WINTER BEHAVIOUR AND POPULATION STRUCTURE OF FIN WHALES (*BALAENOPTERA PHYSALUS*) IN BRITISH COLUMBIA INFERRED FROM PASSIVE ACOUSTIC DATA

by

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Abstract

Fin whales are acoustically active year-round, particularly during the winter breeding season when males produce song as a reproductive display. Little is known about movement patterns and population structure of the fin whale (*Balaenoptera physalus*) in the North Pacific. I used passive acoustic data recorded using bottom-mounted autonomous recording instruments to answer questions about the winter distribution, behaviour and population structure of fin whales in a high-latitude area of the eastern North Pacific Ocean. I found that fin whales are present in British Columbia (BC) waters throughout the winter, and their acoustic behaviour suggests that they are engaging in reproductive and possibly feeding behaviour. The presence of these individuals indicates that not all fin whales migrate south in the winter to low-latitude breeding grounds. I found that the majority of fin whales recorded in BC sang a doublet song with alternating ~13 s and ~17 s intervals between alternating classic and backbeat notes (song Type 2). At the most northerly recording site, and the two offshore sites, I found a few instances of a previously described doublet song type that has longer internote intervals (song Type 1). This suggests that two spatially segregated populations of fin whales are using BC waters, with the population producing song Type 2 being more coastal. Through a literature search, I found evidence of song Type 2 occurring from northern BC to Oregon. Song Type 1 has been documented off Southern California, the Bering Sea and the central North Pacific. My results are consistent with evidence showing that two genetically distinct fin whale populations occur in the eastern North Pacific, and that the population that produces song Type 2 is more closely related to the Southern Hemisphere subspecies of fin whale, than to the other population of fin whales in the North Pacific. My results show that BC waters are important for fin whales year-round, rather than just during the summer feeding season—and that the fin whales in BC likely belong to two distinct populations (one of which may belong to the Southern Hemisphere subspecies) and may require separate plans for their conservation and management.

Preface

Fisheries and Oceans Canada’s Cetacean Research Program (Pacific Biological Station, Nanaimo) provided the passive acoustic data that I analyzed. JASCO Applied Sciences provided me with access to their acoustic analysis program, SpectroPlotter (v. 4.4.30). I performed all of the acoustical and statistical analysis, and prepared the manuscripts, which benefited from comments and edits by co-supervisors Andrew Trites, John Ford, David Hannay and committee member Darren Irwin. Brianna Wright produced the maps for Chapters 2 and 3.

Field research was approved by both the Committee on Animal Care at the University of British Columbia and the Animal Care Committee of the Pacific Biological Station, Fisheries and Oceans Canada. This research was conducted under UBC Animal Care Permit no. A12-0110 and Fisheries and Oceans Canada Marine Mammal Research License no. MML-001. I completed the ethics training requirements of the Canadian Council on Animal Care (CCAC) / National Institutional Animal User Training program (NIAUT) certificate # 5419 – 12.

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Chapter 1: Introduction

1.1 Fin Whale Vocalizations

20-Hz pulses in the ocean were first documented in 1951 by Henry Johnson of the Woods Hole Oceanographic Institution while undertaking ambient noise surveys near Bermuda in the North Atlantic Ocean (Schevill et al. 1964). Subsequent observations revealed that this very distinctive sound was omnipresent at certain times of year (Walker 1964), but the source remained a mystery. Many possible sources such as seismic activity, wave action, barometric pressure fluctuations, major weather events, land based machinery, pile driving, power generators, planes flying overhead and the jet propulsion of giant squid were investigated and ruled out (Walker 1964). Tracking studies revealed that the pulses were produced with very high source levels and originated from widely spaced point sources that travelled at a few knots for extended periods of time, and it was hypothesized that the pulses were of biological origin, likely a species of whale. The pulses were produced with such regular timing, that it was suggested, *"…one of the basic life processes, characterized by an inherently regular rhythm, may be involved – respiration, locomotion, circulation, digestion, or something similar*" (Walker 1964). Interestingly, pulses arranged in a doublet pattern of alternating long and short time intervals were consistently observed. The pattern, and its regularity, were likened to the rhythm of the human heartbeat, and prompted the hypothesis that the pulses were the sounds of the beating heart of a large whale (Walker 1963, 1964).

Since the 1950s, the 20-Hz pulses have been unequivocally attributed to the vocalizations of fin whales (Schevill et al. 1964, Watkins 1981), and the consistent doublet pattern that was initially thought to be the sound of a heart beating is now known to be a stereotyped fin whale song pattern (Watkins et al. 1987). The Oxford English dictionary defines song as "the musical phrases uttered by some birds, whales, and insects, typically forming a recognizable and repeated sequence and used chiefly for territorial defense or for attracting mates". Although fin whale songs are far simpler than the intricate songs of humpback whales or songbirds, they are nonetheless songs. Only males sing (Watkins 1981, Watkins et al. 1987, 2000, Croll et al. 2002), and the timing of song production coincides with the breeding season (November-March; Watkins et al.

1987). While the specific function of fin whale song in reproduction is not clear, it may play a role in mate attraction, advertisement of resources, or male-male competition (Watkins et al. 1987, Croll et al. 2002, Oleson et al. 2014).

Fin whale songs are sequences of 20-Hz notes arranged into patterns with regular intervals between notes, referred to as internote intervals (or interpulse intervals or pulse intervals). Songs can be up to 20 minutes long and can be repeated in bouts that last for hours or days (Watkins et al. 1987). The 20-Hz notes that make up the songs are short (~1 s), downsweeping (Edds 1988), very loud (~171 to 189 dB re 1 μPa at 1 m, Charif et al. 2002, Sirović et al. 2007, Weirathmueller et al. 2013), low frequency pulses (Watkins 1981, Watkins et al. 1987). Although the actual frequency of the 20-Hz notes varies between data sets (Watkins et al. 1987, Thompson et al. 1992, Edds-Walton 1997), they are called 20-Hz notes because fin whale calls described in early studies from the Atlantic were most commonly centered around 20 Hz (Watkins et al. 1987, Edds-Walton 1997, Clark et al. 2002). There are two forms of 20-Hz notes—called the classic and the backbeat notes—with the backbeat occurring at a lower frequency and with a narrower bandwidth relative to the classic note (Clark et al. 2002, Hatch and Clark 2004, Soule and Wilcock 2013). In some regions, fin whale songs have higher frequency components, such as the high frequency upsweep in the western tropical North Atlantic and the northeastern North Atlantic (Hatch and Clark 2004), and the high frequency 20-Hz note component in the Southern Ocean (Širović et al. 2004, Gedamke 2009).

Fin whales arrange 20-Hz notes into songs with very simple patterns. A common fin whale song pattern, called doublet song, consists of alternating classic and backbeat notes, with alternating short and long intervals between the notes (Thompson et al. 1992, Clark et al. 2002, Hatch and Clark 2004). Another common song pattern is the singlet song, which consists simply of one note type repeated at regular intervals (Watkins et al. 1987). Less frequently, songs are composed of triplets or more complicated patterns (Delarue et al. 2013, Soule and Wilcock 2013).

In addition to being used in stereotyped songs with consistent note intervals, fin whales use 20-Hz notes in short series with irregular intervals between the notes (Watkins et al. 1987, Širović et al. 2012). These sounds are common in the summer and are generally produced by animals in groups (Watkins 1981). They are likely used in social interactions and for keeping in contact with conspecifics, but it is not known whether males, females, or both sexes, produce this call type (Watkins 1981, Watkins et al. 1987, McDonald et al. 1995, Edds-Walton 1997). Other lesser known types of non-song fin whale vocalizations include higher frequency downsweeps, ragged low frequency pulses and low frequency rumbles (Watkins 1981, Edds 1988).

1.2 Passive Acoustic Methods

Traditionally, studies of large whales have involved visual surveys, but there are limitations associated with this method. Visual surveys are costly in terms of both time and money—they require trained observers, and many hours of operating costly ships or aircraft to cover even a fraction of the area over which whales range (Mellinger et al. 2007). Visual surveys are limited by daylight and weather conditions, and whales are difficult to detect because they spend the majority of their time underwater. It is also very challenging and costly to obtain biopsy samples from whales, or put satellite tags on these large, fast moving, wide ranging animals.

Because of the limitations associated with visual surveys, there has been an increase in the use of passive acoustic methods, which involves anchoring autonomous recording instruments to the seafloor where they are left to record cetacean vocalizations (Mellinger et al. 2007). Passive acoustic methods are powerful because they collect long-term data at low cost, have the ability to detect whales from great distances, at any time of day or night, and in any type of weather or sea-state. Autonomous acoustic recording instruments can be deployed in remote and offshore areas that would be otherwise inaccessible to researchers for much of the year. Also, they have the potential to be left in place to collect data for up to a full year, providing seasonal coverage that is difficult to achieve with any other method.

Acoustic methods have been shown to detect up to ten times more whales than visual methods, and are particularly useful for detecting rare species that would have a very low probability of being detected visually, and for identifying different cryptic species that would otherwise be difficult to distinguish (Mellinger et al. 2007). By recording vocalizations on passive acoustic monitoring instruments distributed over time and space, it is possible to study the distribution, movements, behaviour, relative abundance and population structure of whales (Mellinger et al. 2007).

Fin whales are excellent candidates for passive acoustic studies because their vocalizations are easily identifiable, they often vocalize for hours at a time, and the low frequencies and loudness of the vocalizations allow them to travel for long distances underwater.

1.3 Fin Whales at High Latitudes in the Winter

Many baleen whales including humpback, grey and right whales undertake regular seasonal migrations between high-latitude summer feeding grounds and low-latitude tropical or sub-tropical winter breeding grounds where they mate and calve (Lockyer and Brown 1981). Although there is some evidence of migration in fin whales (Mizroch et al. 1984, 2009), recent visual and acoustic observations at high latitudes in the winter suggest that their movement patterns may be more complex than other baleen species (Stafford et al. 2007, Mizroch et al. 2009, Simon et al. 2010, Soule and Wilcock 2013, Oleson et al. 2014).

It is not clear why fin whales occur in high latitudes in the winter. One possibility is that these individuals are sexually immature, and therefore do not need to travel to the low-latitude breeding grounds. Another possibility is that travelling long distances to calve in warm, tropical seas is not advantageous for fin whales, and that females remain at high latitudes to calve and breed (see Corkeron and Connor 1999). It is also possible that pregnant females migrate, and females who are not pregnant avoid the energetic cost of migrating south, because they will not require the benefits of the calving grounds. These non-pregnant females may remain on high-latitude feeding grounds during the winter reproductive season, where they may breed, assuming that sexually mature males are present. Alternatively, it is possible that migration of the entire population does occur, but that the migration is staggered, so that at least some whales are present at high latitudes at all times throughout the winter (Mizroch et al. 2009).

Although fin whales are known to occur frequently in British Columbia in the summer months (Gregr et al. 2000, Flinn et al. 2002, Mizroch et al. 2009, Ford et al. 2010a, Ford 2014), recent observations of a small number of fin whales in the winter months (Ford et al. 2010a) has raised the question of whether fin whales are present in this coastal area of the eastern North Pacific year-round. The existence of passive acoustic data sets from British Columbia allowed me to assess this question and to address the questions of what fin whales are doing at high latitudes of the North Pacific in the winter.

1.4 Fin Whale Population Structure

Fin whales in the North Pacific were depleted by commercial whaling in the 20th century. Coastal whaling stations in British Columbia processed at least 7,605 fin whales between 1908 and 1967 (Gregr et al. 2000, COSEWIC 2005) and thousands more were taken by pelagic whaling through the 1970s (COSEWIC 2005). Today North Pacific fin whale numbers are estimated to be 50% below historical abundance, and the species is listed as threatened under the Species at Risk Act in Canada (COSEWIC 2005).

The fin whale is a cosmopolitan species, occurring almost worldwide. However, little is known about fin whale population structure. There are three recognized subspecies: *B. p. physalus* in the Northern Hemisphere, *B. p. quoyi* in the Southern Hemisphere, and *B. p. patachonica*, a pygmy form in the Southern Hemisphere (Committee on Taxonomy 2014). Recent genetic work shows that the Northern Hemisphere fin whales are actually composed of two subspecies, one in the North Atlantic and one in the North Pacific (Archer et al. 2013). The North Pacific subspecies may further be divided into two, possibly three distinct clades, with two clades occurring in the eastern North Pacific (Archer et al. 2013). In the North Pacific, a genetically distinct resident population has been confirmed in the Gulf of California (Bérubé et al. 2002), and there is good evidence for a resident population in the East China Sea, with possible additional resident populations in the Sanriku-Hokkaido and northern Sea of Japan areas (Mizroch et al. 2009).

Although the omnipresence of fin whale song in most of the world’s oceans is well known, relatively little work has been done to describe the characteristics of the songs. Recently, however, there has been increased interest in this field, because patterns of geographic variation in fin whale and other whale songs may be reflective of population structure (Mellinger and Barlow 2003).

Characteristics of fin whale song, such as the pattern, the lengths of the intervals between notes, and the frequency of the notes have been observed to vary between regions (Watkins et al. 1987, Mellinger and Barlow 2003, Hatch and Clark 2004, Delarue et al. 2009, Castellote et al. 2012). Previous studies have found that some characteristics of song notes are specific to ocean basins, and that these characteristics vary within the ocean basins (Hatch and Clark 2004). For instance, a higher frequency song component has been described only in the Southern Hemisphere, and within the Southern Hemisphere. This high frequency component occurs at different frequencies in different regions (Širović et al. 2004, Gedamke 2009).

In some cases, acoustic differences have corresponded to genetic differences between populations, such as in the resident populations of the Gulf of California (Thompson et al. 1992, Bérubé et al. 2002) and the Mediterranean Sea (Bérubé et al. 1998, Castellote et al. 2012). In contrast, a study from the Gulf of St. Lawrence and the Gulf of Maine found differences in song that were consistent with other methods of stock structure assessment such as tagging, pollutant level analysis and photo-identification (Delarue et al. 2009), but no evidence of genetic differentiation based on nuclear and mitochondrial markers was found (Bérubé et al. 1998, Delarue et al. 2009). This may be because population differentiation that is reflected in social signals such as song, may be too recent to be detected in the genetic signature (Delarue et al. 2009). Alternatively, song may not always correspond to genetic differences, but instead may correspond to other forms of population structure, such as feeding aggregations (Delarue et al. 2009). Although the relationship of acoustic and genetic differentiation is not completely understood for fin whales, it has been recommended that in the absence of other data, distinct differences in songs should be used as indicators of population structure when making management decisions (Mellinger and Barlow 2003).

Vocalizations have been used to aid in the description and differentiation of closely related and cryptic species, and different populations within species, for a wide variety of taxa including insects (Wells and Henry 1998, Henry et al. 2002), birds (Irwin et al. 2001, Toews and Irwin 2008) and mammals (Braune et al. 2008, Campbell et al. 2010). In cetaceans, unique vocalizations are produced by different killer whale ecotypes (Ford 1984), and pods within the resident killer whale ecotype can be distinguished by pod-specific dialects (Ford 1991). Sperm whales also show geographic variation in their social sounds (Amano et al. 2014). In baleen whales, geographic variation in blue whale song has been used to characterize population structure worldwide (McDonald et al. 2006), and separate humpback whale breeding aggregations differ in their songs (Garland et al. 2015).

Although there is genetic evidence that two populations of fin whales may exist in the eastern North Pacific, only one song type has been described in detail from Southern California, Hawaii and the Bering Sea (Oleson et al. 2014). The acoustic dataset from British Columbia waters provided me the opportunity to look for evidence other song types, in an area of the eastern North Pacific in which song has not yet been described. It also allowed me to evaluate the population identity and structure of the fin whales in BC based on song types, and to compare songs to acoustic and genetic data from the greater eastern North Pacific, and other ocean basins, in order to examine population structure on a larger scale.

1.5 Research Goals

Although fin whale song is known to occur throughout the North Pacific Ocean, relatively little work has been done to use the song as a means of investigating aspects of fin whale life history. The overall objective of my research was to use song analysis to provide new information on the winter distribution, behaviour and population structure of fin whales in a high-latitude area of the eastern North Pacific Ocean. In Chapter 2, I examined the seasonal occurrence of fin whale song in British Columbia, and evaluated the hypotheses that the whales that remain at high latitudes in the winter are engaging in reproductive and feeding behaviours. In Chapter 3, I addressed the question of whether there are two distinct populations of fin whales in British Columbia, and the greater eastern North Pacific.

The first objective of Chapter 2 was to characterize the song of fin whales in British Columbia over one entire singing season (August to March). To accomplish this, I manually analyzed fin whale 20-Hz notes recorded over one year (2010-2011) at one location (Brooks Peninsula) using a bottom-mounted autonomous passive acoustic recording instrument. I chose to manually analyze the data instead of using automated detection algorithms, as I wanted to ensure that every song, and every note in every song, was accurately measured. As a human analyst, I was able to choose to measure songs that had sufficient signal-to-noise ratios, so that I was sure that I was not missing any notes in the song sequences.

Fin whales are generally thought to migrate south in the winter to low-latitude tropical or subtropical breeding grounds, but observations of fin whales at high latitudes in the winter suggest that their movement patterns may be more complicated. Fin whales are known to occur in BC in the summer, but a few recent observations of fin whales in the winter months in BC (Ford et al. 2010a, Ford 2014) suggest that at least some fin whales remained in this area throughout the winter. Performing measurements of fin whale song over one year allowed me to evaluate the hypothesis that fin whales occur in BC waters year-round.

My second objective was to evaluate the measured songs for evidence of reproductive and feeding behaviour. For this, I measured the seasonal change in song variability and stereotypy, in relation to the breeding period of this species. Singing is a sexual display that is linked to the seasonal fluctuation of testosterone in many species; singing activity and stereotypy (consistency) tend to increase with increasing testosterone levels (Smith et al. 1997, Meitzen et al. 2009, Riebel 2009). Therefore, I expected song to become less variable and more stereotyped as the whales entered breeding condition and moved towards the peak of the breeding cycle. To evaluate whether feeding may be occurring through the winter, I looked for diel patterns in call occurrence. Fin whales have been shown to feed during the day when their zooplankton prey is concentrated at depth, and fin whales have been observed to sing less during the day than at night. This is hypothesized to occur because whales likely do not feed and sing simultaneously, and therefore sing more at night when they are less occupied with feeding (Watkins et al. 1987, Oleson 2005, Stafford et al. 2005, Wiggins et al. 2005, Simon et al. 2010). Therefore, if fin whales feed in BC in the winter, I expected to see a diel pattern of less singing during the day than the night.

The objective of Chapter 3 was to assess the hypothesis that two populations of fin whales use British Columbia waters and the greater eastern North Pacific. To do this, I used passive acoustic data from 8 bottom mounted archival recorders deployed throughout BC waters to determine whether recorded fin whale songs corresponded to the previously described North Pacific fin whale song Types 1 or 2, or other song types. I then undertook a literature search to determine whether song Types 1 or 2, or other song types, had been documented in any other regions of the North Pacific. I extended the analysis to include song samples from other ocean basins, and compared my findings to estimates of genetic differentiation of whales between the North Pacific, North Atlantic and Southern Oceans, and within the North Pacific Ocean.

1.6 Thesis Structure

My thesis contains four chapters: a general introduction (Chapter 1), analysis of fin whale seasonal occurrence and behaviour in British Columbia (Chapter 2), analysis of fin whale population structure in British Columbia and the eastern North Pacific (Chapter 3) and a general conclusion (Chapter 4). The data chapters (Chapters 2 and 3) are written as manuscripts to submit for publication in peer-reviewed journals. Although Chapters 2 and 3 address different questions, there is some overlap in the acoustic analysis methods used, and some data from one recording location (October 2010 and February 2011 from Brooks Peninsula) was used in both chapters.

Chapter 2: Fin whale song indicates year-round presence and winter breeding and feeding behaviour on a high-latitude feeding ground off British Columbia

2.1 Summary

Fin whales (*Balaenoptera physalus*) are generally assumed to migrate between high-latitude summer feeding grounds and low-latitude subtropical winter breeding grounds. However, fin whales are regularly observed in high latitudes in the winter, suggesting that not all individuals migrate. I used passive acoustic data collected over one year (July 2010-July 2011) to evaluate the seasonal presence of fin whales off Vancouver Island, British Columbia. I also sought to assess whether the characteristics of the fin whale calls were consistent with reproductive and feeding behaviours. I found that fin whales consistently produced 20-Hz notes from mid-August through March, and that they made a single distinct song type throughout this entire period consisting of doublets of two 20-Hz note types—the classic note (center frequency of ~23.4 Hz) and the backbeat note (center frequency of ~19.1 Hz)—with two distinct intervals between the notes (~17 s and ~13 s). Song characteristics changed over time (i.e., note intervals increased, frequency decreased, stereotypy increased, and use of irregular interval notes declined) in parallel with the onset (November), peak (December-January) and end of the reproductive period (by March). Diel patterns in calling suggest that fin whales may be feeding in the winter during daylight hours. Overall, the acoustic data indicate that fin whales are present year-round in the coastal regions of British Columbia, and suggest that some individuals mate here during winter, while also taking advantage of feeding opportunities. This suggests that migrating between low-latitude breeding grounds and high-latitude feeding grounds may not be a necessary component of the fin whale's life history strategy.

2.2 Introduction

Many baleen whales including humpback, grey and right whales undertake regular seasonal migrations between high-latitude summer feeding grounds and low-latitude tropical or subtropical winter breeding grounds where they mate and calve (Lockyer and Brown 1981). The same appears to be true for fin whales based on commercial whaling records and more recent visual, acoustic and tagging observations that show movements between high and low latitudes (Mizroch et al. 1984, 2009). However, fin whale movement patterns may be more complex than some other baleen species given that they are regularly seen and heard in high latitudes during winter in the Atlantic and Pacific Oceans (Stafford et al. 2007, Mizroch et al. 2009, Simon et al. 2010, Soule and Wilcock 2013, Oleson et al. 2014).

It is not clear why some fin whales occur at high latitudes in the winter. One possibility is that these individuals are sexually immature, and therefore do not need to travel to the low-latitude breeding grounds. Another possibility is that travelling long distances to calve in warm, tropical seas is not advantageous for fin whales, and that females remain at high latitudes to calve and breed (see Corkeron and Connor 1999). It is also possible that pregnant females migrate, and females who are not pregnant avoid the energetic cost of migrating south, because they will not require the benefits of the calving grounds. These non-pregnant females may remain on high-latitude feeding grounds during the winter reproductive season, where they may breed, assuming that sexually mature males are present. Alternatively, it is possible that migration of the entire population does occur, but that the migration is staggered, so that at least some whales are present at high latitudes at all times throughout the winter (Mizroch et al. 2009).

One means to answer such questions about the winter occurrence and behaviour of fin whales is by passively recording their calls using hydrophones attached to the sea floor (Mellinger et al. 2007). Passive acoustic recording is particularly suitable for use on fin whales at high latitudes in the winter, because this method is not constrained by lack of daylight and harsh weather conditions (Mellinger et al. 2007), and instruments can be deployed in remote areas that are otherwise inaccessible to researchers for much of the year.

Fin whale vocalizations are loud (~171 to 189 dB re 1 μPa at 1 m, Charif et al. 2002, Sirović et al. 2007, Weirathmueller et al. 2013), easily identified, and travel long distances underwater. In fact, fin whales are one of the most vocal marine mammals, particularly during the winter reproductive season (November-March) when they produce stereotyped songs of up to 20 minutes long that can be repeated in bouts that last for hours or days (Watkins et al. 1987). Singing is only exhibited by males (Watkins 1981, Watkins et al. 1987, 2000, Croll et al. 2002), and is considered a reproductive display similar to that of other species such as birds, insects, mice, and humpback whales. While the specific function of fin whale song in reproduction is not clear, it may play a role in mate attraction, advertisement of resources, or male-male competition (Watkins et al. 1987, Croll et al. 2002, Oleson et al. 2014). Although fin whale song is often described as being very stereotyped, the degree of stereotypy and its relationship to the reproductive cycle has not been quantified. Increased singing activity is often cited as an indicator of the reproductive season in fin whales, but seasonal changes in song quality (stereotypy) may be able to provide additional information about reproductive condition and timing of the breeding season in this species.

Fin whale song consists of long sequences of 20-Hz notes with consistent patterns and regular intervals between the notes. These are called 20-Hz notes because fin whale calls described in early studies from the Atlantic were most commonly centered around 20 Hz (Watkins et al. 1987, Edds-Walton 1997), although the actual center frequencies of the 20-Hz note varies between data sets (Watkins et al. 1987, Thompson et al. 1992, Edds-Walton 1997). Some studies have reported two forms of the 20-Hz note that occur at distinct frequencies—called the classic and the backbeat notes—with the backbeat occurring at a lower frequency and with a narrower bandwidth relative to the classic note (Clark et al. 2002, Hatch and Clark 2004, Soule and Wilcock 2013). Fin whales use higher frequency notes in addition to the 20-Hz notes in the Antarctic and Atlantic. However, all fin whale songs have very regular (stereotyped) intervals between their 20-Hz notes—called internote intervals. Songs commonly have one distinct internote interval (called singlets) or two distinct internote intervals (called doublets), and sometimes consist of more complex patterns (Delarue et al. 2013, Soule and Wilcock 2013). In addition to being used in stereotyped songs, fin whales use 20-Hz notes in short series with irregular intervals between the notes (Watkins et al. 1987), but it is not known whether males or females produce this call type. These sounds are common in the summer, are generally produced by animals in groups (Watkins 1981), and are likely used in social interactions and for keeping in contact with conspecifics (Watkins 1981, Watkins et al. 1987, McDonald et al. 1995, Edds-Walton 1997).

