that do not represent call contour. Using two methods not only provides for more robust interpretations but also the opportunity to assess independent approaches to determine which methods to use in future studies. Because objective methods can more easily handle deal with larger data sets and results can be compared between studies, these methods should be the focus of future studies. Hierarchical cluster analyses, an objective method, has some application in classifying graded beluga vocalizations; however, additional research on call perception, similar to research done on bottlenose dolphins, *Tursiops truncatus* (Ralston and Herman 1995; Harley 2008), will aid in categorizing whistles into more discrete categories based on acoustic properties that are biologically relevant to belugas.

Knowledge of a species' calls and calling behaviour may also provide information on its social structure because call characteristics may be linked to social or group organization (Connor et al. 1998). Killer whales and sperm whales form stable social groups that produce group-specific dialects used for group cohesion (Ford 1991; Weilgart and Whitehead 1997; Riesch et al. 2006); whereas, bottlenose dolphins and some terrestrial mammals that form fission-fusion societies have individually distinct calls that may be used to identify individuals, identify kin, and/or maintain contact among individuals when they are out of visual range (bottlenose dolphins: Caldwell & Caldwell 1965; Sayigh et al. 2007; spider monkeys: Ramos-Fernández 2005; African elephants, *Loxodonta africana*: Poole et al. 1988).

This was the first description of calls emitted during different behaviours in Hudson Bay belugas, establishing a basis for studying call meaning and function by providing information on the contexts in which calls are emitted. Whistles were the dominant call type in all behaviours and are therefore important to consider in studying communication between conspecifics. Differences found in relative proportions of whistle contours among behaviours in this study and other odontocete studies (Sjare and Smith 1986b; Weilgart and Whitehead 1990; Hawkins and Gartside 2010), suggest that contour is an important feature in conveying information about the behaviour or the caller. More in-depth research on context-specific calls and call meaning and function is required and knowledge of calls emitted during different behaviours can also be used to infer behaviours in autonomous recordings collected without behavioural observations. More research needs to be done on the use of pulsed and noisy calls;

some differences were found in this study (i.e. in PRR) but a higher sample size is required to make further associations and conclusions.

In future research relating beluga calls to behaviour, it would be valuable to identify the individual or group emitting the calls using either localization methods or targeting groups separated from other belugas. Accurate group size estimates could be obtained and used to calculate call rates for comparison among behaviours and to determine effects of group size on call rates (Cook et al. 2004; dos Santos et al. 2005; Quick and Janik 2008; Díaz López and Shirai 2009).

Acoustics studies on Hudson Bay beluga whales are particularly important because of predicted ecosystem changes. First, reduction of sea ice in Hudson Bay will increase marine vessel traffic, creating a noisier environment. Animals sometimes alter frequency and/or duration of calls in response to increased background noise potentially affecting their communication success (Lesage et al. 1999; Miller et al. 2000; Foote et al. 2004; Nemeth and Brumm 2009). Second, a recent increase in killer whale sightings in Hudson Bay (Higdon and Ferguson 2009) may also have an effect on belugas. Killer whales are a predator of belugas and can have an effect on the acoustic behaviour of their prey (Campbell et al. 1988; Morisaka and Connor 2007).

Passive acoustic monitoring (PAM) of cetaceans is a developing field (review by Mellinger et al. 2007) and may be an effective way to monitor the large area in Hudson Bay where belugas are found over the summer (Richard 2005; Smith 2007; Lewis et al. 2009). PAM monitoring requires information on call types and call characteristics for call detection and further analysis of calls; therefore, information from this study provides

baseline information for PAM studies in Hudson Bay belugas. Acoustic information along with other studies on Hudson Bay beluga provides information towards future monitoring of a population that faces increased boat traffic, killer whale sightings, hydroelectric development and Inuit hunting.

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