Distinct fin whale songs have been described from many of the world's oceans. Although song is consistent within individuals and within regions, the note pattern (i.e., singlets or doublets), internote interval, and sometimes frequency of the songs varies geographically among regions (Watkins et al. 1987, Hatch and Clark 2004). This geographic variation is thought to potentially reflect population structure (Hatch and Clark 2004). The internote intervals of songs within a region have also been shown to evolve seasonally in conjunction with reproductive activity (Watkins et al. 1987, Morano et al. 2012, Oleson et al. 2014), complicating efforts to identify distinct songs for population structure analysis. Little is known about the songs of fin whales in the North Pacific, although one song that evolves seasonally has been described for fin whales off Southern California, Hawaii, and the Bering Sea (Oleson et al. 2014), and a distinct song has been identified in the Gulf of California (Thompson et al. 1992, Hatch and Clark 2004).

In addition to the seasonal patterns in fin whale vocal behaviour that correlate with reproductive activity, diel patterns that may be linked to feeding behaviour have been observed. Fin whale calls appear to be more prevalent during hours of darkness than daylight (Watkins et al. 1987, Simon et al. 2010, Širović et al. 2012), similar to what has been observed for blue whales (Stafford et al. 2005, Wiggins et al. 2005). This has been hypothesized to reflect the fact that fin and blue whales are lunge feeders that primarily feed on zooplankton species that exhibit diel vertical migration patterns. During the day when prey is concentrated at depth (Sato et al. 2013), whales are busy feeding and therefore not singing. At night, when their prey has moved up in the water column and become diffuse, the whales reduce or cease feeding and therefore have more time to sing.

I used passive acoustic recordings from a bottom mounted hydrophone instrument deployed off Brooks Peninsula, Vancouver Island, British Columbia (BC) to investigate the winter presence and vocal behaviour of fin whales in a high-latitude area of the North Pacific. I sought to determine whether whales overwintering in this region were engaged in reproductive behaviour by quantifying changes in fin whale song and its stereotypy over one year (2010-2011) in relation to the reproductive season. I also examined the diel patterns in fin whale call occurrence to determine if they were consistent with the patterns expected for feeding whales. In addition, I provide the first description of fin whale song from British Columbia waters.

2.3 Methods

2.3.1 Data Collection

Passive acoustic data were obtained from the waters off the west coast of Vancouver Island, British Columbia (BC), Canada, at Brooks Peninsula (Figure 2-1) using two Autonomous Underwater Recorders for Acoustic Listening instruments (AURAL, Multi-Electronique, Inc., Rimouski, QC, Canada). The devices were deployed consecutively by the Fisheries and Oceans Canada’s Cetacean Research Program (Pacific Biological Station) in the same location approximately 4.5 km from the nearest point of land on the tip of Brooks Peninsula, in 105 m of water near the edge of the continental shelf (50° 3.616 N, 127° 53.864 W) where the shelf edge comes closer to land than most other places along the BC coast (with the exception of the southwest coast of Haida Gwaii).

The first AURAL deployment recorded from July 15 2010 to April 2 2011. No recordings were collected from April 3 to May 17 2011 (45 days), due to a loss of battery power. The second deployment recorded from May 18 2011 to May 25 2012. I analyzed this deployment up to July 15 2011, so that one full year of data (minus the missing data) were included in this analysis.

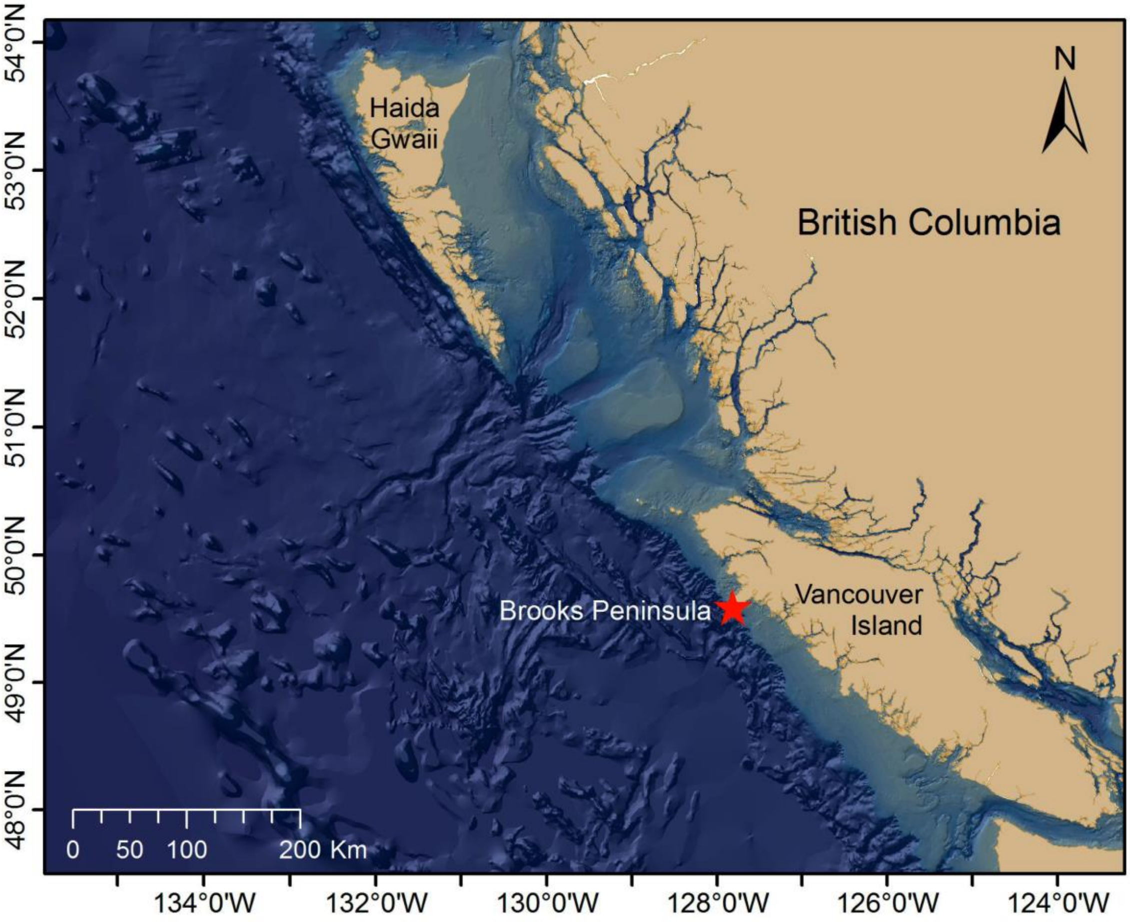

Figure 2-1. Location of passive acoustic recordings (red star) collected by an autonomous, bottom mounted recording instrument from July 15 2010 to July 15 2011 at Brooks Peninsula off the northwest coast of Vancouver Island, British Columbia, Canada.

The AURAL instruments included an HTI-96-MIN hydrophone (High Tech, Inc., Long Beach, MS, USA) with a sensitivity of -165 dB re 1 V/uPa and frequency response of 2 Hz to 30 kHz (specifications are from the manufacturer; hydrophones were not calibrated in the field). The AURALs sampled data at 16,384 Hz with 16-bit resolution, using a recorder gain setting of +16 dB. The instruments were anchored so that the hydrophone was suspended at approximately 10 m above the ocean floor. Data were collected on a 30% duty cycle of 4.5 minutes every 15 minutes. Four 4.5 minute long recordings were saved to each *".wav"* file.

2.3.2 Detection Range Calculation

To obtain a rough estimate of the range at which fin whale vocalizations can be visually detected in a spectrogram, I calculated the distance at which the received level of a fin whale call would exceed the ambient noise level in the frequency range of the call. I first obtained the upper and lower limits, and mid-point, of prevailing ambient spectral levels (decibels relative to 1 μPa in a 1 Hz wide frequency band; dB re 1 $\mu Pa^2/Hz$) at the center frequency of fin whale classic and backbeat notes (as measured in the present study) from the Wenz curves (Wenz 1962). To the lower, upper and mid-point ambient noise spectral levels, I then added 10log(BW), where BW is the bandwidth in Hz (maximum frequency minus minimum frequency in Hz) of the fin whale note, to obtain corresponding ambient noise levels over the frequency band of the note. I then used the simple geometric (spherical) spreading loss formula to find the distance at which the energy in a fin whale call dissipates to the point where its received sound level (level at the recording location) equals the sound level of the ambient noise over the frequency range of the fin whale call, by solving for distance R (in meters):

$$RL = SL - 20\log(R)$$

where RL (in dB re 1 μPA @ 1m) is the received level of the fin whale call at receiver distance R, and SL is the source level of the fin whale call. A source level of 189 dB re 1 μPA @ 1m, measured from eastern North Pacific fin whales (Weirathmueller et al. 2013) was used in this equation. The term -20log(R) represents the transmission loss, or the amount by which the sound level decreases relative to its value at a distance of 1 m from an assumed point source

This simple calculation is intended to provide a rough estimate of the ranges over which fin whales could potentially be detected above ambient noise, and does not account for many variables such as uncertainty in the source levels of the calls, uncertainty in the frequency of the calls, transmission loss due to absorption by the medium (seawater), and refractive effects due to the presence of sound channels and the seabed and sea-surface interfaces. The spherical spreading model assumed here provides conservative estimates of distance relative to those possible in the presence of a sound channel, which could have the effect of trapping sound and allowing for longer propagation ranges (Urick, Robert 1983).

It is also important to note that these calculations provide a range of distances over which fin whale calls just meet or exceed the ambient noise levels, but in the present study, I measured only calls that had higher signal-to-noise ratios than just meeting or exceeding the ambient noise level. Therefore, the calls included in my study likely originated from shorter distances than the estimates calculated, but this is not quantified.

2.3.3 Acoustic Analysis

Each *.wav* file stored by the AURAL consisted of four separate 4.5 min recordings. I first separated the recordings and saved them individually using MATLAB R2009b (The Mathworks Inc 2009). I then down-sampled them to 512 Hz using MATLAB to facilitate the visual analysis of low frequency fin whale vocalizations, and to reduce file size. This resulted in a time-frequency spectrogram of up to 256 Hz, which was high enough to capture all low frequency fin whale vocalizations, but low enough to exclude much unwanted high frequency noise.

I manually reviewed all down-sampled data (30,720 recordings totaling 2,304 h) for the presence of fin whale 20-Hz notes (also referred to as calls in this paper) by visually examining spectrograms using the program Adobe Audition 1.5 (Adobe Systems Inc 2004). When measurable fin whale note sequences were confirmed, I loaded the recordings into the acoustic analysis program, SpectroPlotter Version 4.4.30 (JASCO Applied Sciences 2013), for annotation. Measurable note sequences were those that consisted of at least 5 notes (as in Morano et al., 2012; Soule & Wilcock, 2013; Watkins et al., 1987) and had sufficient signal-to-noise ratio, so as not to miss any calls in the sequence, which would introduce bias into note interval measurements. Also, I only measured sequences that were confidently attributed to being produced by one animal (no overlapping note sequences from multiple whales). Simultaneous calling from multiple whales occurred in the late summer and fall, but was much less common from October through March when whales were singing stereotyped songs.

Each 20-Hz note was identified as a classic note (C note) or backbeat note (B note) based on the relative frequency content and bandwidth of the notes in the doublet songs, with the backbeat being lower in frequency and narrower in bandwidth than the classic note. I looked for high frequency song-type notes such as those observed in the Southern Ocean (Gedamke 2009, Širović et al. 2009) and in the western tropical North Atlantic and northeastern North Atlantic (Hatch and Clark 2004), but did not find any. Although I did observe the 40-Hz call type (Watkins 1981, Širović et al. 2012), I did not include it in the analysis because it is not considered a song component, but rather a social-type sound that is common in the summer. I did not identify any of the lesser known fin whale vocalizations such as the ragged low frequency pulse and low frequency rumble (Watkins 1981, Edds 1988). Notes that had high signal-to-noise ratio were marked for use in analysis of minimum and maximum note frequency and bandwidth analysis.

I annotated fin whale 20-Hz notes in SpectroPlotter following a standardized protocol developed through a collaborative effort to standardize fin whale acoustic analysis (see Rankin et al. 2013, in preparation for detailed protocol). My methods differed from this protocol only in the window type used, and the version of SpectroPlotter used (v. 4.4.30 vs v. 5.0.8), which did not produce measurements of peak frequency. Spectrogram parameters for making annotations were: frequency resolution of 0.1 Hz (providing a true resolution of 0.063 Hz), frame size of 0.1 sec, time step of 0.025 sec, Hanning window type, and rainbow colour scheme. Spectrograms were restricted to a bandwidth of 0 – 50 Hz with a 5 sec window length, and annotations were created using a percent energy selection of 98%. This means that note feature measurements were based on 98% of the energy content (the note) inside the annotation box. Multipath arrivals were not included in the annotation box.

2.3.4 Fin Whale 20-Hz Note Properties

I measured one temporal property (the internote interval) for every fin whale note, and calculated the internote interval (INI) as the time between the centroid time of a note and the centroid time of the following note—irrespective of note type (classic or backbeat). Centroid time was the time at which 50% of the energy in the signal lies before that time, and 50% lies after that time. Intervals greater than 60 s were not considered internote intervals, but were treated as gaps or rests in the song (Watkins et al. 1987) and therefore were not included in the internote interval analysis.

I measured four spectral properties of the 20-Hz notes: center frequency, minimum frequency, maximum frequency and frequency bandwidth. Center frequency was the frequency at which 50% of the signal energy lies above that frequency, and 50% lies below that frequency. Minimum frequency was the lowest measured frequency and maximum frequency was the highest measured frequency of the note. I calculated frequency bandwidth by subtracting the maximum frequency from minimum frequency. I measured center frequency for every note, but I measured minimum frequency, maximum frequency and bandwidth only for notes with high signal-to-noise ratio (SNR) because measurements of these properties were affected by noise.

I examined the temporal and spectral properties of classic and backbeat notes separately according to the interval type that they formed. Classic notes followed by other classic notes (C-C note interval), were examined separately from classic notes followed by backbeat notes (C-B note interval), and backbeat notes followed by backbeat notes (B-B note interval) were examined separately from backbeat notes followed by classic notes (B-C note interval).

2.3.5 Seasonal Occurrence

I described the seasonal occurrence of fin whale 20-Hz notes in the study area by calculating the percentage of days in each month that contained calls. A day was considered to contain fin whale calls whether it contained only a few calls or many calls, of any type. I also described the seasonal occurrence of each type of fin whale call separately.

To analyze seasonal occurrence in terms of the number of distinct calling bouts, the duration of bouts, and the temporal spacing of bouts, I grouped notes into bouts. Following Watkins et al. (1987), I used a time interval of more than 2 hours between any two consecutive notes to distinguish discrete bouts of calling. I considered bouts to be independent events because it was not possible to determine whether the same whale produced different bouts. However, calls occurring when the recorder was off (as part of the duty cycle) might bias the grouping of notes towards higher numbers of shorter bouts.

The duration of each bout was determined as the time in hours between the first and last notes of the bout—and temporal spacing between bouts was the length of time in hours between the last note of one bout and the first note of the next bout. Finally, I tested for changes in occurrence over the calling season by comparing bout durations and bout spacing between months.

2.3.6 Bout Composition

To investigate whether fin whales use irregular notes and stereotyped notes separately, or whether they used them within the same bouts, I examined the composition of bouts by calculating the proportion of each note type (B-C, C-B, C-C, B-B) out of the total number of all notes for each bout. I also tested whether the internote interval and center frequency of the irregular classic note type differed when they were found in mixed bouts as compared to when they were found in bouts consisting only of irregular classic notes.

2.3.7 Seasonal Change in Doublet Song Properties and Stereotypy

To characterize the doublet song and to test for changes over the calling season, I examined three temporal properties of the song: the C-B internote interval, B-C internote interval, and internote interval difference. Internote interval difference was the length of the long interval (C-B interval) minus the length of the short interval (B-C interval). To avoid pseudoreplication, I calculated the mean of each song property for each bout. I also calculated property means only for bouts that had five or more measurements of the property.

I also examined two spectral properties of the doublet song: the center frequency of the backbeat note, and the center frequency of the classic note. However, there were not enough songs in each month with a sufficient number of high quality notes to allow for comparisons of means for minimum frequency, maximum frequency and bandwidth. For mixed bouts (bouts containing both doublets and irregular classic notes and/or singlet backbeat notes), I used only measurements from the doublet notes. I tested for differences in the means of each property between months.

To characterize the stereotypy of the doublet songs (consistency within songs) and to test whether stereotypy changes over the calling season, I calculated the coefficient of variation (CV=SD/mean) of each song property for each song. The CV is a dimensionless number that quantifies the degree of variability relative to the mean. I used CV over other measures of variation because it allows comparison of the variation of song properties that have different mean values and units of measurement. I then tested for differences in the song CVs between months.

As a measure of overall stereotypy per song, I averaged the CV values of the five properties measured for each song. I included only songs with 5 or more measurements for all five properties in this analysis. I then applied a Loess curve to the song means to visualize the change in stereotypy over time.

2.3.8 Diel Occurrence

To test whether fin whale call occurrence varied with daylight condition, and to test whether different patterns existed before and after the onset of the fin whale breeding season, I summed the number of hours containing calls for four categories of the day—dawn, dusk, night and day—before and after October 15. October 15 was chosen because I found that overall song stereotypy was high after mid-October. I defined dawn as the time of twilight between nautical twilight start and sunrise, and dusk as the time of twilight between sunset and nautical twilight end. Night was the time between nautical twilight and sunrise, and day was the time between sunrise and sunset (sunset, sunrise, and twilight information was retrieved from the US Naval Observatory website: http://aa.usno.navy.mil/data/docs/RS_OneYear.php). Because the times of twilight change over the duration of the pre and post October 15 periods, the times of dawn and dusk for each period were defined so that the full range of twilight times that occurred in each period were included (pre October 15: dawn = 0300h through 0600h, dusk = 1700h through 2100h; post October 15 dawn= 0500h through 0800h, dusk= 1600h through 1900h). Hours for which twilight, sunrise or sunset occurred within that hour were included in the dawn or dusk category, instead of the day or night category. Therefore, the hours of dawn and dusk were overestimated, ensuring that only hours of true night and day were included in the night and day categories.

2.3.9 Statistical Analysis

All statistical analyses were performed using ‘R’ version 2.14.1 (R Development Core Team 2011). I used a Box-Cox transformation (‘R’ package MASS) to normalize the data when the assumptions of normality (tested with Shapiro-Wilks test) and heterogeneity of variance (tested with Levene’s test) were not met. Comparisons among months were made using one-way analysis of variance (ANOVA, α=0.05) on the Box-Cox transformed data. For significant effects, post-hoc comparisons between groups were made using a Tukey Honest Significant Difference test. Otherwise, comparisons of medians were made using Mann-Whitney U tests or Kruskal-Wallis tests for non-parametric data. Significant effects found with a Kruskal-Wallis test were followed by a post-hoc test to compare group medians using a pairwise Mann-Whitney U test and the Bonferonni method to correct for multiple comparisons. To investigate diel call occurrence, I used a chi-square goodness of fit analysis to test the hypothesis (α=0.05) that the number of hours containing calls in each daylight category was proportional to the number of hours in that daylight category (expected value). To graphically represent the results, I plotted the standardized residuals of the chi-square analysis (Agresti 2007). All graphics and reported descriptive statistics were based on untransformed data. Spectrograms were generated with SpectroPlotter Version 4.4.30 (JASCO Applied Sciences 2013). All other graphics were generated in R with the ggplot2 package (Wickham 2009).

2.4 Results

2.4.1 Fin Whale 20-Hz Notes

In total, I annotated 10,362 fin whale 20-Hz notes (5,848 classic notes and 4,514 backbeat notes) and found three patterns of notes (Figure 2-2, Figure 2-3). The most common pattern was a doublet consisting of regularly alternating classic and backbeat notes with a longer internote interval (INI) from classic to backbeat note (C-B INI: Mean=17.3 s, SD=3.7, n=3,692) and a shorter internote interval from backbeat to classic note (B-C INI: Mean=12.9, SD=2.4, n=3,894). The second most common pattern consisted of consecutive classic notes with irregular internote intervals (C-C INI: Mean = 17.4, SD=8.0, n=1,509)—and the third note pattern was relatively uncommon and consisted of regularly spaced (singlet) consecutive backbeat notes (B-B INI: Mean=28.8, SD=6.9, n=326). The mean interval between consecutive backbeats of this third pattern was similar to the interval between backbeats in the doublet pattern (i.e., the sum of the long and short doublet intervals = 30.2 s).

The spectral properties of classic notes found in the irregular pattern overlapped significantly with those of classic notes found in the doublet pattern. However, classic notes in the irregular pattern were more variable, higher on average in frequency, and larger in bandwidth than classic notes in the doublet pattern (Figure 2-3). On average, classic notes that occurred in irregular patterns had frequencies that swept down from 34.2 (SD=4.4, n=172) Hz to 20.8 (SD=2.3, n=172) Hz, and had a center frequency of 25.7 (SD=2.7, n=1,509) Hz and a bandwidth of 13.4 (SD=3.2, n=172) Hz. In contrast, the classic notes that occurred in doublet patterns had frequencies that swept down from 30.7 (SD=2.5, n=444) Hz to 19.5 (SD=1.4, n=444) Hz, and had a center frequency of 23.4 (SD=1.6, n=3,692) Hz and bandwidth of 11.2 (SD=2.4, n=444) Hz.

The spectral properties of the backbeat note were distinct from the classic note. Backbeat notes were consistently lower in bandwidth, and minimum, maximum and center frequencies than classic notes (Figure 2-3). The spectral properties (and variation in the properties) of backbeat notes found in the consecutive backbeat note pattern were similar to the properties of backbeat notes found in the doublet pattern (Figure 2-3). On average, backbeats in the consecutive backbeats pattern swept down from 23.4 (SD=1.7, n=37) Hz to 16.0 (SD=0.9, n=37) Hz with a center frequency of 19.0 (SD=1.2, n=326) Hz and bandwidth of 7.4 (SD=1.6, n=37) Hz. Similarly, backbeats in the doublet pattern swept down from 23.5 (SD=1.7, n=279) Hz to 15.8 (SD=1.3, n=279) Hz with a center frequency of 19.1 (SD=1.1, n=3,894) Hz and bandwidth of 7.7 (SD=2.2, n=279) Hz.

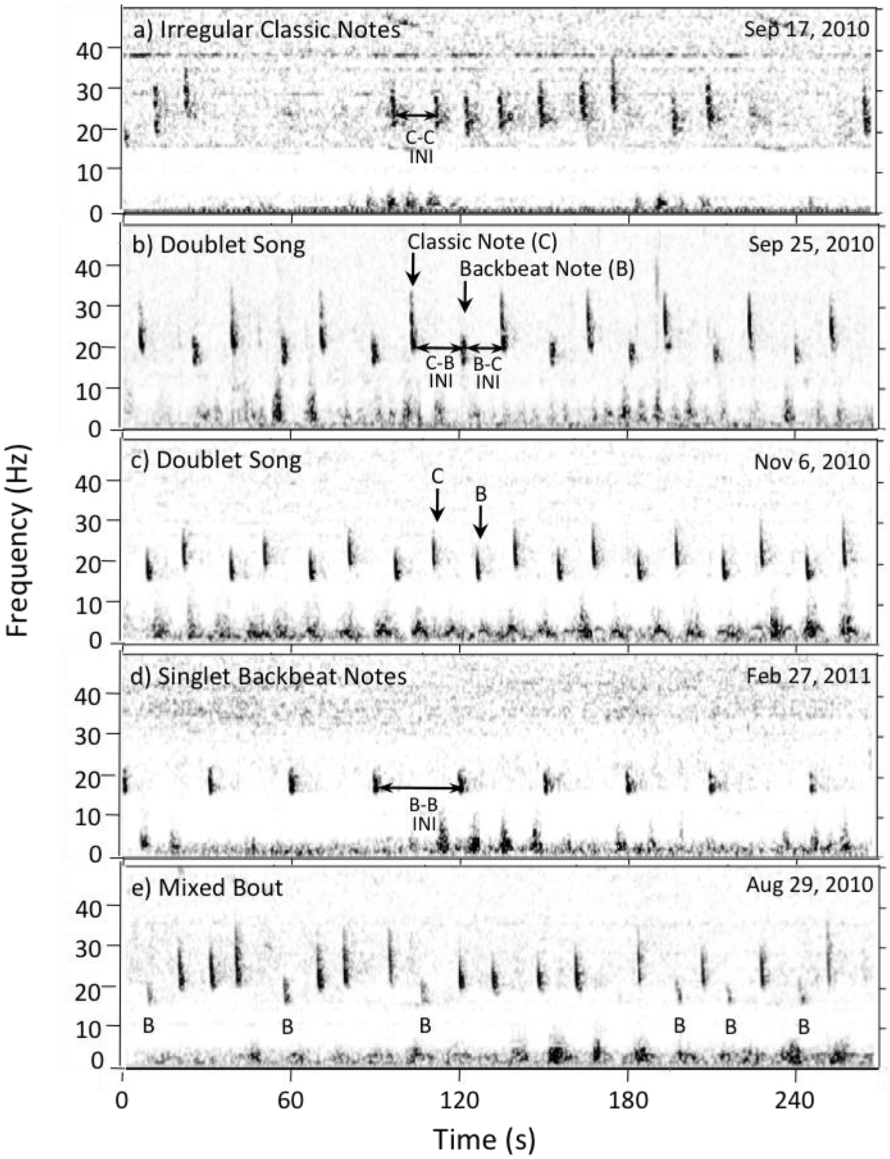

Figure 2-2. Spectrograms of representative examples of fin whale 20-Hz notes recorded off Brooks Peninsula, British Columbia, July 2010 to July 2011. a) Irregular classic notes recorded in September; b) a segment of doublet song showing the alternating classic (C) and backbeat (B) notes and two distinct note intervals, recorded in September; c) a segment of doublet song recorded in November, illustrating the lower frequency of the classic notes as compared to the classic notes in the doublets recorded in September; d) a segment of a singlet backbeat note pattern recorded in February; e) a segment of a calling bout composed of a mix of irregular classic notes and doublet notes recorded in August. The letter “B” indicates backbeat notes in the doublet pattern portion of the mixed bout. Spectrogram parameters were 512 Hz sampling rate, 1024 pt. FFT, 80% overlap, Hanning window function, 0.5 Hz and 0.4 s resolutions.

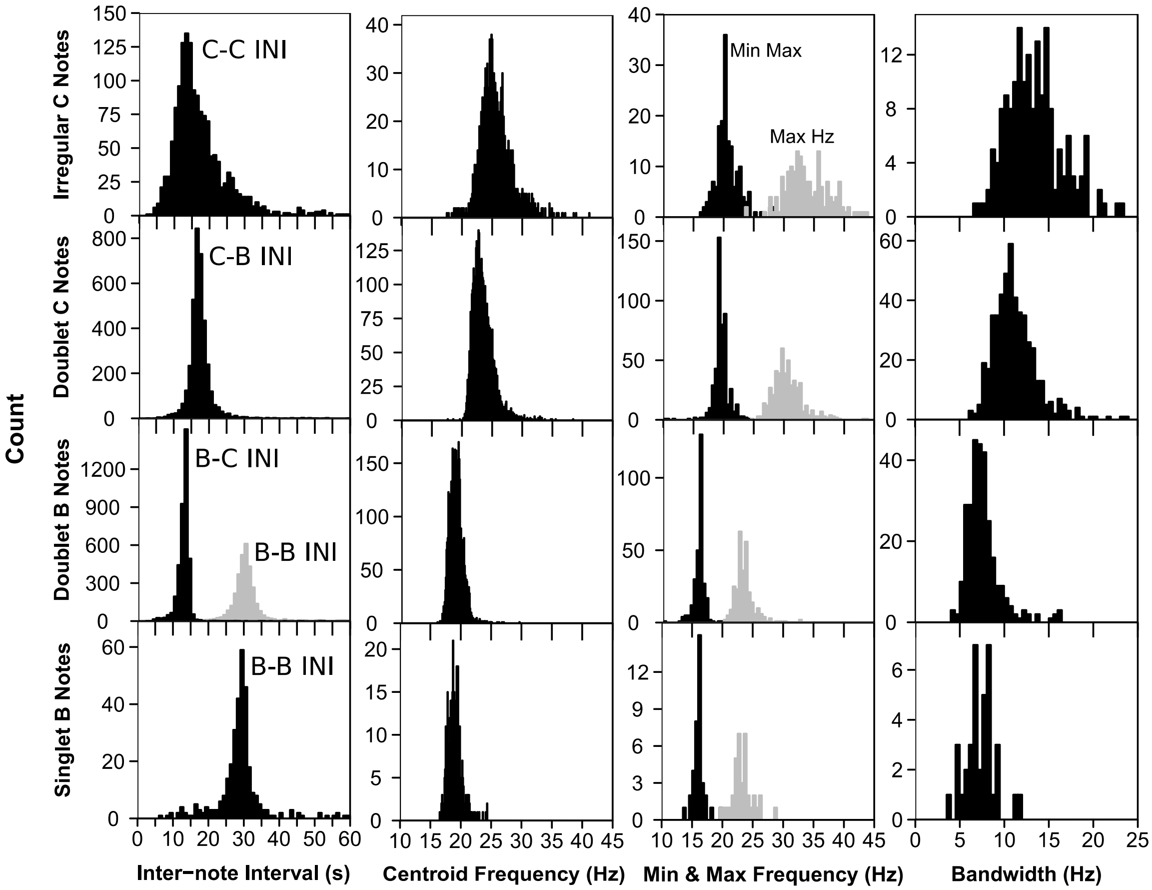

Figure 2-3. Temporal and spectral properties of fin whale 20-Hz notes (classic and backbeat notes) recorded July 2010 to July 2011 at Brooks Peninsula, British Columbia. Each row represents a note type: irregular classic notes, classic notes found in doublets, backbeat notes found in doublets, and singlet backbeat notes. The times between backbeats in the doublet pattern is shown in grey in the doublet backbeat note internote interval plot for comparison with the singlet backbeat note interval. Axes differ between plots. Internote interval histograms have a bin width of 1 s, center frequency histograms have a bin width of 0.1 Hz, and minimum & maximum frequency and bandwidth histograms have a bin width of 0.5 Hz. Only notes with high signal-to-noise ratio were included in the minimum and maximum frequency and bandwidth plots; all notes were included in other plots.

2.4.2 Detection Range

I estimated that the received level of the fin whale classic note, based on a center frequency of 25.1 Hz and bandwidth of 11.2 Hz, would decay to ambient noise levels when the calling whale is at a distance of 1,498 km in low ambient noise levels (at the lower limit of the prevailing ambient noise level), 8.4 km in high ambient noise levels (at the higher limit of the prevailing ambient noise level) and 112 km at average noise levels. The estimated distances for the lower frequency backbeat note (based on a center frequency of 19.7 Hz and bandwidth of 7.4 Hz) where slightly smaller, with a distance of 1,304 km in low ambient noise levels, 4.6 km in high ambient noise levels and 78 km at average noise levels.

The estimated distances at which the calls equal ambient noise levels represent maximum distances for the calls included in this study because calls needed to exceed the ambient noise levels (by some un-quantified amount) in order to be included in the analysis. However, the potential effects of sounds channels, which could increase the detection ranges, are not accounted for.

2.4.3 Seasonal Occurrence

Call Occurrence—Recordings were made between July 15 2010 and July 15 2011, except for the 45 days when recordings were not available from April 3 to May 17 2011. During this ~10.5-month window, 20-Hz notes were only found between August 15 and March 29. The time between the first and last calls (the calling season) spanned 226 days, during which time calls occurred in every week except one week in January (Figure 2-4). Combining all note types revealed that the highest number of calls occurred in September with 1,868 notes detected over 87% of days that month. The number of days that contained fin whale calls decreased slightly in October (58%) and November (53%), and was the lowest in December (35%), January (39%) and March (32%), with February (68%) showing an increase. Only 45% of days in August contained calls. However, of the 17 days in August that occurred after the first call was detected, 14 contained calls (82%).

The occurrence of doublet notes followed a similar pattern with peak daily occurrence in September (73%). The number of days containing consecutive classic notes was low except for August and September when they occurred on more days than doublet notes (Figure 2-4), while the number of days containing consecutive backbeat notes was relatively low each month, with no clear seasonal pattern (Figure 2-4).

Number of Bouts—I measured a total of 222 bouts of calling. The greatest number of bouts occurred in September (n=61), followed by February (n=32). The smallest number of bouts occurred in March (n=13). Remaining months had between 19 and 25 bouts (Figure 2-5).

Bout Duration—Kruskal-Wallis tests showed no significant difference in bout duration between months for all bouts (χ^2=12.99, DF=7, p=0.0724) and for bouts that were longer than the length of one duty cycle (χ^2=11.92, DF=7, p=0.1034; Figure 2-5). Overall, measured bout durations (excluding bouts of less than one record length) tended to be shortest in January (Median=0.6 hr and longest in March (Median=2.3 hr). In August, September and October, all bouts were <4 hrs long. Bouts <4 hrs also occurred throughout the rest of the calling season (November through March) but these months also contained some longer bouts (Figure 2-5). The longest bout duration was 13.5 hrs and occurred in November. 507 notes were recorded from this bout, but accounting for the 30% duty cycle the estimated actual number of notes in this bout is around 1,688.

Temporal Spacing of Bouts—A Kruskal-Wallis test showed a small but significant difference in the length of time between bouts among months (χ^2=17.41, DF=7, p=0.015). A post-hoc Mann-Whitney test with Bonferroni correction showed only September (Median=6.4 hr) and November (Median=14.7 hr) had significantly different bout spacing (p=0.022). Monthly median bout spacing ranged from 6.4 hr in September to 19 hr in October (Figure 2-5). The longest time between bouts was 201.5 hours (8.4 days) and occurred in January. In general, the length of time between bouts appeared to be smaller in the summer (August and September), larger in the fall (October to December), and smaller again the winter (January and February). Time between bouts was most variable in March.

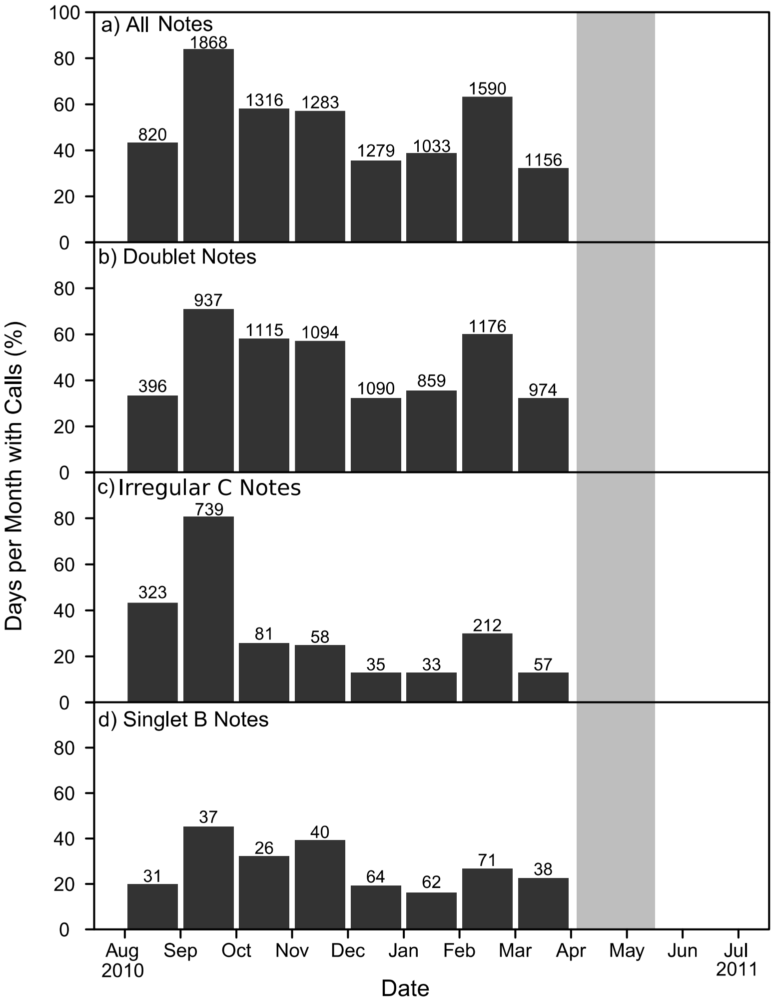

Figure 2-4. Monthly occurrence of fin whale 20-Hz notes recorded at Brooks Peninsula, British Columbia, from July 15 2010 to July 15 2011. Calling started on August 15 2010 and the last call was recorded on March 29 2011. Occurrence is expressed as the percentage of days per month that contained a) 20-Hz notes of any type b) doublet 20-Hz notes, c) irregular classic 20-Hz notes and d) singlet backbeat 20-Hz notes. Numbers at the top of the bars are the total number of calls recorded in that month. Grey shading indicates a period of unavailable data.

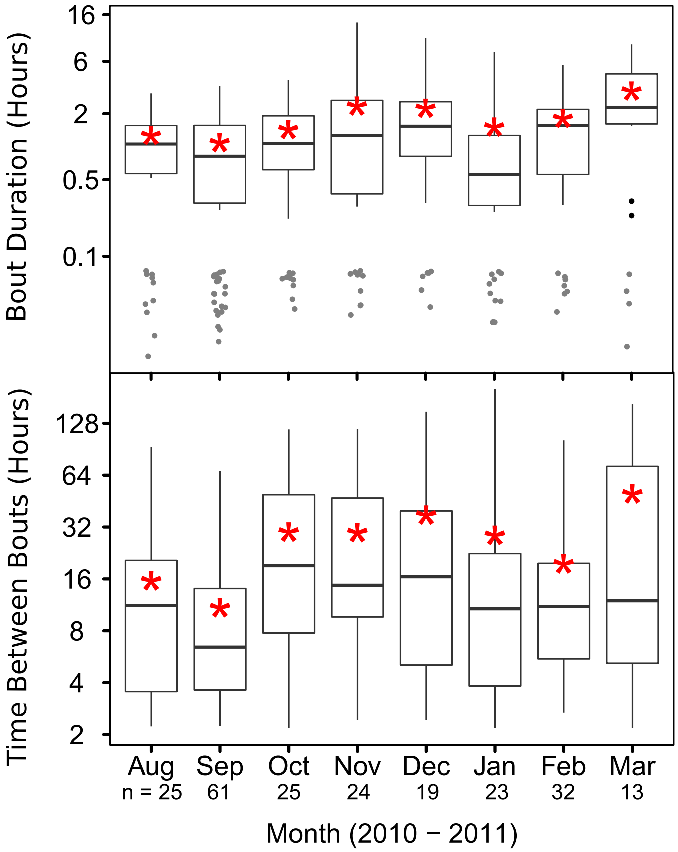

Figure 2-5. The durations of fin whale 20-Hz note bouts (n=222) (top) and the intervals between them (bottom) recorded July 2010 to July 2011 at Brooks Peninsula, British Columbia. Filled grey points are bouts that were one, or less than one, recording length in duration (4.5 min) and were not included in the box and whisker plots of bout duration. For the time between bouts, no data were available for 0-2 hours because distinct bouts were defined as having 2 or more hours of silent time between the end of one bout and the start of the next bout. The box corresponds to the inter-quartile range, with the lower and upper hinges of the box representing the first and third quartiles. The whiskers extend to the highest and lowest values that are within 1.5 times the inter-quartile range from the hinges. Filled black points are outliers. Horizontal bar is the median. Red stars are means. Sample size (number of bouts per month) is indicated underneath each month. The y-axes are on a logarithmic scale.

2.4.4 Bout Composition

The irregular classic note pattern and doublet pattern often occurred together within the same bout of calling, particularly in August and September (Figure 2-6). In August and September, these mixed bouts contained 5% - 95% irregular classic notes (C-C note intervals) with the balance of each bout consisting of doublets (C-B and B-C note intervals) and a small percentage of consecutive backbeat notes (B-B note intervals). From October through March, bout composition was much less variable (Figure 2-6). During this time, many bouts were composed mostly or entirely of doublets (~50% C-B and ~50% B-C intervals). Only five bouts (out of a total of 222 bouts) were composed entirely of consecutive backbeat notes. The majority of consecutive backbeat notes occurred in small numbers within doublet bouts, where it appeared that a classic note was skipped every so often.

Bouts consisting entirely of irregular classic notes (n=20) occurred in August-September and January-February, but not in October, November, December or March. There was no significant difference in bout mean internote interval (Mann-Whitney U test, W=769, p=0.7188) for irregular classic notes that occurred within mixed bouts (median=17.4, interquartile range=14.7-19.8, n=73) as compared to those that occurred in bouts consisting entirely of irregular classic notes (median=17.5, interquartile range=15.1-20.4, n=20). There was a significant difference (Mann-Whitney U test, W=997, p=0.0178) in bout mean center frequency between the mixed bouts (median= 25.3, interquartile range=24.3-26.2, n=73) and pure bouts (median=26.2, interquartile range=25.2-27.6, n=20).

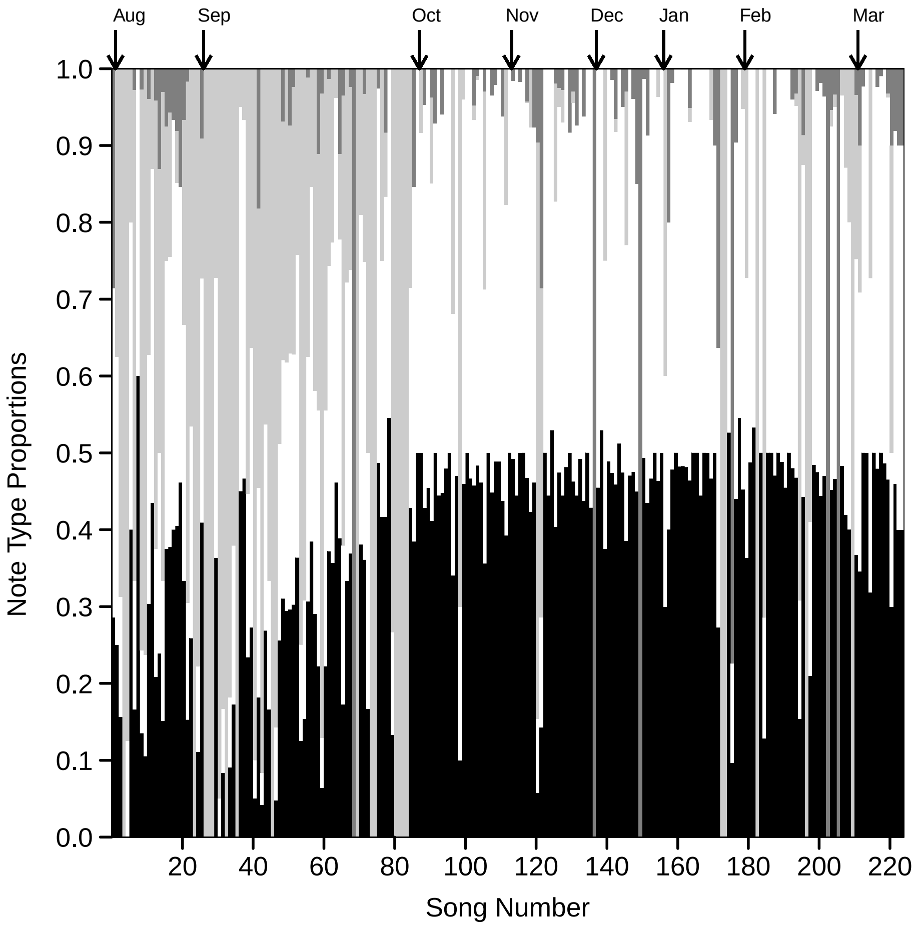

Figure 2-6. Composition of fin whale 20-Hz note bouts (n=222) recorded between July 2010 and July 2011 at Brooks Peninsula, British Columbia. Each vertical bar represents one bout. Black portions of bars represent the proportion of the bout that is composed of the C-B interval, white represents the B-C interval, light grey represents the C-C interval, and dark grey represents the B-B interval. Note the change in composition to songs being composed of about half C-B intervals, and half B-C intervals (the doublet pattern) in October. Arrows at the top of the figure indicate the first song in each month.

2.4.5 Seasonal Change in Doublet Song Properties and Stereotypy

The internote intervals of the doublet song increased slightly over the course of the calling season (Figure 2-7). The C-B interval increased by approximately 2.7 s (from 15.0 s in August to 17.7 s in January), and the B-C internote interval increased by approximately 2.5 s (from 10.9 s in August to 13.4 s in January) with most of the change occurring from August through October (see Table 2-1 for all means and standard deviations). The C-B interval was significantly smaller in August compared to December, January, February and March, and the B-C interval was significantly smaller in August and September compared to the rest of the months.

The difference between the C-B and B-C interval lengths (internote interval difference) decreased from a high in August (5.2 s) to a low in January (3.8 s), and increased again slightly in February and March (Figure 2-7; Table 2-1). The internote interval difference was significantly higher in September than January. The internote interval difference was most variable among songs in August, and this variability resulted in no significant difference being found when comparing August to the other months Figure 2-7.

Classic note center frequency decreased approximately 3.3 Hz from a high in August (26.1 Hz) to a minimum in January (22.8 Hz). Classic note center frequency was significantly higher in August compared to all other months, and higher in September compared to months from October through March (Figure 2-7).

The center frequency of the backbeat note did not change dramatically over the course of the calling season, and did not show a clear trend (Figure 2-7). Although the differences were small, January (19.6 Hz) was significantly higher in frequency than August (18.8 Hz) and March (18.6 Hz).

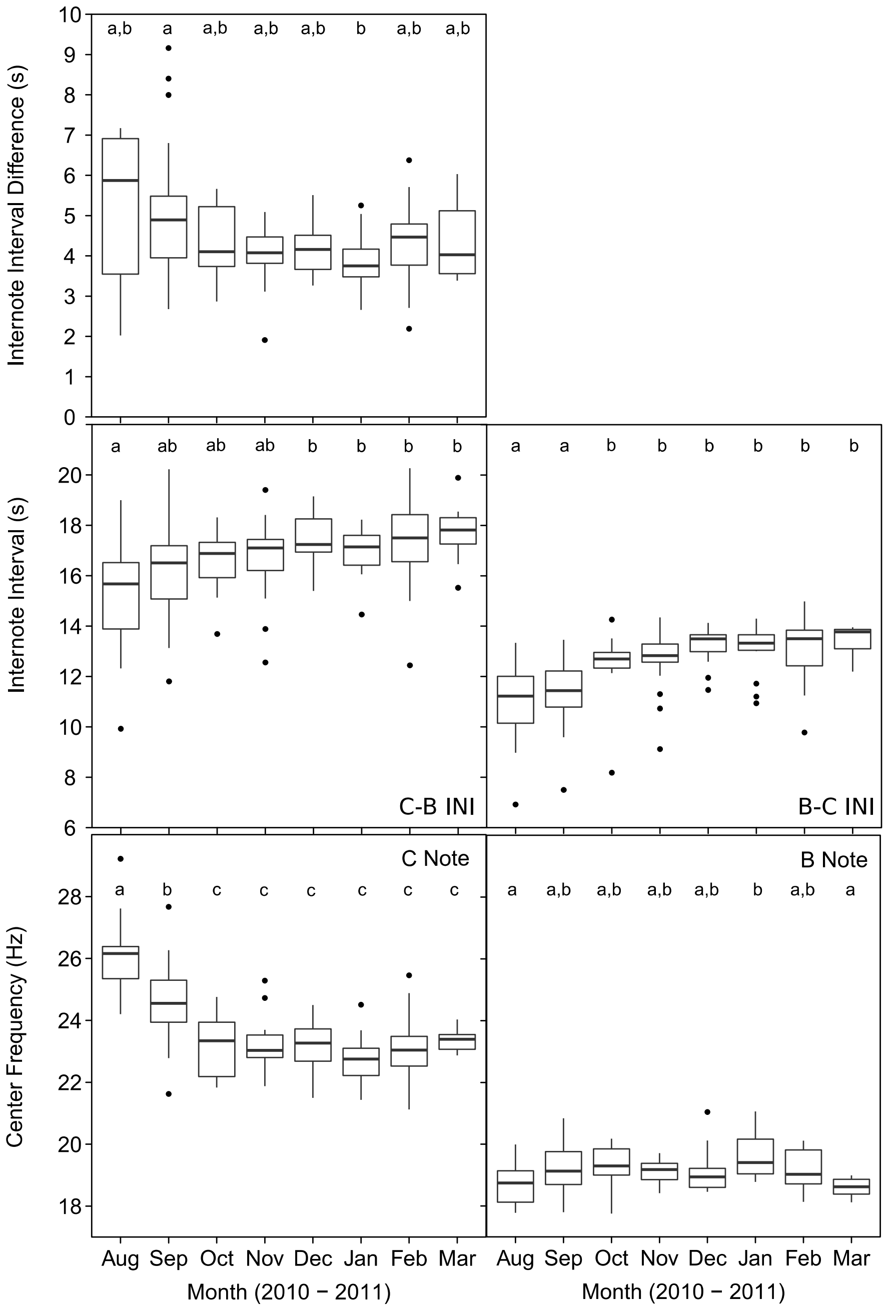

Figure 2-7. Temporal and spectral properties of fin whale doublet songs recorded from July 2010 to July 2011 at Brooks Peninsula, British Columbia. The box corresponds to the inter-quartile range, with the lower and upper hinges of the box representing the first and third quartiles. The whiskers extend to the highest and lowest values that are within 1.5 times the inter-quartile range from the hinges. Filled black points are outliers. Horizontal bar is the median. Different letters indicate significant differences; groups that share a letter do not differ significantly. Summary statistics, significance tests and sample sizes are contained in Table 2-1.

The monthly mean coefficient of variation (CV) of the C-B internote interval, B-C internote interval, internote interval difference and classic note center frequency all decreased from a high in August to a minimum in January, increasing again slightly in February and March (Figure 2-8). The monthly mean CV of the backbeat note center frequency did not show this trend, but was consistently low in all months (see Table 2-1 for all means and standard deviations). In addition to the mean CV being lowest in January for each song property (except backbeat note center frequency), the variation among the CVs in each month was also lowest in January (expressed as standard deviation in Table 2-1). The C-B internote interval CV was significantly higher in August than all other months, and significantly higher in September than November to February, and January was significantly lower than February. The B-C interval CV was significantly lower from October to March than August and September. The CV of internote interval difference was also significantly lower for the months of October to March than for August, and in January, it was significantly lower than both August and September. The CV of the classic note center frequency was significantly higher in August than October to February, and higher in September than November and January. The CV of the backbeat-note center frequency did not significantly differ between months (Table 2-1).

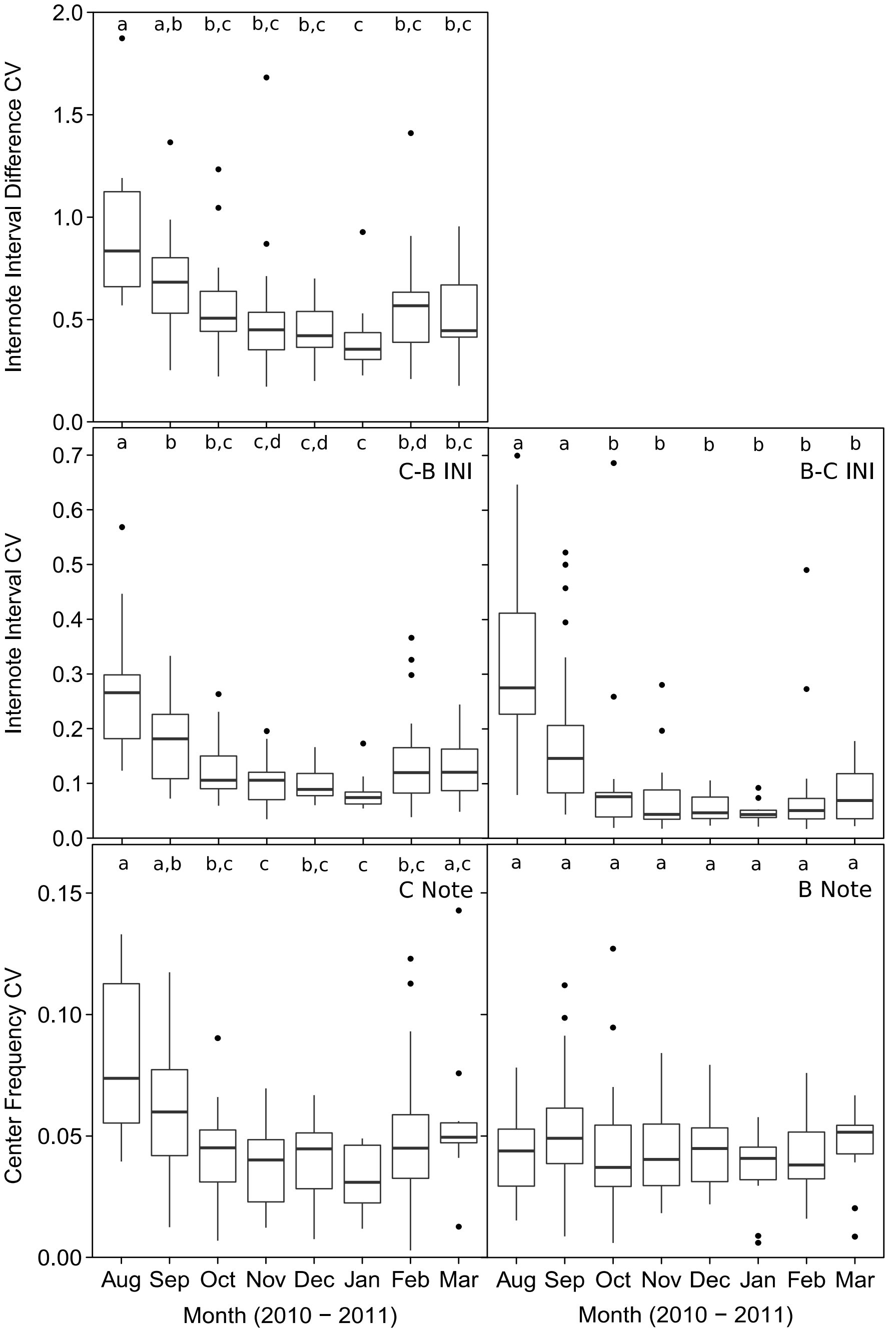

Figure 2-8. Coefficient of variation (CV=SD/mean) of temporal and spectral properties of fin whale doublet songs recorded from July 2010 to July 2011 at Brooks Peninsula, British Columbia. CV is a measure of the consistency (stereotypy) of song properties. Different letters indicate significant differences; groups that share a letter do not differ significantly. Summary statistics, significance tests and sample sizes are contained in Table 2-1.

Table 2-1. Mean, coefficient of variation (CV) and standard deviations of fin whale doublet song temporal and spectral properties by month in 2010-2011. Sample sizes are the number of songs analyzed per month for each song property. Monthly mean, CV and SD are based on song means. Significant differences among months were tested using one-way ANOVA.

				Month					**Statistics**
	Aug	**Sep**	**Oct**	**Nov**	**Dec**	**Jan**	**Feb**	**Mar**	**ANOVA**
Internote Interval Difference (C-B minus B-C interval)									
N	n = 9	n = 26	n = 20	n = 19	n = 16	n = 13	n = 24	n = 10	
Mean	5.2 ± 1.96	5.0 ± 1.66	4.3 ± 0.85	4.1 ± 0.72	4.2 ± 0.67	3.8 ± 0.77	4.3 ± 0.97	4.4 ± 0.98	$F_{7,129}$ =2.68, P=0.013
CV	0.96 ± 0.4	0.68 ± 0.23	0.55 ± 0.25	0.51 ± 0.33	0.45 ± 0.14	0.41 ± 0.18	0.56 ± 0.27	0.53 ± 0.27	$F_{7,129}$ =4.99, P=0
C-B Internote Interval (s)									
N	n = 13	n = 29	n = 21	n = 19	n = 16	n = 14	n = 25	n = 10	
Mean	15.0 ± 2.41	16.3 ± 1.92	16.7 ± 1.09	16.7 ± 1.55	17.4 ± 1.09	16.9 ± 0.97	17.3 ± 1.55	17.7 ± 1.19	$F_{7,139}$ =3.77, P=0.001
CV	0.28 ± 0.13	0.17 ± 0.07	0.12 ± 0.05	0.1 ± 0.04	0.1 ± 0.03	0.08 ± 0.03	0.14 ± 0.08	0.13 ± 0.07	$F_{7,139}$ =11.29, P=0
B-C Internote Interval (s)									
N	n = 14	n = 29	n = 23	n = 22	n = 16	n = 14	n = 25	n = 11	
Mean	10.9 ± 1.66	11.4 ± 1.27	12.6 ± 1.08	12.7 ± 1.18	13.2 ± 0.73	13.0 ± 1.03	13.1 ± 1.2	13.4 ± 0.57	$F_{7,146}$ =12.14, P=0
CV	0.33 ± 0.18	0.18 ± 0.14	0.1 ± 0.14	0.07 ± 0.06	0.06 ± 0.03	0.05 ± 0.02	0.08 ± 0.1	0.08 ± 0.06	$F_{7,146}$ =13.89, P=0
Classic Note Center Frequency (Hz)									
N	n = 13	n = 29	n = 21	n = 19	n = 16	n = 14	n = 25	n = 10	
Mean	26.1 ± 1.33	24.5 ± 1.2	23.2 ± 0.94	23.2 ± 0.79	23.2 ± 0.8	22.8 ± 0.83	23.1 ± 0.97	23.3 ± 0.36	$F_{7,139}$ =20.09, P=0
CV	0.08 ± 0.03	0.06 ± 0.03	0.04 ± 0.02	0.04 ± 0.02	0.04 ± 0.02	0.03 ± 0.01	0.05 ± 0.03	0.06 ± 0.03	$F_{7,139}$ =5.96, P=0
Backbeat Note Center Frequency (Hz)									
N	n = 14	n = 29	n = 23	n = 22	n = 16	n = 14	n = 25	n = 11	
Mean	18.8 ± 0.77	19.2 ± 0.73	19.3 ± 0.63	19.1 ± 0.39	19.1 ± 0.7	19.6 ± 0.72	19.1 ± 0.64	18.6 ± 0.3	$F_{7,146}$ =3.16, P=0.004
CV	0.04 ± 0.02	0.05 ± 0.02	0.04 ± 0.03	0.04 ± 0.02	0.04 ± 0.02	0.04 ± 0.01	0.04 ± 0.02	0.05 ± 0.02	$F_{7,146}$ =0.93, P=0.483

The general trend in overall song CV (the average of the CV's of the five properties for each song) showed a sharp decrease from August to mid-October, leveling out through December with a minimum in January, and increasing again slightly through March (Figure 2-9). Although the general trend shows that CV is increasing after the minimum in January, there are a relatively large of number of songs that have a low overall CV (<0.08). The increase was driven by the addition of a relatively small number of songs that had a high overall CV. This is in contrast to the period of decline in CV from August to mid-October, where most songs had a relatively high CV, and fewer songs had a CV < 0.08 (Figure 2-9).

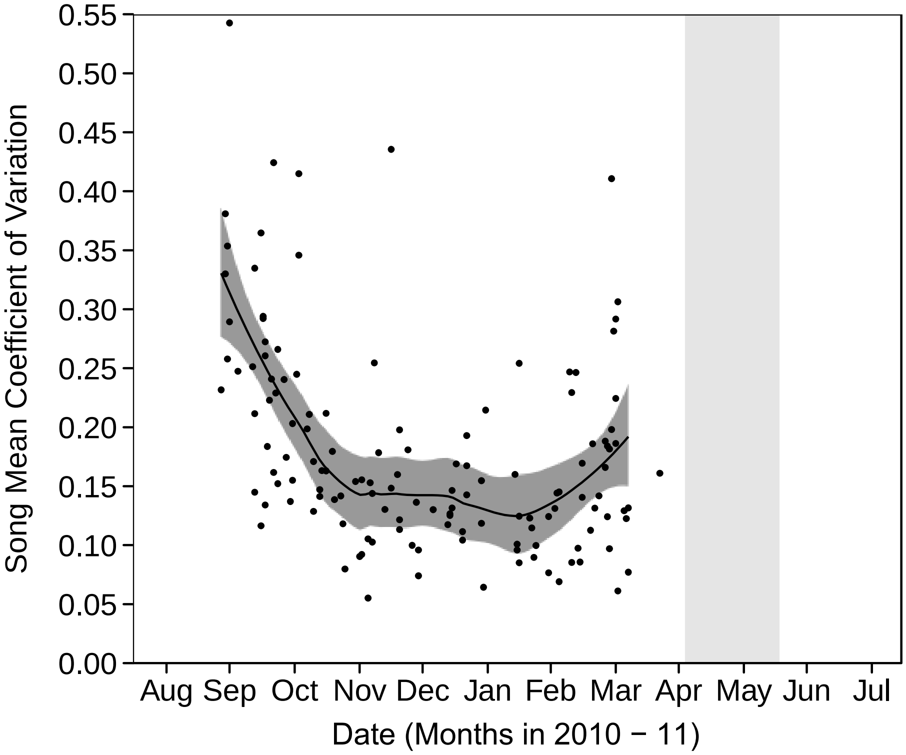

Figure 2-9. Seasonal change in fin whale doublet song stereotypy over the 2010-2011 calling season at Brooks Peninsula, British Columbia. Stereotypy was measured as the coefficient of variation (CV=SD/mean). Each point is a mean of the CV of 5 properties of one song (C-B INI, B-C INI, INI difference, C note center frequency and B note center frequency). Only songs with at least 5 measurements of each property were included (n=138). The black line is a Loess curve fitted (span=0.5) to song means (excluding the last influential data point). The dark shading is the standard error of the Loess curve, and the grey shaded area shows the period of unavailable data.

2.4.6 Diel Occurrence

Diel patterns in call occurrence were tested for, both before and after October 15 2010. Before October 15, hours containing calls were more common during the day and less common at night and dawn (Figure 2-10), though this trend was not significantly different from the null hypothesis (chi-square test, $\chi^2 = 2.74$, $p = 0.434$, df=3). From October 15 onwards, the diel pattern of hours containing calls differed significantly from the null hypothesis of call occurrence being proportional across daylight categories (chi-square test, $\chi^2 = 17.67$, $p = 0.0005$, df=3; Figure 2-10). The significance of this trend reflects the fact that a higher proportion of calls occurred during the night than during the day.

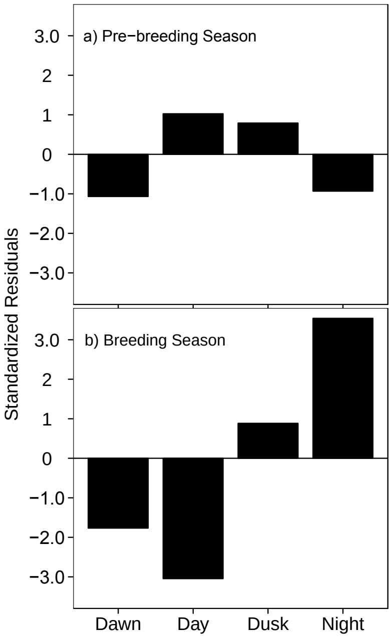

Figure 2-10. Standardized residuals from a chi-squared analysis of the occurrence of fin whale 20-Hz notes in daylight categories of dawn, day, dusk and night for a) calls recorded before October 15 2010 (determined to represent the pre-breeding season in this study) and b) calls recorded after October 15 2010 (determined to represent the breeding season). Positive values indicate daylight categories where the observed occurrence of calls was higher than expected under the null hypothesis that calls were equally likely in each category; negative values indicate categories with lower than expected call occurrence. Patterns in call occurrence were significantly different from the null hypothesis after October 15, with more calls than expected occurring at night, and fewer during the day. The trend in call occurrence in the night and day was opposite before October 15, although it was not a significant trend.

2.5 Discussion

Passive acoustics indicate that fin whales are present throughout the winter off Vancouver Island BC, a region known to support fin whales in the summer. Patterns in their calls suggest that fin whales may remain in British Columbia waters to feed and mate rather than migrate south in the winter. These findings add support to recent observations of others suggesting that fin whale population structure and migration is more complex than previously thought.

2.5.1 Year-Round Presence and Feeding in BC

Historical whaling data (Gregr et al. 2000, Mizroch et al. 2009) and recent visual observations (Ford et al. 2010a, Ford 2014) indicate that fin whales commonly occur in BC during summer (May–October). They were generally believed to migrate south for the winter, but sightings of 8 fin whales in BC between January and March (2006–2008, Ford et al. 2010) and the passive acoustic data I analyzed indicate that some occur here during winter. Thus, it is clear that fin whales are present in British Columbia waters year-round.

The 20-Hz calls recorded in my study from mid-August through March provide evidence that fin whales are present in BC consistently throughout the winter. The absence of 20-Hz calls in the spring and early summer months (May-July) is consistent with other studies showing that fin whales reduce or cease making 20-Hz calls in the summer months (Mizroch et al. 2009, Širović et al. 2012), and does not imply an absence of whales in the area at this time. The abrupt start of calling mid-August likely reflects a change in fin whale calling behaviour rather than the arrival of whales to the area because fin whales were historically killed in this region throughout spring and early summer (Gregr et al. 2000).

The acoustic presence of fin whales in my study is similar to that seen over seven years for blue whales off Vancouver Island (Burtenshaw et al. 2004). The extended presence of these baleen whales suggests that they do not merely pass through these waters, but that this is an important habitat for them (Burtenshaw et al. 2004). The distributions of baleen whales are tightly linked to the availability of prey (Nemoto 1970, Piatt and Methven 1992, Friedlaender et al. 2006, Laidre et al. 2010), and therefore the year-round presence of fin whales in BC is likely related to food availability, as has been suggested for fin whales in the Gulf of Alaska (Stafford et al. 2007). British Columbia's waters are highly productive, with strong and persistent upwelling off Vancouver Island from spring to fall providing the nutrients needed to sustain a high biomass of phytoplankton and zooplankton (Mackas 1992, Gregr and Trites 2001, Burtenshaw et al. 2004). Euphausiids (mainly *Euphausia pacifica* and *Thysanoessa spinifera*) are the primary prey of fin whales in BC (Flinn et al. 2002, Ford 2014), and are found consistently along the shelf break from February to November (Mackas 1992) and sometimes over the shelf from August to November. The waters of British Columbia are a known summer feeding ground for fin whales (Gregr et al. 2000, Flinn et al. 2002, Mizroch et al. 2009, Ford 2014). With zooplankton biomass persisting through much of the year (February-November), it is possible that at least some fin whales choose to remain at these high latitudes, potentially feeding throughout the winter (or fasting during times of low prey abundance) rather than migrating south.

The pattern of less singing during daylight hours, and more singing during hours of darkness (in winter, from mid-October through March) at Brooks Peninsula, is consistent with that expected for fin whales that are feeding. The two dominant euphausiid species in BC waters (*E. pacifica* and *T. spinifera*) undertake daily vertical migrations (which continues throughout the winter for *E. pacifica;* Sato et al. 2013), concentrating at depth during the day and becoming more scattered near the surface at night (Mackas 1992). It is hypothesized that lunge feeding baleen whales sing less during the day because they are busy feeding (Watkins et al. 1987, Oleson 2005, Stafford et al. 2005, Wiggins et al. 2005, Simon et al. 2010). As a lunge feeder, it is more cost-effective to feed on dense concentrations of prey during the day (Goldbogen et al. 2011), and engage in other behaviours, such as singing, at night when prey are scattered and feeding is less efficient. This is supported by tagging studies showing that during the day, fin and blue whales perform feeding dives which become shallower at dusk as the prey migrates towards the surface, with whales switching to resting behaviour near the surface at night (~20:00 to 03:00 h) with no indication of feeding (Goldbogen et al. 2011, Friedlaender et al. 2015). This is further supported by other observations of daily feeding patterns that coincide with the vertical migration of prey (Nemoto 1970), and observations of fin whales engaging in more social activity and resting near the surface in hours of darkness than in the day (Watkins 1981, Watkins et al. 1987).

Fin whales feeding outside of the summer feeding season have also been observed elsewhere by others (Brodie 1975, Canese et al. 2006, Ladrón de Guevara et al. 2008, Simon et al. 2010), adding support to the growing body of evidence that fin whales may not follow the traditional model of feeding in the summer at high latitudes and fasting during the winter at low-latitude breeding grounds (Mizroch et al. 2009).

Although not statistically significant (due perhaps to insufficient sample sizes), I found that fin whales called more often during daylight hours than hours of darkness prior to mid-October—an opposite pattern to that observed during the winter breeding season. Prior to mid-October, 20-Hz calling was irregular and after mid-October, 20-Hz calling was almost exclusively stereotyped song. Differences in the function of these call types, or changes in whale behaviour before and after transitioning into the breeding season may explain the differing patterns in diel call activity. In blue whales, different call types have been shown to exhibit different diel patterns, with feeding calls occurring more often, and song-type calls occurring less often, during the day (Oleson et al. 2007). Future studies should consider seasonal changes in behaviour when investigating diel calling patterns.

Fin whales produce 20-Hz calls seasonally with peaks in calling activity often observed to coincide with the peak of reproduction in December and January (Watkins et al. 1987, 2000). However, the greatest numbers of 20-Hz calls were recorded at my study site in August and September. This peak in call occurrence coincides with the time of presumed peak in feeding activity, and may reflect a seasonal abundance of whales in the study area. This is consistent with whaling data that show that fin whales returned to BC waters each summer, with most whales present in July and August (Gregr et al. 2000, Gregr and Trites 2001).

Seasonal movements into coastal BC waters may reflect the arrival of fin whales from offshore or from southern waters, or a combination of both. Whaling data show that fin whales were captured farther from shore from April to June, and were obtained closer to shore from July to September (Gregr et al. 2000), suggesting a possible inshore-offshore movement pattern. However, a study tracking fin whales through a seismometer network about 250 km south and 150 km west of my study area showed that fin whales travelled northwards from August to October (Soule and Wilcock 2013). This northward movement is consistent with the northward movement of blue whales that follow the northward bloom of primary production from Southern California in June, to Oregon and Washington in September (Burtenshaw et al. 2004).

Proportionally fewer calls were recorded during the peak of the breeding season (December-January) than during late summer (August-September), which might simply mean that fewer fin whales were present here during winter. However, other factors may influence the number of calls recorded seasonally. For example, in contrast to the calls recorded in late summer and fall, the songs I recorded in winter rarely overlapped with each other, which is consistent with other observational and tracking studies that have shown that that singing fin whales are always well separated spatially (Walker 1963, Patterson and Hamilton 1964, Watkins 1981, Watkins et al. 1987, Soule and Wilcock 2013). This suggests that the song from one male may suppress singing in nearby males, or act as a spacing mechanism between singing males, as has been proposed for humpback whales (reviewed in Helweg et al. 1992). This phenomenon may have contributed to lower numbers of calls being recorded during the peak reproductive season. Additionally, the increased singing activity of fin whales during the peak of breeding season contributes to higher levels of ambient noise in the frequency range of fin whale calls. This increased noise was evident in my study, and potentially reduced the number of calls during the peak breeding season with great enough signal-to-noise ratio to include in my study.

Based on an estimated detection range of 8.4 km for fin whale classic notes in high ambient noise conditions (high ambient noise due to increased singing activity as discussed above), the potential area that could be monitored by the hydrophone would be 222 km^2 (calculated by Area= Πr^2, where r is the detection range). However, because the hydrophone was located near to shore, this area is reduced by approximately one half, to 111 km^2. Therefore, in an area of about 100 km^2, usually only one male is singing at a time. This is within the range of densities of singing whales that have been reported by others (e.g., one singer per 777 km^2, Patterson and Hamilton 1964; one singer per several hundred square miles, Walker 1963; singers spaced by at least 5 km, Watkins et al. 1987), and may be an indication of the density of males in the area near the continental shelf off Vancouver Island, but it is not possible to know how many males are present and not singing.

It is important to note that interpretations of seasonal trends in call occurrence may be confounded by seasonal changes in calling behaviour. Fin whale calling activity changes seasonally, and other studies have found different patterns in fin whale occurrence and abundance based on acoustic and visual methods (Širović et al. 2012). In this study, I found that aspects of fin whale calling behaviour also change seasonally (see below). At this time, it is unclear whether the trends I observed in call occurrence correspond to changes in whale abundance, calling behaviour, or a combination of both. Studies incorporating methods such as satellite tagging, photo identification and visual abundance surveys will be needed to better understand the relationship between call occurrence and whale occurrence, and to better elucidate the seasonal occurrence of fin whales year-round in BC.

2.5.2 A Distinct Song from Fin Whales in BC

Fin whale song varies geographically, among and within ocean basins, and is thought to reflect population identity (Watkins et al. 1987) as has been suggested for blue whales (McDonald et al. 2006). The main way in which fin whale songs vary geographically is in the pattern (e.g., singlets or doublets) and internote interval lengths (Hatch and Clark 2004). Worldwide, internote intervals of fin whale songs range from about 6 to 46 seconds (Watkins et al. 1987, Hatch and Clark 2004). In the North Pacific, a variety of song internote intervals have been reported (Northrop et al. 1968, Thompson et al. 1992, McDonald et al. 1995, Hatch and Clark 2004, Soule and Wilcock 2013, Brodie and Dunn 2015), but no clear spatial or temporal patterns in the song indicative of population structure have been discovered (Hatch and Clark 2004). However, most of these studies have lacked adequate sample size, detail of analysis, or temporal coverage, and have not attempted to describe seasonal variation in the internote intervals.

A doublet song that changes significantly in internote interval over the course of the singing season has been recently identified for fin whales over multiple years in three widely spaced areas of the North Pacific (Southern California, Hawaii and the Bering Sea; Oleson et al. 2014). The internote intervals of this song are about 20 s and 26 s in October, increasing to about 28 s and 33 s in February. The similarity, and synchronous changes of the songs in these widely spaced regions suggests that one broadly ranging population is responsible for producing the song (Oleson et al. 2014). In my study off Brooks Peninsula, the fin whale song consisted of a doublet pattern with internote intervals of ~13 and ~17 s (13/17 s song), with a very minimal change over the course of the singing season (see below). These intervals are very different than those found for the song from Southern California, Hawaii, and the Bering Sea, over the entire duration of the calling season. This clear and consistent difference in song types suggests that the fin whales occurring in my study area may belong to a different population than those whales in California, Hawaii, and the Bering Sea. The internote intervals I recorded were very similar to the intervals reported from the eastern North Pacific in 1966 (Cummings and Thompson unpublished, in: Thompson et al. 1992), suggesting that this song—and therefore this population of whales—may have been present in this region for 50 years or more. Fin whale song in other regions has been observed to remain relatively stable over 5-10 years (Watkins et al. 1987, Oleson et al. 2014), but stability over periods as long as 5 decades has not been previously investigated.

In contrast to my findings, a recent study tracking singing fin whales over one year through a seismometer array located offshore of northern Washington (only about 300 km south of my study area) failed to detect the 13/17 s doublet song pattern (Soule and Wilcock 2013). About half of the whales tracked off Washington had internote intervals centered around 24 s and 30 s, which are comparable to the intervals found in Southern California, Hawaii and the Bering Sea—although these intervals were not found in the traditional doublet pattern of alternating long and short intervals, but had more complex arrangements (Soule and Wilcock 2013). A smaller number of songs recorded off Washington were singlets with 24-25 s internote intervals, which were interpreted as being produced by the same population of whales that produced the song with 24 s and 30 s internote intervals. This is also consistent with the findings from Southern

California, Hawaii, and the Bering Sea, where singlets had the same internote interval as the short interval of the doublet song, and were considered a variant of the doublet song (Oleson et al. 2014). In addition to the internote intervals centered around 24 and 30 s, a few of the songs tracked off Washington had internote intervals of 13 and 24 s with no consistent doublet pattern (Soule and Wilcock 2013). The 13 s interval is similar to what I recorded in British Columbia. However, Soule & Wilcock (2013) surmised that this 13 s interval could have been caused by a 25 s caller “interrupting” a whale with a longer interval song, and therefore may not represent a true song interval. Thus, the relationship between the song from offshore of Washington, the song from Southern California, Hawaii and the Bering Sea, and the song from my study area in BC, is unclear at this time.

Given the close proximity of the Washington study (Soule and Wilcock 2013) to my study area, the differences in the internote intervals are interesting, and suggest that fin whale song may vary on a fine spatial scale. The seismic network off of the Washington coast is far offshore, and in deep waters (>2000 m) that contain hydrothermal vent fields (Soule and Wilcock 2013), whereas my study area is near-shore, in relatively shallow water on the edge of the continental shelf. The differences in songs between these two areas could indicate that different populations, or different age or sex classes are using these two different habitats, or that the behaviour of whales in these areas is different. More work describing the calling behaviour and song characteristics from other areas off the Washington and BC coasts are needed in order to investigate these possibilities.

In addition to the doublet song, I found five occurrences of stereotyped singlet note sequences consisting of backbeats spaced at regular intervals of about 29 s. The relative rarity of this song type, and the similarity of the note interval to the interval between backbeats in the doublet song, leads me to believe that it is not a unique song type, but rather a variant of the doublet song in which the classic notes have been left out. This conclusion is consistent with previous studies that have found singlet variants of doublet songs (Soule and Wilcock 2013, Oleson et al. 2014). However, my results differ in that the internote interval of the singlet is the sum of the two doublet intervals, rather than being equal to the shorter interval.

2.5.2.1 Irregular Calling

The irregular interval call type in my study (consecutive classic notes sweeping down from ~34 Hz to ~20 Hz, with irregular internote intervals) is consistent with the “20-35 Hz irregular repetition interval” call type that makes up about 90% of fin whale calls in the summer at higher latitudes of the North Pacific (McDonald and Fox 1999). This call type occurred in significant numbers only in the summer months of August and September in my study, but made up only ~40% of all 20-Hz notes. Irregular interval notes were also observed from August to October south of my study area off Washington (Soule and Wilcock 2013), where most whales producing these call types were travelling faster and in straighter paths than whales producing more song-like calls—indicating that they were transiting through the study area (Soule and Wilcock 2013). This irregular interval call type is generally produced by animals in groups (Watkins 1981) and is likely used in social interactions and for keeping in contact with conspecifics (Watkins 1981, Watkins et al. 1987, Edds-Walton 1997).

Although the irregular interval and song type 20-Hz notes are often described as discrete call types, with different seasonal patterns and behavioural contexts, I found similarities that suggest that these calls were not mutually exclusive. Both call types were first detected on the same day, and last detected in the same week of my study period. There was also no point in time where the irregular interval notes occurred without doublet pattern notes. I found that the irregular interval and doublet call types not only occurred during the same periods, but that they often occurred within the same bout, particularly in August and September when irregular notes were most common. Although some instances of these mixed bouts may have been an artifact of data analysis (all calls that are separated by <2 hours were considered the same bout), I often observed seamless transitions from one call type to the other, sometimes multiple times within a bout. These mixed bouts had consistent signal-to-noise ratios, indicating one animal was the source of the calls. Fin whale bouts containing both irregular and regular note interval patterns in another study off Vancouver Island were confirmed to originate from a single individual by tracking the source of the sounds through a seismometer array (Soule and Wilcock 2013).

In addition to being found in the same bouts, irregular interval notes and doublet notes that occur in August and September share some note interval and frequency characteristics. Although the internote intervals of the irregular interval call type in my study were variable when compared with stereotyped song calling, the note intervals clearly clustered around a central value of about ~ 15 s—a value that lies nearly perfectly between the ~13 s and ~17 s internote intervals of the doublet song. The range of the majority of the internote intervals of the irregular call type overlaps the full ranges of the doublet song internote intervals.

The irregular and doublet call types are also similar in frequency during the months of August and September. I found that the center frequency of the classic note in the doublet pattern changed significantly over the calling season, with center frequency in August (26.1 Hz) and September (24.5 Hz) being higher than in October to March (~23 Hz). The center frequencies of classic notes in the irregular pattern (~25.7 Hz) are very similar to the center frequencies of the classic notes in the doublet pattern in August and September. The similarities in internote intervals and frequency, and the fact that irregular and doublet call types often occur within the same bout, indicates that the irregular call type is not independent from the song-type calling. Further, non-independence of the two call types suggests that the irregular call type may also carry population information, and irregular interval calling should not be overlooked in future studies of fin whale acoustics.

Although songs are accepted as being male reproductive displays produced in the fall and winter during the breeding season (Watkins et al. 1987, Croll et al. 2002), song-type calling that occurs at high latitudes in the summer during the feeding season as observed in my study, suggests that either reproductive activity extends outside of the breeding season, or that song-type calling may have functions other than serving as a reproductive display (Clark et al. 2002). However, when song type calling occurs in the summer at high latitudes, I found that it is linked to, and produced in conjunction with, irregular-type calling which is considered a contact call and is associated with socializing whales (Watkins 1981, Edds-Walton 1997). I also found that characteristics of the doublet song are different and more variable (less stereotyped) in the summer (August-September), compared to the winter breeding season when irregular interval calling decreases and songs become stereotyped (see below). This suggests that the doublet song has a function other than reproductive display when produced in the summer, and that it does not necessarily indicate breeding outside of the reproductive period. This is supported by unpublished data on fetus sizes of fin whales killed in British Columbia, which suggest that this population rarely breeds out of season (Pike 1963, unpublished data).

Like fin whales, humpback whales have been observed to start to singing in August and September, prior to the onset of their breeding season (Gabriele and Frankel 2002). In birds, environmental (primarily day length) and social cues stimulate increases in circulating sex steroid levels and reproductive development several weeks before the actual onset of breeding season (reviewed in Tramontin and Brenowitz 2000), and a similar process is thought to occur in humpback whales (Clark and Clapham 2004, Wright and Walsh 2010). Testosterone levels in mature North Atlantic fin whales have been found to increase significantly from June through August (Kjeld et al. 2006), so fin whale song prior to the breeding season may simply be a function of increasing hormone levels prior to the breeding season.

For humpback whales, it has been speculated that singing in late summer may allow individuals from different breeding areas to converge on a common song prior to the next breeding season while they are still together on the feeding grounds (McSweeney et al. 1989). Unlike humpback whale song (Payne and Payne 1985), fin whale song does not change significantly from year to year (Watkins et al. 1987, Morano et al. 2012, Oleson et al. 2014) so the song convergence hypothesis likely does not apply to fin whales. The function or behavioural context of song-type calling outside of the breeding season is unknown for fin whales.

2.5.3 Seasonal Change in Song Suggests Reproductive Activity

2.5.3.1 Seasonal Change in Song Properties

Most of what little is known of fin whale reproduction is based on commercial whaling data from the Southern Hemisphere (Lockyer and Brown 1981). It has revealed that fin whales are seasonal breeders that mate over about a five month period in the winter (Laws 1961, Mizroch et al. 1984). In the North Atlantic and North Pacific, calving peaks in November and December, conception is estimated to peak in December or January, and the gestation period is 11 to 12 months (Lockyer 1984, Kjeld et al. 2006). Like other seasonally breeding birds and terrestrial and marine mammals (Atkinson and Yoshioka 2007, Yoshimura 2013), fin whales have an annual cycle of testes activity (Laws 1961, Lockyer 1984) and testosterone levels (Kjeld et al. 2006, Atkinson and Yoshioka 2007) which peak around the time of peak conception (Laws 1961).

The breeding season for fin whales in the North Atlantic is estimated to occur from approximately November to March, and corresponds with increased singing activity (Watkins et al. 1987, Morano et al. 2012). In many seasonally breeding vertebrates that use song as a reproductive display such as birds (Meitzen et al. 2009), fish (Forlano et al. 2014), and humpback whales (Clark and Clapham 2004, Wright and Walsh 2010, Vu et al. 2012), changes in singing activity and behaviour are linked to circulating steroid hormone levels. Seasonal changes in song can include changes in call rate, temporal and spectral properties of the song notes, and the consistency (stereotypy) with which individuals produce the temporal and spectral properties of the notes (Meitzen et al. 2009).

The seasonal changes that I and others have found in internote intervals of fin whale songs coincide with the reproductive season (Watkins et al. 1987, Morano et al. 2012, Oleson et al. 2014). In each study, the seasonal change involved a lengthening of internote intervals over the singing season, but the patterns of change differed. In Bermuda, intervals initially decrease from September to October, increase gradually from November to April, then decrease in May and June (Watkins et al. 1987). In the western North Atlantic, intervals were short from September to January (although appearing to increase slightly during this time), and over the course of one month in February, transitioned to a longer interval present from March to May (Morano et al. 2012). In the song found in three regions of the North Pacific, intervals increase steadily over the singing season until February, leveling off in March until the end of singing (Oleson et al. 2014). The internote intervals of the fin whale songs found in my study off British Columbia increase gradually over the singing season, with most change occurring in August and September, and leveling off in December until the end of the study period in March.

Although the two songs reported in the North Pacific (i.e., my study and Oleson et al., 2014) show a similar gradual increase, and leveling of intervals, the amount of change that occurred was very different. The intervals of the song in my study increased by ~2.6 s in total, whereas the intervals for the song described from California, Hawaii and the Bering Sea increased by ~2 seconds per month, for a total change of ~8 s (Oleson et al. 2014). The differences in the patterns of change in these songs highlight the importance of describing seasonal change for each distinct song type found, for the purpose of aiding population identification studies. Going further, it could be hypothesized that differences in patterns and rates of change in the songs could reflect population level differences in singing behaviour or physiological changes related to breeding. If this is the case, quantifying seasonal change in fin whale song may help to provide an additional indicator of population structure in fin whales.

Because internote intervals have been identified as being the most geographically variable property of fin whales song, and therefore having the most potential for population identification, seasonal changes in song properties other than internote interval have not yet been investigated. I found that other properties of the doublet song, including the internote interval difference and center frequency of the classic note also changed. Both of these properties decreased in August and September, and then remained relatively stable from October through March, with a slight dip in January, and slight increase in February and March. This suggests that the fin whale song undergoes multiple changes over the breeding season.

The center frequency of the backbeat note was the only song property that I examined that did not show a clear seasonal trend. Center frequencies of the backbeat note were higher in January than other months, in contrast to the classic note, which had frequencies that were lowest in January compared to other months. This may indicate that the song tends towards frequencies of the classic and backbeat notes becoming more similar at the peak of the breeding season. Additionally, the backbeat note center frequency was unique in that it was very consistently produced (highly stereotyped) throughout the entire singing season, suggesting either a physiological constraint on producing the frequencies of this note, or that it serves an important function that does not benefit from changing seasonally.

2.5.3.2 Seasonal Change in Song Stereotypy

The degree of song stereotypy, or in other words, how consistent an individual is in producing a song or elements of a song, is considered a measure of performance skill (Byers et al. 2010). It is thought that consistency may reflect an individual's fitness, age or dominance, and that it may be used by females to aid in mate selection (Riebel 2009). In birds and in other vertebrates, sex steroid hormones are involved in male sexual behaviour, including the regulation of vocal consistency (Riebel 2009, Sakata and Vehrencamp 2012). In birds, song stereotypy has been correlated with testosterone levels in the lab (Meitzen et al. 2009) and in the wild (Smith et al. 1997). Although fin whale song is often described as being very stereotyped, the degree of stereotypy and seasonal changes in stereotypy in relation to the reproductive cycle have not been quantified.

As expected, I found that the stereotypy of internote intervals, interval difference and classic note frequency of the fin whale doublet song changed over the course of the singing season. Stereotypy of each song characteristic increased most quickly in August and September, leveled off from October to December, peaked in January and then increased somewhat in February and March. Overall song stereotypy (a combined measure of the stereotypy of all song characteristics for each song) showed a clear trend of stereotypy increasing from the beginning of the singing season to mid-October, leveling off through December, and peaking in mid-January. Although the general trend in stereotypy decreased again in February and March, a relatively large number of highly stereotyped songs were still occurring.

Unpublished commercial whaling data for fin whales killed in the summer months off Vancouver Island suggest that 75% of conceptions occurred between mid-November and mid-March, with a peak in January (Pike 1956, unpublished data). The pattern of song stereotypy fits with this pattern of conception, providing support for the timing of the breeding season for this population: song becomes stereotyped around the time of the start of the breeding season (November) and remains stereotyped to the end of the breeding season (March), and the peak in stereotypy occurs during the time of peak conception (January). Observations of fin whales caught off Norway and Iceland suggest that average conception times may vary between stocks (Meredith and Campbell 1988).

The finding that increased song stereotypy coincides with the estimated peak of the breeding season of the population of fin whales in BC, suggests that acoustic analysis could potentially be used as a tool to investigate population level differences in breeding times.

Fin whales that remain in northern latitudes over the winter have been suggested to represent non-receptive females or non-reproductive juveniles (Edds-Walton 1997). However, my data indicate that males were present during winter in British Columbia, given that only males are known to produce stereotyped songs. Also, no sex specific differences in distribution have been observed for fin whales to date (Bérubé et al. 1998). Furthermore, the multiple concurrent changes in fin whale calling behaviour that coincide with the reproductive season (i.e., decreased use of irregular calls after September, increasing internote intervals, decreasing internote interval difference, classic note center frequency increasing song stereotypy) suggest that the individuals producing song are undergoing the seasonal reproductive changes that are expected for mature males in breeding condition.

A very small number of songs had internote intervals that were classified as outliers in my analysis. It is possible that these songs were from immature whales that have not fully learned or acquired the song. However, it is not known whether fin whales learn song, whether immature whales sing, or whether internote intervals evolve as a whale matures, so it is not possible to attribute these outliers to immature whales. Differences in songs from immature and adult whales may be expected to occur in the frequency characteristics of the song because the frequency of vocalizations generally decrease with increased body size among species (Fletcher 2004, May-Collado et al. 2007) and within species (Linhart and Fuchs 2015). Smaller, immature whales would be expected to vocalize at higher frequencies than the larger adult whales. However, very few songs that were outliers in note frequency were identified, especially in the lower backbeat note, which immature whales would likely have the greatest difficulty producing.

2.5.4 Study Limitations and Future Research

The data for my study were collected using an autonomous passive acoustic recording instrument that was anchored to the seafloor on the continental shelf in relatively shallow water (~100 m), near to shore (<5km). In shallow water, the propagation of low frequency sounds is complicated by the signal interacting with surface and bottom reflections, thereby causing some distortion of the fin whale calls, and possibly reducing the effective range of the hydrophone (Watkins 1981). Placing the hydrophone in deeper water off the continental shelf may have improved the quality of the low frequency fin whale recordings and increased the range of the hydrophone.

I estimated that fin whale calls could be detected above ambient noise levels when whales were as far from the hydrophone as ~1,500 km (for the classic note, in low ambient noise conditions) resulting in a potentially very large circular area over which fin whales can be detected. However, because the hydrophone was located only about 5 km from shore, the area monitored by the hydrophone was substantially reduced (by almost one half). Placing the hydrophone farther from shore would have allowed for the monitoring of a larger area, and may have resulted in more songs being recorded.

Although the duty cycle imposed on the recorder reduced power usage allowing for longer-term recording, and reduced analysis time, it resulted in an incomplete record. Continuous recording would have been beneficial for capturing short bouts that may have been missed in duty cycle recording. Continuous recording would also have allowed larger samples of measurements from each bout to be obtained, and for more accurate measurements of bout length and times between bouts to be made. However, most songs during the period of interest (winter) were likely sampled because fin whale songs are relatively long (~20-minute songs in bouts that can last hours to days) compared to the duty cycle.

My study is a detailed analysis of one year of data from one location. The strength of this design is that the level of detail resulted in accurate measurements and a good understanding of fin whale song patterns that higher-level studies may not achieve. However, my study is somewhat limited temporally and spatially.

Patterns of seasonal occurrence are known to vary for fin whales, and more years of data are required to understand the range of seasonal occurrence patterns for my study location. Unlike the songs from humpback whales which change from year to year (Payne and Payne 1985), fin whale song patterns and note intervals have been observed to be relatively stable from year to year within regions (Watkins et al. 1987, Morano et al. 2012, Oleson et al. 2014). Therefore, it is likely that the song described in my study will persist. However, fine scale changes occurring over long time periods (decades) are possible, as has been documented for the frequency of blue whale calls (McDonald et al. 2009, Gavrilov et al. 2012).

The area sampled by the hydrophone in my study was small relative to the ranges of fin whales, and the area of British Columbia's waters and the greater North Pacific. Because little is known about the population structure of fin whales in the North Pacific, it is possible that different song types will be found at different locations if different populations occur there. Therefore, the results of my study are specific to the area and population of whales that was sampled off Brooks Peninsula, BC.

Sei whales produce low frequency downsweeps that are similar to fin whale calls, and passive acoustic data collected autonomously lack concurrent visual observations to confirm that calls are attributed to the correct species. However, I believe that the calls in my study were correctly identified as fin whales. Sei whales are extremely rare in BC waters (Ford 2014), so it is unlikely that this species is responsible for the large number of calls I detected. The calls produced by sei whales in Hawaii are similar to the "20-35 Hz irregular repetition interval" fin whale call type (McDonald and Fox 1999, Rankin and Barlow 2007), but they are not known to make lower frequency downsweeps that could be confused with the fin whale backbeat note. I also found that both the irregular interval call type and backbeat call type often occurred within the same bout, which again makes it unlikely that these calls were produced by sei whales. Furthermore, in October 2012 I recorded the irregular interval call type and the doublet call type in the visual presence of fin whales in BC waters approximately 300 km from my study area, in Caamaño Sound.

2.5.5 A Resident Population?

The results of my study show that fin whales are present in BC year-round, and that these whales appear to be feeding and engaging in reproductive activity over the winter. However, it is not clear whether the fin whales that occur in northern latitudes in the winter represent year-round resident individuals, or if staggered migration patterns occur that result in at least some whales being present at all times (Mizroch et al. 2009).

Evidence for non-migratory, resident populations of fin whales is available from various regions (Brodie 1975, Thompson et al. 1992, Bérubé et al. 2002, Mizroch et al. 2009, Castellote et al. 2012). In the North Pacific, a resident population has been confirmed in the Gulf of California, and there is good evidence for a resident population in the East China Sea, with possible additional resident populations in the Sanriku-Hokkaido and northern Sea of Japan areas (Mizroch et al. 2009).

The possibility that a year-round resident fin whale population uses BC waters is interesting to consider. Because only male fin whales sing, I show conclusively that male fin whales are present in BC through the winter. Since song in fin whales appears to be related to reproduction, it follows that females are probably also present in the winter, and that mating is likely occurring. Whether calving also occurs consistently in the same high-latitude areas is less clear. The whaling records show that pregnant female fin whales in BC were near term at the end of September (Gregr et al. 2000). Unpublished calculations based on the whaling data estimate that 75% of births in this population occur between mid-October and mid-February, with a peak in December (Pike 1956, unpublished data), and young calves have recently been sighted in BC waters (John K. B. Ford, Cetacean Research Program, Fisheries and Oceans Canada, personal communication). Fin whales with newborn calves have also been observed at high latitudes off northern Norway in the North Atlantic, suggesting that fin whales may not require tropical waters for calving (Bérubé et al. 1998) unlike the highly migratory baleen whales such as right whales and humpback whales (Lockyer and Brown 1981). Thus, it is possible that female fin whales that remain in northern latitudes over the winter calve in these areas. While it is also possible that non-pregnant females remain at northern latitudes to breed, and that pregnant females migrate south to give birth, no breeding grounds have been identified for fin whales, suggesting that calving does not occur in specific regions, but rather occurs over a wider area.

Although it is physiologically and ecologically possible for a resident population of fin whales to exist in BC, and the acoustic evidence presented here may support this, more study is needed. Satellite tagging studies could determine whether individual whales remain here year-round, or migrate south. Collaborative photo-identification studies with groups working in low latitudes may also reveal patterns of migration between the two regions. In addition, biopsy sampling could determine whether the whales that occur in BC are genetically different from other fin whales in the North Pacific, particularly those that sing a distinct song. Further acoustic studies will also help to map the spatial extent of the song identified in this study, and determine whether the whales producing the song identified in my study occur in a localized region, or range widely.

2.6 Conclusions

The analysis I undertook of passive acoustic recordings off Vancouver Island provide the first detailed description of the song of fin whales in British Columbia waters. It adds to the increasing evidence that fin whale movements and residency patterns are more complex than previously thought. In particular, my findings support the hypothesis that at least some fin whales in the North Pacific remain on high-latitude feeding grounds during the winter, where they appear to take advantage of both breeding and feeding opportunities. However, it is not known whether these fin whales belong to a larger population in which other individuals are migratory, or whether these whales belong to a distinct non-migratory population. Resolving this question is important for the recovery and management of this threatened species.

Chapter 3: Song analysis reveals acoustic population structure of fin whales in the eastern North Pacific

3.1 Summary

Genetic evidence suggests there may be two distinct populations of fin whales (*Balaenoptera physalus*) in the eastern North Pacific, but other evidence to support this population structure is lacking. I measured the internote intervals of fin whale doublet songs recorded in October and February (2006 – 2012) at 8 locations in British Columbia (BC) using bottom-mounted archival passive acoustic recording instruments. I found two song types with distinct intervals between the notes—Type 1 (with a ~25 s short interval and a ~30 s long interval) previously recorded in Southern California, Hawaii and the Bering Sea; and Type 2 (with a ~13 short and ~17 s long interval) previously recorded off Vancouver Island, BC. Song Type 2 was common and occurred at all coastal and offshore BC recording sites, while song Type 1 was relatively rare and occurred only at the two offshore sites and at the most northerly site. Comparisons with fin whale songs from other regions in the North Pacific suggest that the fin whales singing the Type 2 songs range along the coast of North America from the Gulf of Alaska to Oregon. Similarities in song Type 2 and Southern Hemisphere song, suggest the population singing song Type 2 may be closely related to the Southern Hemisphere fin whale subspecies, as suggested by previous genetic work. Comparison of fin whale doublet songs from the North Pacific, North Atlantic and Southern Oceans showed that all songs share a curious common trait—the duration of the long interval is always ~5 seconds greater than the short interval, regardless of the duration of the short interval. This ~5-sec rule appears to be highly conserved across all subspecies in all ocean basins. My results provide support for the presence of at least two populations of fin whales in the eastern North Pacific, with the more coastal population that ranges from the Gulf of Alaska to Oregon potentially being closely related to the Southern Hemisphere subspecies.

3.2 Introduction

Fin whales (*Balaenoptera physalus*) are a cosmopolitan species consisting of three subspecies: *B. p. physalus* in the Northern Hemisphere, *B. p. quoyi* in the Southern Hemisphere, and *B. p. patachonica*, a pygmy form in the Southern Hemisphere. However, genetic evidence suggests that there are actually two subspecies in the Northern Hemisphere (one in the North Atlantic and one in the North Pacific), and that the North Pacific subspecies may further consist of two clades in the eastern North Pacific. The possibility that two clades of fin whales occur in the eastern North Pacific is consistent with observations of fin whales taken by commercial whalers in British Columbia that found whales with two blood types, suggesting that they may belong to two different breeding populations (Pike 1963, unpublished; Fujino 1964). Furthermore, fin whales taken from BC were thought to belong to two groups — a summer-resident group consisting of smaller sized fin whales (possibly juveniles) that was feeding in BC, and larger fin whales thought to be migratory (Pike and MacAskie 1969, Gregr et al. 2000). Unfortunately, little else is known about these fin whales to help distinguish the extent to which they may or may not be distinct populations and reproductively isolated (Archer et al. 2013).

Vocalization is an important form of communication in many animals, and often serves as a pre-mating barrier to reproduction (Wells and Henry 1998). Courtship songs can serve to identify the species, subspecies and even population or social group of the calling individual—and have been used by biologists to describe and differentiate between cryptic species and populations of insects (Wells and Henry 1998, Henry et al. 2002), birds (Irwin et al. 2001, Toews and Irwin 2008) and mammals (Braune et al. 2008, Campbell et al. 2010). Among cetaceans, killer whale ecotypes (Ford 1984), and pods within the resident killer whale ecotype, can be distinguished by pod-specific dialects (Ford 1991); and social sounds of sperm whales have been shown to vary geographically (Amano et al. 2014). For baleen whales, blue whales from nine regions have nine distinct songs (McDonald et al. 2006), and breeding humpback whales sing different songs in different ocean basins (Garland et al. 2015). As for fin whales, two different song types have been described in the eastern North Pacific Ocean (Oleson et al. 2014 and Chapter 2), which may correspond to the presence of two distinct populations.

Male fin whales produce short, low frequency, down-sweeping notes called 20-Hz notes (Watkins et al. 1987). During the winter breeding season in the Northern Hemisphere (November to March), fin whales arrange 20-Hz notes into simple one or two note songs, with very regular intervals between the notes (internote intervals). Songs can have one interval type (singlet song) or alternating long and short intervals (doublet song). These doublet songs usually consist of two forms of the 20-Hz note—the classic note and slightly lower frequency backbeat note—with the classic note occurring after the short interval, and the backbeat note occurring after the long interval.

Worldwide, internote intervals are the most variable aspect of fin whale songs, and differences in internote intervals have been hypothesized to correspond to different populations (Watkins et al. 1987, Thompson et al. 1992, Mellinger and Barlow 2003, Hatch and Clark 2004, Delarue et al. 2009, Castellote et al. 2012). Differences in internote intervals have been shown to correspond to genetically differentiated populations of resident fin whales in the Gulf of California (Thompson et al. 1992, Bérubé et al. 2002) and the Mediterranean Sea (Bérubé et al. 1998, Castellote et al. 2012). In contrast, a study from the Gulf of St. Lawrence and the Gulf of Maine found differences in song that were consistent with other methods of stock structure assessment such as tagging, pollutant level analysis and photo-identification (Delarue et al. 2009), but no evidence of genetic differentiation was found (Bérubé et al. 1998, Delarue et al. 2009). This suggests that song may not always correspond to genetic differences, but may instead correspond to other forms of population structure such as feeding aggregations (Delarue et al. 2009). Although the relationship of acoustic and genetic differentiation is not completely understood for fin whales, distinct differences in songs are recommended as indicators of population structure in the absence of other data (Mellinger and Barlow 2003).

The two doublet song types described for fin whales in the eastern North Pacific have distinct internote intervals. One song type (referred to as song Type 1) has been described from Southern California, Hawaii and the Bering Sea, and is known to change significantly over the course of a singing season (September to March), with internote intervals increasing from about 21 s and 26 s in October to about 28 s and 33 s in February (Oleson et al. 2014). A second song type (referred to as song Type 2) has been described off Vancouver Island, BC, and has internote intervals of ~13 s and ~17 s that change little over the course of a breeding season (Chapter 2).

My primary goal was to use acoustic analysis to determine whether two populations of fin whales occur in British Columbia. Using passive acoustic data from 8 bottom mounted archival recorders deployed throughout BC waters, I determined whether recorded fin whale songs corresponded to the previously described North Pacific fin whale song Types 1 or 2. I also compiled all known reports of fin whale doublet songs from the North Pacific to examine the geographic ranges of the song types. Finally, I combined all available data on fin whale doublet songs from the Atlantic, Pacific and Southern Oceans to assess the extent to which differences in fin whale songs relate to the genetic differentiation of fin whale subspecies and clades. Collectively, the analyses lend support to using acoustics as a tool to determine population structure in fin whales and provide new information about the population identity of fin whales in British Columbia.

3.3 Methods

3.3.1 Data Collection

Passive acoustic data were obtained from various years between 2006 and 2012 at eight locations in British Columbia waters (Table 3-1, Figure 3-3). The locations were chosen to represent offshore, inshore and shelf edge habitats. In the North Pacific Ocean, fin whales sing from September through March, but songs were only analyzed for two months—October and February—which captured the beginning and end of the fin whale singing season, and the change of the song internote intervals over this period (Oleson et al. 2014; Chapter 2). Analyzing two months of data for each site allowed multiple locations to be analyzed.

With the exception of the deployment at Union Seamount, which used a PATC (Passive Acoustic Tracking of Cetaceans) recording instrument (Vagle et al. 2004, Ford et al. 2010b), all acoustic recordings were made using Autonomous Underwater Recorders for Acoustic Listening instruments (AURAL, Multi-Electronique, Inc., Rimouski, QC, Canada) deployed by Fisheries and Oceans Canada’s Cetacean Research Program (Pacific Biological Station, Nanaimo). The instruments were anchored to the sea floor at various depths, and recorded data autonomously under battery power, except for the instrument at Langara Island, which was connected to a land-based solar power source.

The AURAL instruments included an HTI-96-MIN hydrophone (High Tech, Inc., Long Beach, MS, USA) with a sensitivity of -165 dB re 1 V/uPa and frequency response of 2 Hz to 30 kHz (specifications are from the manufacturer; hydrophones were not calibrated in the field). The AURALS sampled data at 16,384 Hz with 16-bit resolution, using a recorder gain setting of +16 dB. The instruments were anchored so that the hydrophones were suspended at approximately 10 m above the ocean floor. Data were collected using various duty cycles and saved as *".wav*" files.

3.3.2 Acoustic Analysis

I down-sampled the recordings to 512 Hz using MATLAB to facilitate the visual analysis of low frequency fin whales vocalizations, and to reduce file size. This resulted in a time-frequency spectrogram of up to 256 Hz, which was high enough to capture all low frequency fin whale vocalizations, but low enough to exclude much unwanted high frequency noise.

I manually reviewed all down-sampled data for the presence of fin whale doublet song by visually examining spectrograms using the program Adobe Audition 1.5 (Adobe Systems Inc 2004). When measurable song sequences were confirmed, I loaded the recordings containing the songs into SpectroPlotter Version 4.4.30 (JASCO Applied Sciences 2013) for annotation. Measurable songs consisted of at least 5 notes (as in Morano et al., 2012; Soule & Wilcock, 2013; Watkins et al., 1987) and had sufficient signal-to-noise ratio to ensure that no calls in the sequence would be missed, which would bias the note interval measurements. In addition, I only measured songs that I could confidently attribute to one animal, but simultaneous high signal-to-noise ratio songs from multiple whales that made it impossible to discern which notes belonged to which song were uncommon. Each 20-Hz note in each doublet song was identified as a classic note (C note) or a backbeat note (B note) based on the relative frequency content and bandwidth of the notes, with the backbeat being lower in frequency and narrower in bandwidth than the classic note. I did not consider other fin whale song types (e.g., singlets), other song note types (e.g., high frequency song notes; Antarctic ref), or other fin whale vocalizations (e.g., higher frequency downsweeps, ragged low frequency pulses and low frequency rumbles; Watkins 1981, Edds 1988) in this analysis.

I annotated the fin whale calls in SpectroPlotter following a standardized protocol developed through a collaborative effort to standardize fin whale acoustic analysis (see Rankin et al. 2013 in preparation for detailed protocol). My methods differed from this protocol only in the window type used, and the version of SpectroPlotter used (v. 4.4.30 vs. v. 5.0.8), which did not produce measurements of peak frequency. Spectrogram parameters for making annotations were: frequency resolution of 0.1 Hz (providing a true resolution of 0.063 Hz), frame size of 0.1 sec, time step of 0.025 sec, Hanning window type, and rainbow colour scheme. Spectrograms were restricted to a bandwidth of 0 – 50 Hz with a 5 sec window length, and annotations were created using a percent energy selection of 98%. This means that note feature measurements were based on 98% of the energy content (the note) inside the annotation box. Multipath arrivals were not included in the annotation box.

3.3.3 British Columbia Song Analysis

I calculated the internote interval (INI) for all consecutive notes in the doublet songs (classic to backbeat note, and backbeat to classic note). Internote interval was the time between the centroid time of one note and the centroid time of the following note. Centroid time was the time at which 50% of the energy in the signal lies before that time, and 50% lies after that time. Intervals greater than 60 s were not considered internote intervals, but were treated as gaps or rests in the song (as per Watkins et al. 1987) and therefore were not included in the internote interval analysis.

To facilitate comparison with the song type described in Oleson et al. (2014), I calculated the median of the long and short internote intervals for each song, rather than the mean. I then plotted each song as the median of the long interval vs. the median of the short interval, and compared the intervals to the internote interval ranges of the songs previously described from the North Pacific by Oleson et al. (2014; referred to as North Pacific Song Type 1), and by me (Chapter 2; referred to as North Pacific song Type 2).

Again to facilitate comparison with Oleson et al. (2014), I defined the ranges of internote intervals for each song type, for the months of October and February, using the

Median Average Deviation (MAD). MAD is the median of the absolute deviations from the median, and provides a measure of variability that is robust and resilient to outliers.

For song Type 1 (Oleson et al. 2014), the medians of the long and short internote intervals and MADs were provided for October and February for three locations over multiple years. To calculate a range of internote interval values for this song type that encompassed the full range of variability seen in the data set, I calculated the median minus MAD for the month with the smallest internote intervals, and median plus MAD for the month with the largest internote intervals, for both the long and short interval. I performed this calculation separately for the months of October and February, to produce ranges for each month that reflected the different internote intervals for these months as a result of seasonal change in the intervals.

To calculate internote interval ranges for song Type 2 (described from Brooks Peninsula, Chapter 2), I calculated the median and MAD for the long and short internote intervals in the months of October and February at Brooks Peninsula, BC. I then calculated ranges as median minus MAD and median plus MAD for the long and short intervals for October and February, as for song Type 1.

After calculating interval ranges, I categorized the songs as being Type 1 or Type 2 by determining whether the long and short intervals of the song fell within or near the range of internote interval values calculated for each song type (keeping in mind that being calculated as median ± MAD, the ranges encompass most, but not all of the variability that would be expected for these song types).

3.3.4 North Pacific Song Analysis

I gleaned all possible fin whale doublet song internote intervals from existing literature to look for evidence of Type 1 and 2 songs from other locations in the North Pacific, as well as other possible doublet song types (see Table A-1 for all measurements and sources). The ways in which publications reported internote intervals varied, with most publications providing only general descriptions of common internote intervals, and some providing ranges or actual measurements. When publications provided only spectrograms of samples of song recordings, I measured internote intervals from the spectrogram. Similar to the BC song data, I attempted to determine whether the reported internote intervals matched to either song Type 1 or song Type 2.

3.3.5 North Pacific, North Atlantic and Southern Ocean Song Analysis

As for the North Pacific analysis, I gleaned all possible fin whale doublet song internote intervals from studies conducted elsewhere in the world (see Table A-1 for all measurements and sources). I also investigated broad patterns in the doublet internote intervals across ocean basins from the summarized BC data, the Oleson et al. (2014) data, and all published internote intervals. BC data were summarized by calculating the median internote interval values for each month, year, and location, for each song type (i.e., where song Type 1 and song Type 2 occurred in the same month and location, median internote intervals were calculated separately for each song type). Finally, I used linear regression to describe the relationship between the long note interval (classic to backbeat note) and the short interval (backbeat to classic note).

3.3.6 Statistical Analysis

Simple linear regression was performed in ‘R’ version 2.14.1 (R Development Core Team 2011). Spectrograms were generated with SpectroPlotter Version 4.4.30 (JASCO Applied Sciences 2013). All other graphics were generated in R with the ggplot2 package (Wickham 2009).

3.4 Results

3.4.1 Fin Whale Doublet Song in British Columbia Waters

Type 1 (described in Oleson et al. 2014) and Type 2 (described in Chapter 2) doublet songs both occurred in British Columbia waters (Figure 3-1,Table 3-1). Song Type 2 was recorded at all sites and in all months that contained song, except at Union Seamount (although a limited amount of data was available for this location). I found only 7 instances of the song Type 1—one at Union Seamount, two at Bowie Seamount, and three at Langara Island (Table 3-1, Figure 3-2). The two song types occurred in the same month at the same location only at Bowie Seamount in February, 2012. However, the song types did not occur on the same days — song Type 2 occurred throughout the day of February 12, then song Type 1 occurred on February 14, 17 and 22, followed again by song Type 2 on February 23, 24 and 25.

The greatest number of songs were recorded at Brooks Peninsula, followed by Bowie Seamount and Triangle Island (Table 3-1). Although the Caamaño Sound and Squally Channel recordings contained relatively fewer numbers of songs, the presence of fin whales in these areas was significant—Caamaño Sound and Squally Channel are located in protected inshore waters, not typical of fin whale habitat (Figure 3-3). In contrast, the Cape St. James recordings—which contained even fewer numbers of fin whale songs—was expected to contain more songs due to its location near the shelf edge. The small number of songs in the recordings from Langara Island should be interpreted cautiously, as this instrument suffered from electronic interference in the frequency range of fin whale calls and also, the hydrophone was not at the ideal depth or location for recording fin whale calls.

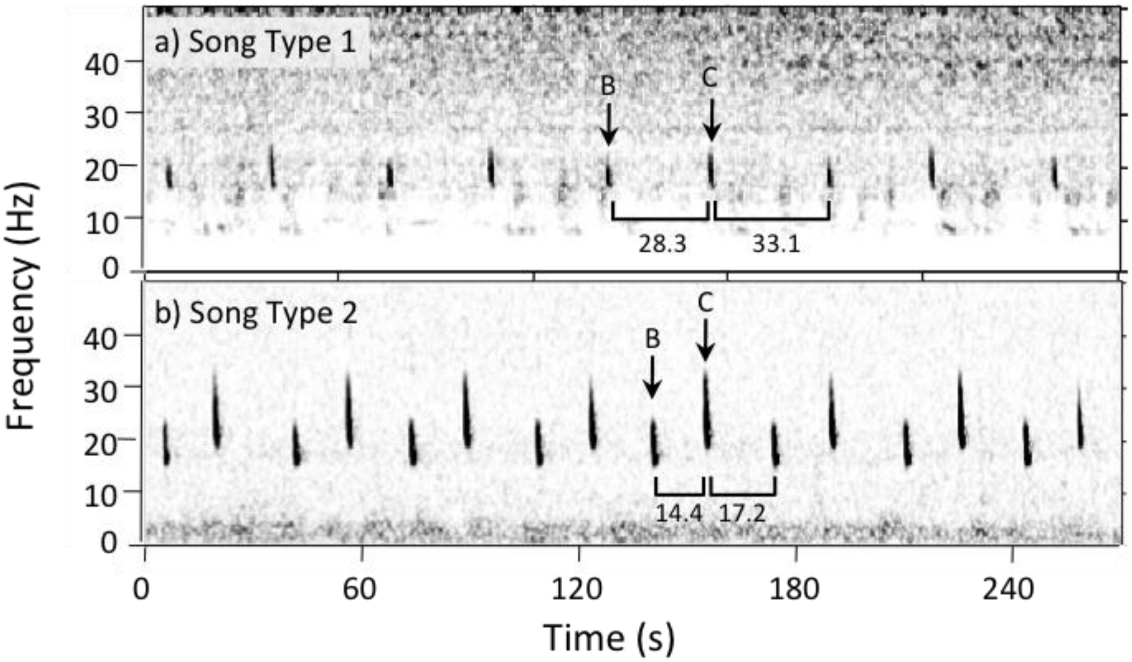

Figure 3-1. Spectrograms of representative examples of the fin whale doublet song types recorded in British Columbia. a) Song Type 1 recorded at Union Seamount, February 15, 2006, b) Song Type 2 recorded at Bowie Seamount, February 25, 2012. The letter B indicates the backbeat note type and the letter C indicates the classic note type. Examples of the internote intervals between the two note types are given.

Table 3-1. Passive acoustic data analyzed from British Columbia waters, including locations, dates analyzed, duty cycles (minutes of recording/recording cycle length in minutes) and water depth (m). Number of doublet songs and number of notes measured are given for songs of each type (Type 1 and Type 2). NA denotes months in which recordings were not available and zeros indicate that recordings were available and analyzed but no measurable Type 1 or Type 2 doublet songs were found.

Deployment	**Location**	**Duty Cycle**	**Water Depth**	**Dates Analyzed**	**Number of Songs (notes) Type 1**	**Number of Songs (notes) Type 2**
Bowie Seamount	53 18.332 N	9/15	235	Oct 2011	0 (0)	11 (504)
	135 37.398 W			Feb 2012	3 (52)	6 (542)
Langara Island 1	54 14.2 N	10/30	NA	Oct 2009	3 (39)	0 (0)
	132 57.7 W			Feb 2010	0 (0)	0 (0)
Langara Island 2	54 14.2 N	10/30	NA	Oct 2010	0 (0)	0 (0)
	132 57.7 W			Feb 2011	0 (0)	0 (0)
Langara Island 3	54 14.2 N	4.5/15	NA	Oct 2011	0 (0)	1 (7)
	132 57.7 W			Feb 2012	0 (0)	0 (0)
Caamaño Sound	52 51.032 N	7/30	20	Oct 2011*	0 (0)	8 (378)
	129 19.652 W			Feb 2012	0 (0)	0 (0)
Squally Channel	53 5.8 N	9/20	20	Oct 2012*	0 (0)	3 (289)
	129 18.7 W			Feb – NA	NA	NA
Cape St. James 1	52 2.017 N	7/30	100	Oct 2009	0 (0)	0 (0)
	131 12.054 W			Feb 2010	0 (0)	0 (0)
Cape St. James 2	52 2.009 N	9/30	98	Oct 2010	0 (0)	2 (50)
	131 12.056 W			Feb 2011	0 (0)	1 (28)
Triangle Island	50 44.879 N	4.5/15	148	Oct 2011	0 (0)	9 (348)
	129 10.565 W			Feb 2012	0 (0)	5 (128)
Brooks Peninsula	50 3.616 N	4.5/15	105	Oct 2010	0 (0)	23 (1052)
	127 53.864 W			Feb 2011	0 (0)	25 (1016)
Union Seamount	49 32.703 N	60/60**	320	Oct – NA	NA	NA
	132 42.380 W			Feb 2006*	1 (60)	0 (0)
Total					7 (151)	94 (4342)

* Caamaño Sound recording began October 18 2011, Squally Channel recording ended October 18, 2012, Union Seamount recording began February 9 2006.

** The duty cycle was interrupted intermittently for 10 minutes when high frequency sounds were detected.

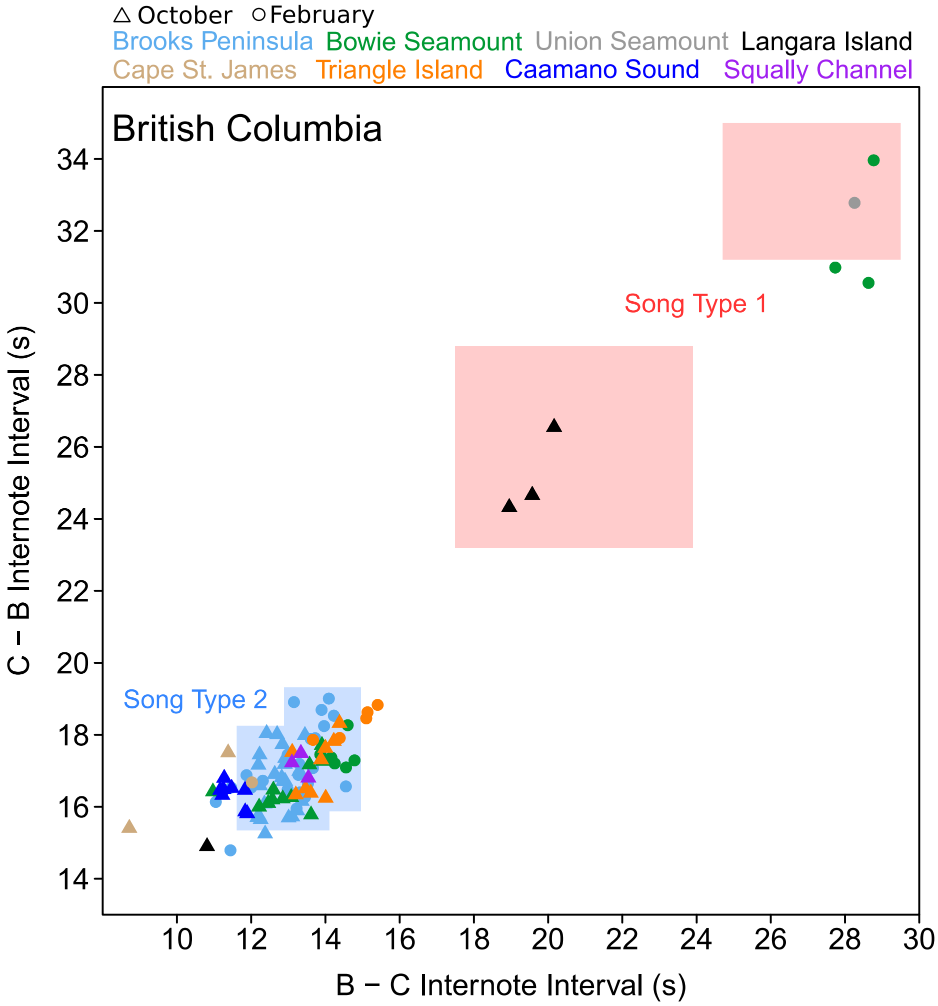

Figure 3-2. Internote intervals of fin whale doublet songs measured from recordings made in October and February of various years in British Columbia waters. Each data point is a song plotted as the median of the song's long interval measurements (C-B internote interval) vs. the median of the song's short interval measurements (B-C internote interval). Colours represent recording locations and shapes represent the months of October (triangles) and February (circles). The light red boxes show the range (calculated as median ±MAD) of the internote intervals for October (lower box) and February (upper box) for song Type 1 (derived from song measurements in Oleson et al. 2014), and the light blue boxes show the range of the internote intervals for October (lower box) and February (upper box) for song Type 2 (derived from song measurements in Chapter 2).

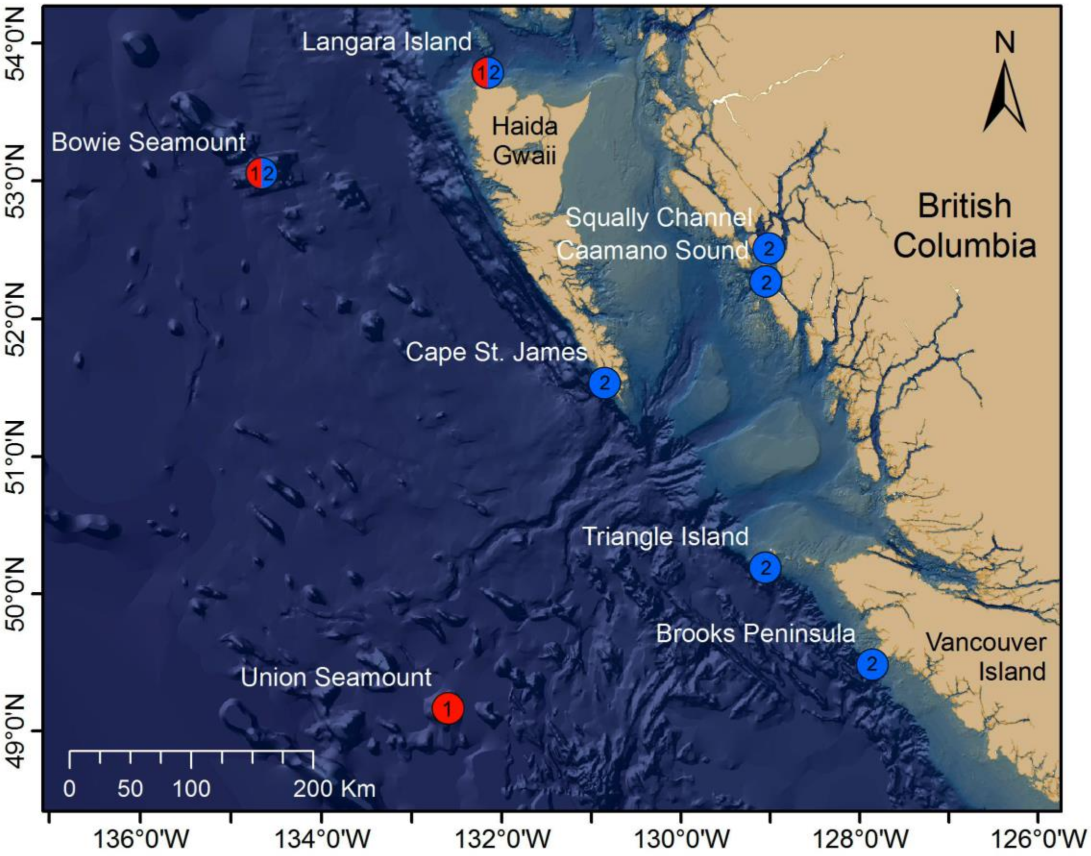

Figure 3-3. Locations of passive acoustic recordings from British Columbia waters. Recordings were analyzed from the months of October and February in various years (2006, and 2009 – 2012) for each location (see Table 3-1). Coloured circles indicate the presence of song Type 1 (red) and song Type 2 (green) at that recording location (see Table 3-1).

3.4.2 Fin Whale Doublet Song in the North Pacific Ocean

Song Type 1—Song Type 1 has been previously described from Southern California, Hawaii and the Bering Sea (Oleson et al. 2014). I found examples of fin whale doublet song with internote intervals that are consistent with song Type 1 in five other previously published studies (Figure 3-4; Table A-1). Consistent with the Oleson et al. (2014) study, one example was from Southern California (INI ~ 23/27, Clark and Fristrup 1997), two were from the central North Pacific (INI ~ 26/32 McDonald and Fox 1999; INI ~24/28, Thompson and Friedl 1982, Thompson et al. 1992), and one was from the Gulf of Alaska or Bering Sea (INI ~ 24/28, Hatch and Clark 2004). An additional example was found off Japan in the western North Pacific (INI ~ 29/34, André et al. 2011).

Song Type 2—I found examples of fin whale doublet song with internote intervals that are consistent with song Type 2 in five published studies (Figure 3-4; Table A-1). These examples were from the general "eastern North Pacific" (INI ~ 12/16, Cummings and Thompson 1966, cited in Thompson et al. 1992), from a network that spanned from Vancouver Island to California (INI ~ 16/18, Weirathmueller and Wilcock 2014), approximately 500 km offshore of Vancouver Island, British Columbia (INI ~ 13/17, Stafford et al. 2007), coastal Washington (INI ~ 11/15, Sirović et al. 2011) and coastal Oregon (INI ~ 14/16, Haxel et al. 2013).

Other Song Type: Gulf of California—Fin whales in the Gulf of California are considered a unique population, with song that is distinct from song in the rest of the North Pacific (Thompson et al. 1992, Hatch and Clark 2004, Mizroch et al. 2009). Fin whale doublet songs in the Gulf of California differ from other doublet songs in that they do not consist of alternating classic and backbeat notes (Thompson et al. 1992, Hatch and Clark 2004). The notes are all of relatively similar frequency content, but they have two distinct note intervals. Doublet song recorded from the Gulf of California on August 8, 1987 (prior to the fin whale singing season) had internote intervals of ~ 5 and 17 s (Thompson et al. 1992). This sample was not included in Figure 3-4 and Table A-1 because it was only recorded on one day in the summer, outside of the fin whale singing season. Internote intervals in February and March of 1999-2000 (late in the singing season) were ~ 4 and 10 s for 97 measured songs (Hatch and Clark 2004). These note intervals were smaller than note intervals from song Type 1 and song Type 2.

Other Song Type: Central North Pacific—Doublet internote intervals reported in three studies from the central North Pacific fall between the range of reported internote intervals for the North Pacific song Type 1 and song Type 2 (Figure 3-4, Table A-1) The authors of one of the studies stated that although the modes of the internote intervals were 16 s and 20 s, the short interval ranged from 14 to 18 s and the long interval ranged from 20 to 30 s (Northrop et al. 1968). They recorded fin whale calls from September through April, so it is possible that these ranges represent a seasonal change in the internote intervals. The values reported by the other two studies fall within these ranges (INI ~ 15/22 s, Patterson and Hamilton 1964; INI ~ 17/23 s, Thompson and Friedl 1982, Thompson et al. 1992), suggesting that this may represent a third distinct song in the central North Pacific, in which the lengths of the internote intervals fall between the North Pacific song Types 1 and 2.

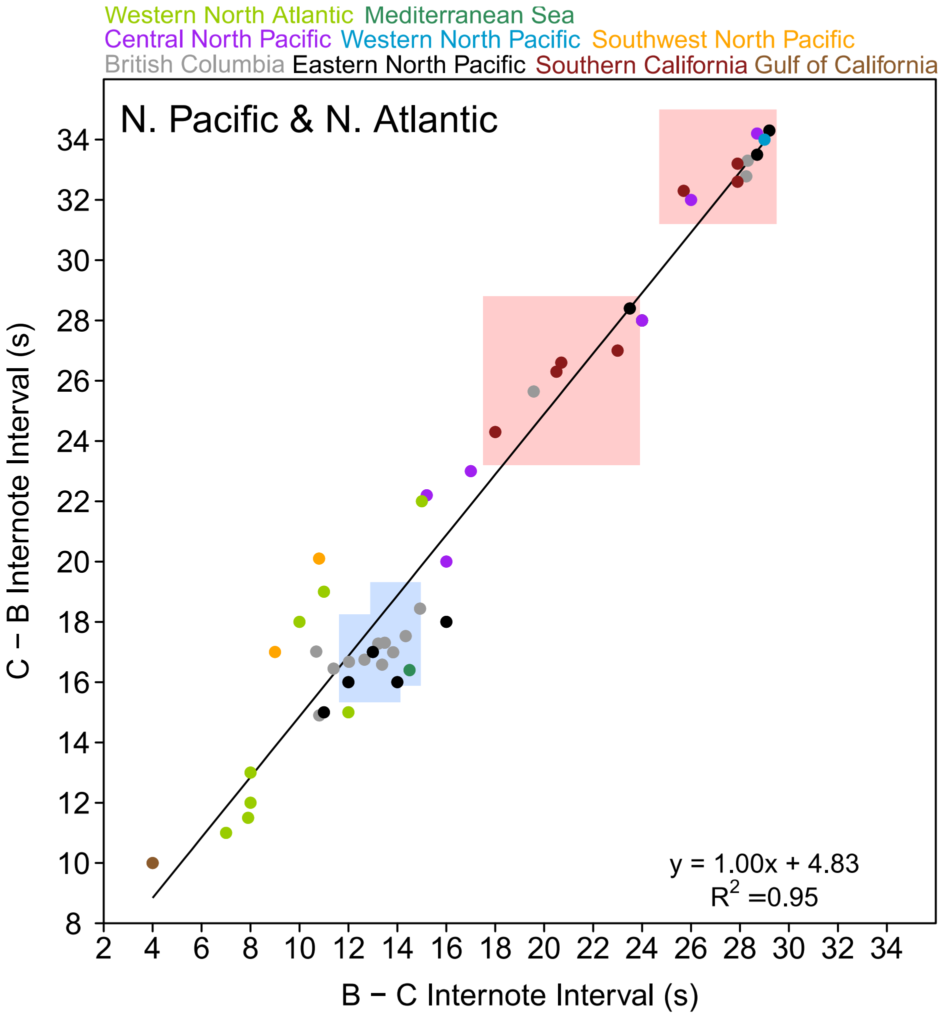

Figure 3-4. Internote intervals of fin whale doublet songs from the North Pacific and North Atlantic Oceans. Data points from British Columbia are medians of the long and short interval for October and February for each location that I analyzed in this study. All other data points are from previously published studies from various years and months (sources are located in Table A-1). Colours represent regions. The light red boxes show the range (calculated as median ±MAD) of the internote intervals for October (lower box) and February (upper box) for song Type 1 (Oleson et al. 2014), and the light blue boxes show the range of the internote intervals for October (lower box) and February (upper box) for song Type 2 (Chapter 2).

3.4.3 Song in the South Pacific, North Atlantic and Southern Oceans

Southwest Pacific—Internote intervals of doublet songs from two studies in the southwest Pacific do not fall within the range of either North Pacific song Type 1 or song Type 2 (Figure 3-4, Table A-1). A study in the Lau Basin off Tonga reported mean internote intervals off 10.8 s and 20.1 s, with the short interval ranging from 8 to 13.5 s and the long interval ranging from 18.4 to 22.9 (Brodie and Dunn 2015). The study occurred over a full year and fin whale calls were present from June to October (the Southern Hemisphere winter) so it is possible—although not explicitly stated—that these ranges represent a seasonal change in the internote intervals. A study off New Zealand provided a short example of fin whale song with internote intervals that correspond closely to this range (INI ~ 9/17s, McDonald 2006).

The songs recorded off Tonga and New Zealand do not correspond to the North Pacific song Type 1 or 2, suggesting that they may represent a distinct song type. However, internote intervals of this song type are more similar to the North Pacific song Type 2 than to song Type 1.

Indian Ocean and Southern Ocean—A study off western Australia in the Indian Ocean, and off Antarctica in the Southern Ocean, reported singlet fin whale song (Gedamke 2009). Although internote intervals were not provided and doublets were not mentioned in this study, it is evident from the example spectrograms given that they do occur. When backbeats occur, it appears that the internote intervals of the doublets that they create are very similar to those of the North Pacific song Type 2 (INI ~ 13/17 s; Figure 3-5). Furthermore, fin whale singlet song in the Scotia Sea region of the Southern Ocean has been reported to have internote intervals of 13 s (Sirovic et al. 2006).

The songs from the Indian and Southern Oceans contain high frequency components not found in the North Pacific songs (Figure 3-5; Gedamke 2009). Measurements from these songs were not included in Figure 3-4 and Table A-1 because of the extremely small sample sizes available.

Western Tropical North Atlantic—A study that included song samples from the western tropical Atlantic (in the region of the Caribbean) reported fin whale song with an internote interval of ~ 13 s between regular (classic) notes (Hatch and Clark 2004).

Although the short and long doublet intervals were not measured in this study, it is evident from the example spectrogram given that they do occur, and that the internote intervals of the doublets that they create are very similar to those of the North Pacific song Type 2 (Figure 3-5). Additionally, internote intervals of 30 s are evident in the figure of intervals between regular (classic) notes, which corresponds to the interval between classic notes of North Pacific song Type 2. The songs from the western tropical North Atlantic contain high frequency components not found in the North Pacific songs (Figure 3-5; Gedamke 2009). Measurements from these songs were not included in Figure 3-4 and Table A-1 because of the extremely small sample sizes available.

Western North Atlantic and Mediterranean Sea—Three interval types reported from the area of New England (INI ~ 7/11 s, Watkins 1981; INI ~ 8/12 s, Walker 1963; INI ~ 7.9/11.5 s, Watkins et al. 1987), and one from Bermuda (INI ~ 8/13 s, Watkins et al. 1987), were very similar to each other. The intervals of these songs were smaller than the North Pacific song Type 2 (Figure 3-4, Table A-1).

One study reported three different doublet interval types (INI ~ 11/19 s, INI ~ 12/15 s, and INI ~ 15/22 s, Patterson and Hamilton 1964) co-occurring in the area around Bermuda, with no seasonal patterns in the presence of the interval types. Another study reported similar intervals from an uncertain location but likely near New England (INI ~ 10/18 s, Watkins 1981). These intervals appear to be longer than the other intervals reported primarily from the area off New England. These intervals are more similar to the North Pacific song Type 2 than Type 1 (Figure 3-4, Table A-1).

Intervals reported in one study from the Mediterranean Sea are similar to those of the North Pacific song Type 2 (INI ~ 14.5/16.4 s, Clark et al. 2002; Figure 3-4, Table A-1).

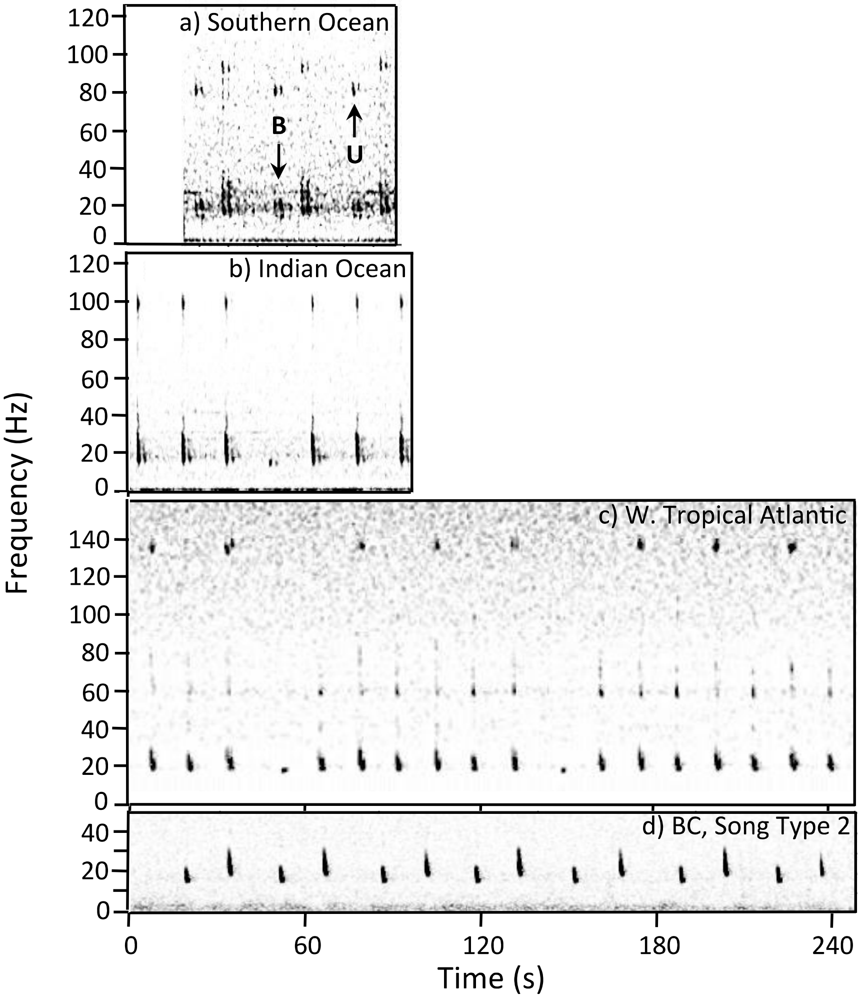

Figure 3-5. Spectrograms of fin whale song recorded from other ocean basins. a) Southern Ocean (modified from Gedamke 2009), b) Indian Ocean, off Australia (modified from Gedamke 2009), c) Western Tropical North Atlantic (modified from Hatch and Clark 2004), d) song Type 2 from British Columbia for reference to the other spectrograms. The letter B in panel 'a' identifies the backbeat note, which is also present in all other panels below. The letter U identifies the high frequency upsweep note that is present in panels 'a' to 'c'. Spectrograms have been resized to the same time and frequency scales for comparison. Note the similar internote intervals around the backbeats in each panel.

3.4.4 Common Pattern

The internote intervals of the doublet songs compiled from around the world ranged from 4 to 30 s for the short interval and 10 to 34 s for the long interval. Across this wide range of internote intervals, there is a significant, positive, linear relationship between the long and short internote intervals ($y=1.00x+4.83$, $p = 0.0$, $R^2 = 0.95$). In other words, the long interval is about 5 seconds (4.8 s) longer than the short interval, irrespective of the length of the short interval (Figure 3-4). Although sample size is limited, the relationship appears to be tighter at the high end of the internote interval range than the low end (Figure 3-4).

3.5 Discussion

Two fin whales songs types (Type 1 and Type 2) can be heard in British Columbia, of which song Type 2 appears to be more common. The whales producing song Type 2 range coastally from at least northern BC to southern Oregon, while song Type 1 has been recorded in the Bering Sea, Hawaii, and Southern California (Oleson et al. 2014), but is less common in BC—occurring only a few times at the offshore sites and the most northerly site. These two song types may correspond to the two genetic clades of fin whales that have been identified in the eastern North Pacific (Archer et al. 2013).

Similarities and differences in fin whale doublet song from within the North Pacific, and among other ocean basins, correspond to estimates of genetic divergence, suggesting that fin whale song reflects population structure, at least at the subspecies level. However, at the species level, there appears to be a common pattern in the doublet song that is shared by fin whales around the world, whereby the long interval of the doublet is consistently about 5 seconds longer than the short interval. The significance of this highly conserved characteristic of fin whale songs across all confirmed and potential subspecies is unexplained and warrants further study.

3.5.1 Fin Whales in British Columbia

The two song types I recorded in British Columbia waters suggest that there are two populations of fin whales that are somewhat spatially segregated. The fin whales that produced song Type 2 (the putative “Type 2 population”) occurred throughout coastal

British Columbia, from sheltered inshore coastal inlets, along the shelf edge, and offshore to Bowie Seamount. However, I only detected song Type 1 from whales (the putative "Type 1 population") at the two offshore recording locations and the most northern BC recording location near the shelf edge. This suggests that the Type 2 population may use coastal waters more often than the Type 1 population, which occurred mostly offshore. Additional recordings of song Type 2 from coastal areas of Washington (Sirović et al. 2011) and Oregon (Haxel et al. 2013) suggest that the Type 2 population ranges coastally at least from northern BC, south to Oregon.

The possible spatial segregation of the two potential fin whale populations in British Columbia may mean that the Type 2 population was affected by commercial whaling to a greater extent than was the Type 1 population. Commercial whaling in BC was primarily shore-based, with ships catching and taking whales back to the shore stations for processing. This meant that whales occurring coastally near the stations would have been more likely to be taken than whales that occurred farther from shore.

The majority of fin whales taken by whalers in BC were off the northwestern coast of Vancouver Island, near the Coal Harbour Whaling station (Gregr and Trites 2001, Ford 2014). The highest density of kills was centered around Brooks Peninsula, where song Type 2 was the only song type recorded in 2010 (Chapter 2). This song type was previously recorded prior to 1966 (Cummings and Thompson 1966, cited in Thompson et al. 1992) suggesting that this population was present during the whaling era (1905-1967), and has persisted to this day.

I recorded significantly more fin whale songs at Brooks Peninsula than at other recording locations in BC. This, together with the fact that the majority of fin whales were also killed here, suggests it was and continues to be an important area for fin whales due possibly to the upwelling of nutrient rich waters that result in a highly productive environment that supports the zooplankton consumed by fin whales (Gregr and Trites 2001).

Fin whales are usually found in deep water, near or beyond the shelf break, so the presence of Type 2 fin whales in Caamaño Sound and Squally Channel is notable because these narrow coastal mainland inlets are on the continental shelf, approximately 150 km from the nearest shelf edge. However, these inlets are very deep and may provide suitable foraging habitat. Fin whales were historically hunted in Caamaño Sound and Squally Channel, and sightings in recent years suggest that they appear to be re-occupying this inshore habitat (DFO 2012).

3.5.2 North Pacific Fin Whale Population Structure

All of the doublet fin whale songs recorded to date in the North Pacific Ocean group into 4 song types—of which most are either Type 1 or Type 2. A third song type (North Pacific Type 3) may occur in the central North Pacific with internote intervals that fall between the Type 1 and Type 2 songs—while a fourth song type (with very short internote intervals and no backbeat notes) has been recorded in the Gulf of California (Thompson et al. 1992, Hatch and Clark 2004). This Type 4 song has been previously associated with a distinct resident population of fin whales and likely reflects the genetic divergence between these whales and the rest of the North Pacific fin whales (Thompson et al. 1992, Bérubé et al. 2002, Hatch and Clark 2004, Mizroch et al. 2009).

The three North Pacific Ocean song types are consistent with genetic data (from mitochondrial DNA) that supports the presence of two, and possibly three separate clades of fin whales in the eastern North Pacific (Archer et al. 2013). Two of these clades (Clade A and C) are genetically very different, with 108 fixed differences between them (Archer et al. 2013). Individuals belonging to these two clades were sampled from the eastern North Pacific, along the coast of North America from the Bering Sea south to the Southern California Bight and Gulf of California.

The two common song types from the eastern North Pacific, song Types 1 and 2, may correspond to the North Pacific fin whale Clades A and C. The position of the third clade (Clade B) in the phylogenetic tree is uncertain, and is based on only two individuals sampled in Hawaii and the Gulf of California (Archer et al. 2013). It is possible, however, that this third clade corresponds to song Type 3 that occurs in the central North Pacific.

It is probable that song Type 1 and song Type 2 correspond to the two distinct clades of fin whales identified in the eastern North Pacific. Furthermore, it is likely that song Type 1 is from Clade A and song Type 2 is from Clade C, based on Clade C fin whales being sampled more often north of Pt. Conception, California, and Clade A being sampled more often south of Pt. Conception (Archer et al. 2013). This explanation fits with the finding that song Type 2 occurs at least from BC to Oregon (with no published confirmed records of Type 2 songs from Southern California)—and that song Type 1 occurs in Southern California (in addition to Hawaii and the Bering Sea; Oleson et al. 2014).

Another compelling argument for assigning song Type 2 to Clade C lies in the evolutionary history of fin whales in the North Pacific. According to the mitogenomic data, Clade A diverged from all other fin whales about 1.94 million years ago (Archer et al. 2013). The other fin whales then evolved into the North Atlantic and Southern Hemisphere whales. The North Pacific Clade C fin whales then branched off from the Southern Hemisphere subspecies, likely due to an individual that migrated from the Southern Ocean to the North Pacific about 0.37 million years ago (Archer et al. 2013). Clade C whales are therefore more genetically similar to Southern Hemisphere whales than to the Clade A North Pacific whales (Archer et al. 2013). This is consistent with my finding that the North Pacific song Type 2 is more similar to the Southern Hemisphere songs than to North Pacific song Type 1, suggesting that the Type 2 whales correspond to the Clade C whales.

Although the mitogenome data show that Clade A and Clade C are genetically distinct from each other, nuclear DNA is needed to confirm the evolutionary history suggested by the mitochondrial DNA (for example see Shaw 2002), and to determine whether there is gene flow between the two clades (Archer et al. 2013). Limited gene flow in nuclear markers would mean that Clade C could be considered part of the Southern Hemisphere subspecies (*B. b. quoyi*), and that Clade A is a new subspecies (Archer et al. 2013). Studies of nuclear DNA are not yet available, but the significant difference between song Types 1 and 2 suggest that fin whales are likely able to discriminate between their respective A and C Clades based on song, which could potentially limit gene flow. Courtship songs of many species serve to advertise the identity of the singer, ensuring that matings between incompatible species are prevented (Wells and Henry 1998). However, the extent to which differing song types impede mating between fin whales is unknown.

On a broader scale, the early divergence of the North Pacific clade A fin whales from all other fin whales in the North Pacific, Southern Ocean, and North Atlantic, is consistent with song Type 1 internote intervals (assumed to represent Clade A) being distinct from other songs from the North Pacific, Southern Ocean, and North Atlantic. Many songs from the North Pacific, Southern Ocean, and North Atlantic (excluding those from Clade A in the North Pacific), have strikingly similar internote intervals (Figure 3-5), which may possibly reflect their more recent divergence from each other, than from North Pacific Clade A. Additionally, high frequency notes have been found only in songs from the Southern Hemisphere and the Atlantic Ocean, possibly reflecting a common ancestor (that is not shared with North Pacific Clade A whales), that used high frequency notes. The congruence in these broad genetic and acoustic patterns suggest that similarities and differences in song may provide indicators of genetic relationships in fin whales.

While on a broad scale (subspecies level), genetic patterns (based on the mitogenome) and acoustic patterns appear to agree, population structuring at a finer scale may be reflected in more subtle song differences and therefore may be more difficult to detect. In the western North Atlantic, differences in the songs of fin whales that are not genetically differentiated, may correspond to distinct feeding aggregations within the larger population (Delarue et al. 2009). More detailed analysis of internote intervals, and other song characteristics such as frequency, may thus reveal differences that are more subtle than the obvious differences between song Type 1 and 2.

Although the two song types identified in the North Pacific are consistent with the genetic evidence of two clades of fin whales occurring in the eastern North Pacific, it is possible that the song types may not be indicative of subspecies structuring, but some other form of population structuring, such as different age classes or reproductive statuses. Based on whaling data from the Southern Hemisphere, it was noted that immature animals tend to travel nearer to the coast than mature animals (Pike 1956, unpublished data). It is possible that fin whale age classes segregate by distance from shore, and that song Type 1 represents mature whales that occur offshore and that song Type 2 represents immature individuals that occur closer to shore. However, the whales that produced song Type 2 were likely sexually mature given that their singing behaviour became increasingly stereotyped as the breeding season progressed (Chapter 2). The BC whaling data show that a larger proportion of immature whales occurred here than at higher latitudes such as the eastern Aleutian Islands (Pike 1956, 1963, unpublished data), suggesting possible age segregation by latitude. However, the smaller sized whales in BC may simply reflect the lower length limits for the BC whaling stations (Pike 1956). Additionally, the majority of whaling occurred in the summer months (April to October), and information on segregation in the winter (when singing occurs) is unavailable. In recent years, a number of female fin whales with young calves have been observed in near-shore waters of BC, showing that mature whales do occur here (John K. B. Ford, Cetacean Research Program, Fisheries and Oceans Canada, personal communication).

3.5.3 A Highly Conserved Pattern

Despite the differences in fin whale songs that seem to correspond to subspecies level genetic differentiation, all songs from all ocean basins from which data are available, shared two common traits, or “rules”. The first is that the long interval of the doublet is about 5 seconds longer than the short interval, irrespective of the length of the short interval (5-sec rule). The second rule is that the backbeat note (the lower frequency, narrower bandwidth note) always follows the long interval. Aside from some variation around the 5 s rule, no exceptions to these rules were found (except that doublets in the Gulf of California did not use backbeats), showing that these rules are highly conserved within this species.

The 5-sec rule was the most strictly followed at the longest internote intervals observed (short INI of ~ 29 s and long INI ~34 s), which is opposite to the naïve expectation that it would be more difficult to maintain a 5 second difference in interval lengths as the intervals get longer. This shows that fin whales are capable of producing notes at consistent intervals, even at very long intervals. The greater variation around the 5-sec rule at shorter intervals may be explained by the fact that songs with short intervals came from various populations of whales (i.e., North Pacific, southwest Pacific and North Atlantic), which may have slight variations of the 5-sec rule (e.g., one population may follow a 4-sec rule, and another may follow a 6-sec rule). Most fin whale songs sampled in BC fell below the 5-sec line (i.e., < 5-sec rule), while samples from elsewhere (including some samples from the North Atlantic and the samples from the southwest Pacific) fell above the line (i.e., > 5-sec rule). Variations on the 5-sec rule may represent a new and unexplored characteristic of fin whale song that has the potential to provide population information.

The significance of the 5-sec rule is unclear. Based on its relatively conserved nature across subspecies, it is possible that this song trait functions in species recognition. However, it is difficult to imagine how the 5-sec rule may act as a species-specific identifier, because of the changing nature of the relationship of the long and short interval across interval lengths. Songs with short intervals (like those from song Type 2) have obviously different interval lengths, while the difference is much less apparent at longer intervals (like those from song Type 1). Thus, the 5 second difference in lengths is likely more difficult to detect in songs with long internote intervals.

Whether or not the 5-sec rule carries species recognition information, its presence across subspecies suggests a genetic or innate origin of the pattern. Short time constants associated with time perception and motor skills occur in humans and animals. Humans experience temporal intervals of 2-5 seconds long as units, and human speech and movement is associated with a 2-3 second time constant (reviewed in Gerstner and Goldberg 1994). Movement and time perception in some mammals have time constants of 1 to 4 seconds (Gerstner and Goldberg 1994, Gerstner and Fazio 1995) that are believed to indicate the presence of a time regulating neural system that has been highly conserved in mammals (Gerstner and Goldberg 1994). The ~5 second difference in the long and short intervals found for fin whales may indicate a similar conserved time constant. Several neural interval timing mechanisms have been proposed for humans and animals (Mauk and Buonomano 2004, Buhusi and Meck 2005, Goel and Buonomano 2014), and the presence of a mechanisms such as these may explain the consistency of fin whale note intervals within songs of an individual, and within individuals in a population. This may also explain why different populations may exhibit slight variations to the 5-sec rule, whereby selection or genetic drift within populations may have acted on the interval timing mechanism, resulting in variations on the 5 s rule.

Alternatively, the 5-sec rule may simply be the by-product of some unknown physiological constraint to vocal production. However, this too is difficult to evaluate because the mechanism of vocal production in fin whales is unknown. Fin whales, like humpback whales, have a laryngeal sac that is separated from the trachea and lungs by a structure homologous to the vocal fold in terrestrial mammals, called the U-fold (Reidenberg and Laitman 2007). In humpback whales, vocalizations are thought to be produced by forcing air back and forth between the lungs and laryngeal sac across the U-fold (Reidenberg and Laitman 2007, Mercado et al. 2010, Adam et al. 2013). This proposed mechanism of sound production allows humpback whales to create a highly diverse repertoire of sounds. Although fin whales may also produce 20-Hz notes by forcing air across the U-fold, it leaves the question as to why the fin whale repertoire is so small and simple compared to the humpback whale. Nor does this method of sound production provide a physiological explanation as to why there is a greater length of time between the production of a classic and backbeat note, than between a backbeat and classic note. Physiological constraints on vocal production do not explain why fin whales can produce interval lengths from 4 to 34 s, as well as irregular interval lengths in non-song contexts.

In contrast to the highly conserved 5-sec rule, the actual durations of the internote intervals vary considerably between populations, and may reflect a song trait that is not genetically based, but may rather be learned and transmitted culturally within populations. Cetaceans are among the few mammals that are known to possess vocal learning capabilities, and although nothing is known about whether fin whales have the ability to learn songs, the closely related humpback whale is known for it’s song learning capabilities, and cultural transmission of songs across ocean basins (Garland et al. 2013, Janik 2014).

3.5.4 Study Limitations and Future Research

My comparisons of genetic and acoustic patterns were limited in a number of ways. First, the number of published song samples was limited, samples were unevenly distributed by region, and many regions were not represented. Second, the measurements of note intervals from many of these studies were based on an unknown number of songs and notes, with no estimates of variability or seasonal change, and little information on how the intervals were calculated (e.g., measured from a spectrogram, or "eye-balled"). In many cases, no measurements of internote intervals were provided, which resulted in me measuring internote intervals, to the best of my ability, from the spectrograms provided.

Because the doublet song has been described in detail from the North Pacific, my comparisons were based on doublet songs alone. However, it is well known that fin whales in the North Pacific, North Atlantic and Southern Ocean also produce song consisting of singlets. Additionally, because internote intervals have been shown to be the song parameter with the most potential for revealing population differences, my analysis focused only on internote intervals. Analysis of singlet song may provide additional information or help to clarify the comparisons made here.

Similarly, analysis of other song parameters, such as spectral characteristics of the notes (e.g., minimum and maximum frequency, center frequency, and frequency sweep), may also provide ways of distinguishing song types. North Pacific song notes have been observed to have a greater frequency sweep than North Atlantic song notes (Thompson et al. 1992). Although I did not measure this, it appears that the song Type 1 and Type 2 that I recorded in British Columbia have different frequency characteristics. For example, song Type 2 notes appear to be slightly higher in frequency overall than Type 1 notes, and the difference in frequency of the classic and backbeat notes is greater in song Type 2 than Type 1 (Figure 3-1).

Although my study provides support for the existence of two populations of fin whales in the eastern North Pacific, more work is needed to unequivocally assign song Type 1 and 2 to Clade A or C. This could be achieved by taking genetic samples from singers of both song types during the fin whale singing season (October to March), and comparing them to the genetic profiles of Clade A and C. Obtaining song samples and assigning them to individuals may be possible by attaching digital acoustic tags to whales. However, the success of this approach is dependent on 1) being able to tag males (only males sing), 2) the whale producing song during the relatively short tagging period, 3) the process of tagging not affecting singing behaviour, and 4) the ability to obtain a biopsy from the tagged whale. Directional sonobouys may also be used to obtain recordings with direction information, so that songs may be assigned to individuals.

3.6 Conclusions

Song analysis has provided new information on the acoustic population structure of fin whales in British Columbia waters, and the greater eastern North Pacific. The result of two distinct song types with differing distributions is consistent with two genetically distinct clades of fin whales, which may be different subspecies (Archer et al. 2013), inhabiting the eastern North Pacific. The occurrence of two fin whale subspecies within the same ocean basin would have significant implications, and pose unique challenges, for the conservation and management of fin whales in the North Pacific.

If further studies confirm that: 1) there is little or no gene flow between Clades A and C, 2) that the two distinct song types correspond to the two clades, 3) that their habitat use is different (i.e., offshore vs. coastal in BC), and 4) that their distributions are different (i.e., ranges in the North Pacific), the clades may qualify as separate Designatable Units in Canada (as determined by the Committee on the Status of Endangered Wildlife in Canada, COSEWIC). Due to their differing evolutionary histories, potentially differing exploitation histories, and apparent habitat use differences, it is likely that the two populations have different abundances, recovery trends, biological and ecological limitations, and anthropogenic threats that would need to addressed separately.

Confirmation of differences between clades may result in the Clade C fin whales in the North Pacific being classified as belonging to the Southern Hemisphere subspecies, and the Clade A whales being classified as its own subspecies (Archer et al. 2013). The geographic isolation of the Clade C fin whales and the Southern Hemisphere whales would further create a unique situation for management of this subspecies.

The correspondence of song differences (at least in internote intervals of doublet song) and estimates of genetic differentiation (at least in the mitogenome) provide an indicator that differences in song may be a marker of genetic differentiation. This suggests that song analysis contributes to understanding the population structure of fin whales.

Chapter 4: Conclusions

4.1 Summary of Research Findings

The overall objective of my research was to use song analysis to provide new information on the winter distribution, behaviour and population structure of fin whales in a high-latitude area of the eastern North Pacific Ocean. I found that fin whales occurred in British Columbia (BC) consistently through the winter, and suggest that these whales are engaging in reproductive and feeding behaviours. I found that two song types occurred in BC, suggesting the presence of two distinct populations. The population producing song Type 2 was common throughout coastal BC and this population may range south to at least Oregon. Surprisingly, comparison of song characteristics and genetic evidence (Archer et al. 2013) suggest that this population may belong to the Southern Hemisphere fin whale subspecies. The population producing song Type 1, which has previously been described from Southern California, Hawaii and the Bering Sea (Oleson et al. 2014), occurred in BC only at the offshore and most northerly sites.

4.1.1 Winter Presence and Behaviour

To characterize the song of fin whales in British Columbia over one entire singing season, I manually analyzed fin whale 20-Hz notes recorded over one year (2010-2011) at one location (Brooks Peninsula, off the northwest coast of Vancouver Island) using a bottom-mounted autonomous passive acoustic recording instrument. I found that fin whales occurred in BC consistently through the winter, with 20-Hz notes occurring from mid-August through March. Fin whales at this location produced a single distinct song type consisting of a doublet pattern with alternating classic notes (center frequency of ~23.4 Hz) and backbeat notes (center frequency of ~19.1 Hz), with alternating internote intervals of ~17 s and ~13 s.

My study represents only the second detailed description of fin whale song in the North Pacific (see Oleson et al. 2014). The song type that I described was distinct from the other previously described song type from Southern California, Hawaii and the Bering Sea, which has short and long internote intervals that increase from about 20 s and 26 s in October, to about 28 s and 33 s in February (Oleson et al. 2014).

As a measure of reproductive behaviour, I measured the seasonal change in singing behaviour and stereotypy in relation to the breeding period of this species. Singing is a sexual display that is linked to the seasonal fluctuation of testosterone in many species (Riebel 2009, Sakata and Vehrencamp 2012). As I expected, I found that singing behaviour and song characteristics became less variable and more stereotyped as the whales entered the breeding season (November). The peak in stereotypy coincided with the estimated peak in breeding activity for this species (January; Pike 1963, unpublished). The presence of stereotyped song (a reproductive display) shows that reproductively active males occur in BC through the winter, suggesting that reproductive activity occurs at high latitudes of the eastern North Pacific, contrary to the traditional belief that baleen whales migrate south to calve and mate (Lockyer and Brown 1981).

Fin whales have been shown to feed during the day when their euphausiid prey is concentrated at depth, and sing mostly at night when feeding is less efficient (Watkins et al. 1987, Oleson 2005, Stafford et al. 2005, Wiggins et al. 2005, Simon et al. 2010). I found that during the winter breeding season (mid-October to March), fin whales made more calls during hours of darkness, a pattern that is consistent with what is expected for feeding whales.

In summary, my analysis of passive acoustic recordings off Vancouver Island in Chapter 2 provided the first detailed description of fin whale song from British Columbia waters, and is only the second detailed description of fin whale song from the North Pacific. The findings add to the increasing evidence that fin whale movements and residency patterns are more complex than previously thought. In particular, my findings support the hypothesis that at least some fin whales in the North Pacific remain on high-latitude feeding grounds during the winter, where they appear to take advantage of both breeding and feeding opportunities. This suggests that migrating between low-latitude breeding grounds and high-latitude feeding grounds may not be a necessary component of the fin whale’s life history strategy.

4.1.2 Population Structure

Analysis of passive acoustic data from October and February (near the beginning and end of the fin whale singing season) from 8 bottom mounted passive acoustic recorders deployed throughout BC waters in various years between 2006 and 2012, revealed that two distinct song types, and therefore possibly two populations, of fin whales occur in this region of the eastern North Pacific. I found that the majority of fin whales sang the doublet song that I described in Chapter 2 (which I refer to as song Type 2). At the most northerly recording site, and the two offshore sites, I found a few instances of the other previously described doublet song type from the North Pacific (which I refer to as song Type 1; Oleson et al. 2014). I found no evidence of any doublet song that did not fit the description of either of these two song types. This suggests that two spatially segregated populations of fin whales are using BC waters, with the population producing song Type 2 being more coastal.

Through an extensive literature search, I found evidence of song Type 2 occurring from northern BC to Oregon. The population producing song Type 2 appears to occur more coastally than the population that produced song Type 1. I also found evidence of song Type 1 from Southern California, the Bering Sea and the Central North Pacific, which has been previously documented (Oleson et al. 2014). The two song types are consistent with mitogenomic evidence showing that two genetically distinct fin whale populations occur in the eastern North Pacific (referred to as Clade A and Clade C; Archer et al. 2013).

Comparing the two North Pacific song types to song samples from the Southern Ocean revealed that North Pacific song Type 2 was more similar to Southern Ocean fin whale song than to North Pacific song Type 1. This is consistent with the mitogenomic evidence showing that North Pacific fin whale Clade C is more closely related to the Southern Hemisphere subspecies than it is to North Pacific Clade A (Archer et al. 2013). Therefore, I hypothesize that song Type 2 corresponds to Clade C. Surprisingly, this implies that the fin whale population that is most common in BC waters, may belong to the Southern Hemisphere subspecies.

To date, correlations between song differences and genetic population structure have been found in only two populations, for the Gulf of California resident population (Thompson et al. 1992, Bérubé et al. 2002) and in the Mediterranean Sea (Bérubé et al. 1998, Castellote et al. 2012). Although the correspondence of acoustic and genetic similarity that I found has not yet been tested, it provides support for the hypothesis that genetic differences in fin whales are reflected by differences in song, and suggests that song analysis may be a valuable tool for investigating population structure in fin whales.

4.2 Strengths, Weaknesses and Limitations

The strength of my study lies in the method that I used to analyze the passive acoustic data. I manually analyzed the data instead of using automated detection algorithms because I wanted to ensure that every song and every note in every song was accurately measured. Although automated detection methods provide unparalleled speed and efficiency in analyzing large data sets, and they are often quite accurate, the gold standard for accurate acoustic analysis is the human being. For my study it was very important to correctly measure the internote intervals of the fin whale song to obtain an accurate estimate of the internote interval lengths and their variation. Automated detection algorithms can be susceptible to the influence of ambient noise, and this could have resulted in notes with low signal-to-noise ratio being missed, causing inaccurate measurements of the times between notes. Additionally, non-target noises can trigger false detections, also causing erroneous interval measurements. As a human analyst, I was able to choose to measure songs that had sufficient signal-to-noise ratios, so that I was sure that I was not missing any notes in the song sequences.

Although I measured all fin whale song in my detailed analysis of one recording location in Chapter 2, I found only doublet type songs. Therefore, I restricted my analysis in Chapter 3 to only doublet song types. However, it is well known that fin whales in the North Pacific, North Atlantic and Southern Ocean also produce songs consisting of singlets and other patterns (Watkins et al. 1987, Delarue et al. 2009, Castellote et al. 2012, Morano et al. 2012, Oleson et al. 2014). Analysis of singlets and other song types may provide additional information or help to clarify my analysis.

Another weakness in my study was the limited temporal and spatial coverage of the data that I analyzed. In Chapter 2, I analyzed data from just one year at one recording location, and in Chapter 3 I analyzed only the months of October and February at multiple sites. This was the result of the tradeoff between volume and accuracy: either manually analyze a limited amount of data accurately, or use automated detectors to analyze a large amount of data less accurately. Analysis of more full years of data, from more locations throughout BC would provide a clearer picture of the seasonal occurrence, behaviour and population identity of whales using these waters.

A major limitation of passive acoustic data is that there are no concurrent visual observations to confirm inferences made from vocalizations that are recorded. Studies that perform simultaneous behavioural and acoustic observations are needed in order to be able to correlate vocalizations with behaviours, but these are lacking (Mellinger et al. 2007). Therefore, the context of many vocalizations are inferred based on knowledge of other species or based on the analysis of patterns that correlate to known behavioural patterns. Also, acoustic data come with no information on the vocalizing animal, such as its sex, age, or reproductive status, which limits the extent to which data can be interpreted (except in the case of song, where it has been shown that only male fin whales sing).

4.3 Applications and Importance of Study

My finding that possibly two populations of fin whales use British Columbia waters has implications for conservation and management. With the song Type 2 animals occurring more coastally than the song Type 1 animals, it is possible that the two putative populations were differentially affected by whaling, and therefore may exhibit different abundance and recovery trends. Furthermore, differences in the spatial distribution of the two populations mean that they may experience different anthropogenic threats that need to be mitigated separately. For example, the coastal population may be at greater risk of ship strikes. Similarly, the two populations may experience different biological and ecological limitations. For example, prey availability and foraging behaviour may differ between shallower coastal waters and deep offshore waters, possibly resulting in different energy needs and expenditures.

My finding that fin whales occur in BC throughout the winter may spur further winter research efforts. Visual surveys, photo-identification, satellite tagging and other efforts occur predominately in the summer months, due to the challenges of working on the ocean in the winter at high latitudes. However, confirming that fin whales are present through the winter, and showing that they seem to be present consistently in the area of Brooks Peninsula off the northwest coast of Vancouver Island, may provide some incentive for putting more effort into winter research.

My research provides support for the use of passive acoustics as a tool in population structure analysis for fin whales. The identification of two very distinct and distinguishable song types, which seem to correspond to estimates of genetic differentiation, suggests that song analysis should be seriously considered for future studies of fin whale population structure.

4.4 Future Research

In order to confirm my hypothesis that the population of whales that occurs commonly in BC waters—the population that produce song Type 2—corresponds to the fin whale Clade C described by Archer et al. (2013), simultaneous genetic and acoustic samples need to be taken. These samples should be taken during the fin whale singing season, between October and March. Singing whales will need to be identified unequivocally, and then biopsy sampled. This could be difficult because fin whales often occur in groups. Targeting solitary whales may not be worthwhile because fin whales are less likely to sing if there no conspecifics near by (Watkins 1981, Watkins et al. 1987, Soule and Wilcock 2013). Assigning song to individuals may be possible by attaching digital acoustic recording tags to the whales. However, the success of this approach hinges on 1) being able to tag males (only males sing; Croll et al. 2002), 2) the whale producing song during the relatively short tagging period, 3) the process of tagging not affecting singing behaviour, and 4) the ability to obtain a biopsy from the tagged whale. Directional sonobouys may also be used to obtain recordings with direction information, so that songs may be assigned to individuals, but careful concurrent visual observations with position data need to be recorded.

Through my literature search, I found small samples of song from Washington and Oregon that match song Type 2. In order to confirm that song Type 2 occurs consistently in these regions, dedicated studies of fin whale song over the winter singing season should be performed. This is important in order to determine the range of the population that produces this song type. Coordinated studies in multiple locations along the coast of North America may be able to detect whether seasonal shifts in calling between locations occur, which would indicate migratory movements.

Analyzing passive acoustic data from more locations in BC would provide a better picture of how fin whales use these waters. It is known that fin whales use BC waters to feed in the summer, and through visual surveys, important feeding locations can be identified for the purpose of defining critical habitat. However, my research shows that fin whales also use BC waters in the winter. Expanded acoustic monitoring efforts will aid in identifying important winter habitats, so that critical habitat may be defined year-round for fin whales. Additionally, studies to confirm my hypotheses that fin whales are feeding and breeding at high latitudes in the winter will help to define the function of winter critical habitats. Direct visual observations of fin whale behaviour during the winter would be needed in order to achieve this. Analyzing dive patterns using digital acoustic recording tags may also be effective for detecting winter feeding behaviour. Tags with video-recording capability may document feeding, as has been done for blue whales (Goldbogen et al. 2013).

Further examining the presence of fin whales in the coastal inlets of BC is important in light of increasing industrial development plans along this coast. Information on the seasonal occurrence of whales in these areas, and the importance of this habitat, is needed in order to evaluate the potential effects of increased shipping and anthropogenic activity on the whales that use these inlets. The risk of ship strikes and increased noise in the frequency range of fin whales vocalization, are possible effects associated with this industrial activity in coastal waters where fin whales occur. Passive acoustic data collection would provide a method to assess the occurrence of whales and ships, and to measure the noise levels produced by shipping.

Now that two eastern North Pacific fin whale song types have been identified, and the temporal and spectral properties of the songs have been described in detail over the course of complete singing seasons, it is possible to design automatic detection algorithms that can identify the song types, even as they evolve seasonally. This will allow for the efficient analysis of large data sets, and will facilitate the execution of the future acoustic studies that I have proposed.

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Appendices: Supplementary Tables

Table A-1. Fin whale doublet song internote interval measurements (short/long interval) from my study in British Columbia waters (BC) and from previously published literature. For previous publications, the location, month, year and instrument used to make recordings are given where available. NA denotes information that was unavailable. If I (BK) made internote interval measurements from a spectrogram figure, and the date of the recording was not given, the range of dates of fin whale detections, or range of the study period, is given instead. The internote intervals reported in each publication are given along with a description of the type of measurement made (general observation by the authors, acoustic measurement by the authors, or measurements made by me from example spectrograms).

Location	Month	Year	Internote Intervals	Measurement Type	Instrument Type	Source
North Pacific Doublet Song Type 2						
Offshore BC, Bowie Seamount	Oct	2011	13.4/16.6	BK's measurements (n= 11 songs)	AURAL Autonomous moored hydrophone	Koot, this study
Offshore BC, Bowie Seamount	Feb	2012	14.3/17.5	BK's measurements (n= 6 songs)	AURAL Autonomous moored hydrophone	Koot, this study
Coastal BC, Langara Island	Oct	2011	10.8/14.9	BK's measurements (n= 1 song)	AURAL Autonomous moored hydrophone	Koot, this study
Inshore BC, Caamaño Sound	Oct	2011	11.4/16.4	BK's measurements (n= 8 songs)	AURAL Autonomous moored hydrophone	Koot, this study
Inshore BC, Squally Channel	Oct	2012	13.2/17.3	BK's measurements (n= 3 songs)	AURAL Autonomous moored hydrophone	Koot, this study
Coastal BC, Cape St. James	Oct	2010	10.7/17.0	BK's measurements (n= 2 songs)	AURAL Autonomous moored hydrophone	Koot, this study

Location	**Month**	**Year**	**Internote Intervals**	**Measurement Type**	**Instrument Type**	**Source**
Coastal BC, Cape St. James	Feb	2011	12.0/16.7	BK’s measurements (n= 1 song)	AURAL Autonomous moored hydrophone	Koot, this study
Coastal BC, Triangle Island	Oct	2011	13.8/17.0	BK’s measurements (n= 9 songs)	AURAL Autonomous moored hydrophone	Koot, this study
Coastal BC, Triangle Island	Feb	2012	14.9/18.4	BK’s measurements (n= 5 songs)	AURAL Autonomous moored hydrophone	Koot, this study
Coastal BC, Brooks Peninsula	Oct	2010	12.6/16.7	BK’s measurements (n= 23 songs)	AURAL Autonomous moored hydrophone	Koot, this study
Coastal BC, Brooks Peninsula	Feb	2011	13.5/17.3	BK’s measurements (n= 25 songs)	AURAL Autonomous moored hydrophone	Koot, this study
Offshore British Columbia	Nov	2001	13/17	BK measured from 4.5 min spectrogram	PMEL moored autonomous hydrophone	(Stafford et al. 2007)
Vancouver Island BC, to California	NA	2011-2013	16/18	General statement of dominant intervals	Ocean bottom seismometer network	(Weirathmueller and Wilcock 2014)
Coastal Washington	Oct	2008	11/15	BK measured from 50 s spectrogram	HARP autonomous moored hydrophone	(Sirović et al. 2011)
Coastal Oregon	Sep-Dec	2010-2011	14/16	BK measured from 10 min spectrogram	Autonomous moored hydrophone	(Haxel et al. 2013)

Location	Month	Year	Internote Intervals	Measurement Type	Instrument Type	Source
Eastern North Pacific (specific location unknown)	Aug-May	N/A (prior to 1966)	12/16	Typical values reported by author	N/A	Cummings and Thompson 1966, cited in (Thompson et al. 1992)
North Pacific Doublet Song Type 1						
Coastal BC, Langara Island	Oct	2009	19.6/25.6	BK's measurements (n= 3 songs)	AURAL Autonomous moored hydrophone	Koot, this study
Offshore BC, Bowie Seamount	Feb	2012	28.3/33.3	BK's measurements (n= 3 songs)	AURAL Autonomous moored hydrophone	Koot, this study
Offshore BC, Union Seamount	Feb	2006	28.3/32.8	BK's measurements (n=1 song)	PATC Autonomous moored hydrophone	Koot, this study
Gulf of Alaska	Jan, May, Oct-Dec	1999-2001, 2003	24/28	BK measured from 5 min spectrogram	PMEL moored autonomous hydrophone	(Hatch and Clark 2004)
Southern California	Oct	1995	23/27	BK measured from 5 min spectrogram	Towed horizontal line array	(Clark and Fristrup 1997)
Southern California	Oct	2000	20.7/26.6	Measurements made by author (values are medians)	ARP autonomous moored hydrophone	(Oleson et al. 2014)
Southern California	Feb	2001	25.7/32.3	Measurements made by author (values are medians)	ARP autonomous moored hydrophone	(Oleson et al. 2014)
Southern California	Oct	2001	18/24.3	Measurements made by author (values are medians)	ARP autonomous moored hydrophone	(Oleson et al. 2014)

Location	Month	Year	Internote Intervals	Measurement Type	Instrument Type	Source
Southern California	Feb	2002	27.9/33.2	Measurements made by author (values are medians)	ARP autonomous moored hydrophone	(Oleson et al. 2014)
Southern California	Oct	2002	20.5/26.3	Measurements made by author (values are medians)	ARP autonomous moored hydrophone	(Oleson et al. 2014)
Southern California	Feb	2003	27.9/32.6	Measurements made by author (values are medians)	ARP autonomous moored hydrophone	(Oleson et al. 2014)
Bering Sea	Oct	2005	23.5/28.4	Measurements made by author (values are medians)	HARP autonomous moored hydrophone	(Oleson et al. 2014)
Bering Sea	Feb	2001	29.2/34.3	Measurements made by author (values are medians)	ARP autonomous moored hydrophone	(Oleson et al. 2014)
Bering Sea	Feb	2002	28.7/33.5	Measurements made by author (values are medians)	ARP autonomous moored hydrophone	(Oleson et al. 2014)
Central North Pacific - Hawaii	Feb	2001	28.7/34.2	Measurements made by author (values are medians)	ARP autonomous moored hydrophone	(Oleson et al. 2014)
Central North Pacific	Aug-Mar	1992-1993	26/32	BK measured from 2.7 min spectrogram	Autonomous moored hydrophone	(McDonald and Fox 1999)

Location	Month	Year	Internote Intervals	Measurement Type	Instrument Type	Source
Central North Pacific – Hawaii	Aug-Mar	Before 1978-1981	24/28	Durations of sum of long and short interval reported in (Thompson and Friedl 1982). Typical values of long and short intervals reported in Thompson et al. (1992)	NA	(Thompson and Friedl 1982, Thompson et al. 1992)
Western North Pacific – Japan	Apr	2010	29/34	BK measured from 7 min spectrogram	Sea floor observatory	(André et al. 2011)
Other – Gulf of California						
Gulf of California	Feb, Mar	1999-2000	4/10	Measurements made by author (n= 97 songs)	“Pop-up” Autonomous moored hydrophone	(Hatch and Clark 2004)
Other – Central North Pacific						
Central North Pacific – Eniwetok, Midway, Wake, Oahu	Sep- Apr	1965-1966	16 (14,18) / 20 (20,30)	Typical values reported by author. Values are mode (min/max)	PMR MILS Hydrophones and analog recordings	(Northrop et al. 1968)
Central North Pacific – Oahu	Dec	1960	15/22	Typical values reported by author	PMR MILS Hydrophone	(Patterson and Hamilton 1964)
Central North Pacific - Hawaii	Aug-Mar	1978-1981	17/23	Durations of sum of long and short interval reported in Thompson and Friedl (1982). Typical values of long and short intervals reported in Thompson et al. (1992)	Bottom mounted hydrophone recorded to tape recorder with speed of 2.4 cm/s (or 2,4 and 8 x higher speeds), and spectrographic analyzer	(Thompson and Friedl 1982, Thompson et al. 1992)

Location	Month	Year	Internote Intervals	Measurement Type	Instrument Type	Source
Other – Southwest Pacific						
Western Tropical Pacific – Lau Basin, Tonga	Jun-Oct	2009-2010	10.8 (8-13.5) / 20.1 (18.4-22.9)	Measurements by author. Values are mean (min/max)	Ocean bottom seismometers	(Brodie and Dunn 2015)
Southwest Pacific – Northern New Zealand	Jun-Sep	1997	9/17	Author gave 150 s example (12 notes) and typical values	Autonomous moored hydrophone	(McDonald 2006)
Other – North Atlantic						
Western North Atlantic – Most likely Massachusetts, but Pacific possible	Oct-May	1958- 1980	7/11	Typical values reported by author	Various – near surface and bottom mounted hydrophones	(Watkins 1981)
Western North Atlantic– Most likely Massachusetts, but Pacific possible	Oct-May	1958-1980	10/18	Typical values reported by author.	Various – near surface and bottom mounted hydrophones	(Watkins 1981)
Western North Atlantic – South of New England	Oct	1959	8/12	Typical values (with some seasonal dependence noted) reported by author	Autonomous moored hydrophone and oscillographic traces	(Walker 1963)
Western North Atlantic – Maine	Dec	1957	7.9/11.5	Measurements made by author (n=25).	Near-surface single and array hydrophone	(Watkins et al. 1987)

Location	Month	Year	Internote Intervals	Measurement Type	Instrument Type	Source
Western North Atlantic – Bermuda	Nov	1978	8/13	BK measured from figure.	Near-surface single and array hydrophone	(Watkins et al. 1987)
Western North Atlantic –Bermuda	Nov-Mar	1959-1962	15/22	Typical values reported by author. Most common doublet type (20-30% of all calls)	Autonomous moored hydrophone and multichannel Ampex magnetic tape recorder	(Patterson and Hamilton 1964)
Western North Atlantic –Bermuda	Nov-Mar	1959-1962	12/15	Typical values reported by author. Less common doublet type	Autonomous moored hydrophone and multichannel Ampex magnetic tape recorder	(Patterson and Hamilton 1964)
Western North Atlantic –Bermuda	Nov-Mar	1959-1962	11/19	Typical values reported by author. Less common doublet type.	Autonomous moored hydrophone and multichannel Ampex magnetic tape recorder	(Patterson and Hamilton 1964)
Other - Mediterranean Sea						
Ligurian Sea	Sep	1999	14.5/16.4	Measurements made by author (C-B n=21, B-C n=19).	“Pop-up” Autonomous moored hydrophone	(Clark et al. 2002)