INDIVIDUAL KILLER WHALE VOCAL VARIATION DURING
INTRA-GROUP BEHAVIORAL DYNAMICS

A Dissertation in
Acoustics
by
Dawn M. Grebner

© 2009 Dawn M. Grebner

Submitted in Partial Fulfillment
of the Requirements
for the Degree of

Doctor of Philosophy

December 2009
The dissertation of Dawn M. Grebner was reviewed and approved* by the following:

David L. Bradley
Professor of Acoustics
Dissertation Advisor, Chair of Committee

Dean E. Capone
Associate Professor of Acoustics

Susan E. Parks
Assistant Professor of Acoustics

Jennifer L. Miksis-Olds
Assistant Professor of Acoustics

Timothy J. Kane
Professor of Electrical Engineering

John K. B. Ford
Program Head of Cetacean Research
Pacific Biological Station, Fisheries and Oceans Canada
Special Signatory

Anthony A. Atchley
Professor of Acoustics
Chair of the Graduate Program in Acoustics

*Signatures are on file in the Graduate School.
Abstract

The scientific goal of this dissertation was to carefully study the signal structure of killer whale communications and vocal complexity and link them to behavioral circumstances. The overall objective of this research sought to provide insight into killer whale call content and usage which may be conveying information to conspecifics in order to maintain group cohesion. Data were collected in the summers of 2006 and 2007 in Johnstone Strait, British Columbia. For both individuals and small groups, vocalizations were isolated using a triangular hydrophone array and the behavioral movement patterns were captured by a theodolite and video camera positioned on a cliff overlooking the hydrophone locations.

This dissertation is divided into four analysis chapters. In Chapter 3, discriminant analysis was used to validate the four N04 call subtypes which were originally parsed due to variations in slope segments. The first two functions of the discriminant analysis explained 97% of the variability. Most of the variability for the N04 call was found in the front convex and the terminal portions of the call, while very little variability was found in the center region of the call. This research revealed that individual killer whales produced multiple subtypes of the N04 call. No correlations of behaviors to acoustic parameters obtained were found. The aim of the Chapter 4 was to determine if killer whale calling behavior varied prior to and after the animals had joined. Pulsed call rates were found to be greater pre- compared to post- joining events. Two-way vocal exchanges were more common occurring 74% of the time during pre-joining events. In Chapter 5, initiated and first response to calls varied between age/sex class groups when mothers were separated from an offspring. Solo mothers and calves initiated pulsed calls more often than they responded. Most of the no vocal responses were due to mothers who were foraging. Finally, observations of the frequency split in N04 calls discussed in Chapter 6 showed that the higher frequency component (HFC) was always associated with sideband 7 (SB7) of the lower frequency component (LFC). Insight into Northern Resident killer whale intra-group vocal dynamics would aid our understanding of vocal behaviors of many other marine mammal species that rely on vocal exchanges for prey capture, group movement or survival. This is the first study to focus on killer whale vocal
content and usage as it pertains to intra-group dynamics for 1) mother and offspring separations and 2) for all individuals prior to joining events, as well as 3) individual usage in a diverging pulsed call. It is also the first time the N04 call has been parsed into subtypes.
# Table of Contents

List of Figures ix  
List of Tables xii  
Acknowledgments xiii  

**Chapter 1 Introduction**  
1.1 Relevance of this Study ................................. 1  
1.2 History of Killer Whales ............................... 4  
1.3 Behavioral Movement ................................. 6  
1.4 Auditory and Vocal Behavior .......................... 8  
  1.4.1 Types of Vocalizations ............................ 9  
1.5 Communication Theory of Vocal Production .......... 11  
1.6 Maintaining Group Cohesion ........................... 12  
  1.6.1 Discrete Pulsed Calls ............................ 12  
  1.6.2 Selective Pressures ............................... 16  
1.7 Study Species and Location ........................... 17  
1.8 Thesis Outline ........................................ 20  

**Chapter 2 Site, Methods & Analysis: In Depth**  
2.1 Part I: Johnstone Strait, British Columbia, Canada .... 21  
  2.1.1 Description of Location ............................ 21  
  2.1.2 Oceanography of Johnstone Strait .................. 22  
  2.1.3 Sound Speed Profiles ................................ 26  
  2.1.4 Water and Weather Conditions .................... 28  
    2.1.4.1 Water Visibility ............................ 28  
  2.2 Part II: Acoustic Recording System ................... 29  
    2.2.1 Sensitivity, Frequency Response, Bandwidth, and Gain 29  
    2.2.2 Power Supply .................................... 30  
    2.2.3 Hydrophone Array Setup .......................... 31
Chapter 3 Discrete Pulsed Call Variation

3.1 Introduction ........................................... 52
3.2 N04 Subtypes and Acoustic Parameter Variation .............. 56
  3.2.1 Results ........................................... 61
    3.2.1.1 Acoustic Parameter Variation ................. 62
3.3 Predominant Sideband Energy and Its Usage .................. 69
  3.3.1 Results ........................................... 69
3.4 Social Circumstances .................................. 73
  3.4.1 Pre-joining Events ................................ 73
    3.4.1.1 Results .................................... 73
  3.4.2 Mother and Offspring Separations ...................... 74
    3.4.2.1 Results .................................... 74
3.5 Discussion ............................................. 75

Chapter 4 Intra-Group Joining Events

4.1 Introduction ........................................... 82
4.2 Calling Exchange Behavior ................................ 86
  4.2.1 Call Rates ........................................ 86
    4.2.1.1 Results .................................... 87
  4.2.2 Vocal Exchanges ................................... 88
    4.2.2.1 Results .................................... 89
4.3 Call Type Usage ....................................... 89
  4.3.1 Results ........................................... 90
    4.3.1.1 N04 Usage During Behavioral Movements ....... 94
4.4 Discussion ............................................. 94

Chapter 5 Mother and Offspring Separations

5.1 Introduction ........................................... 98
5.2 Call Production During Encounters and Bouts ................. 102
  5.2.1 Results ........................................... 102
## List of Figures

1.1 Mean auditory brainstem response (ABR) and behavioral audiograms . . 9
1.2 Example of four discrete pulsed calls . . . . . . . . . . . . . . . . . . . . . 14
1.3 Northern Resident family tree and predominant discrete pulsed call pro-
duction . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . 15
1.4 Map of the Northern Resident habitat off British Columbia, Canada . . . 18
2.1 Map of Johnstone Strait region, British Columbia, Canada . . . . . . . . 22
2.2 Map of Pizza and Eagle Points . . . . . . . . . . . . . . . . . . . . . . . . 23
2.3 Cross-sectional bathymetry schematic of Johnstone Strait near Kelsey Bay 24
2.4 Sound speed profiles for 2006 and 2007 . . . . . . . . . . . . . . . . . . . . 27
2.5 Hydrophone array location between Pizza and Eagle Points . . . . . . . . 32
2.6 Schematic of a representative bottom-mounted hydrophone array used in
summers 2006 and 2007 . . . . . . . . . . . . . . . . . . . . . . . . . . . . 33
2.7 Snapshot of adult female captured from video camera . . . . . . . . . . . 34
2.8 Photograph of mother and juvenile captured off Eagle Point . . . . . . . . 35
2.9 Bathymetric map of 2 male killer whale movement tracks of matriline A36 36
2.10 Equilateral triangular hydrophone array cartesian coordinates . . . . . . 38
2.11 Bathymetric map of 2 male killer whale movement tracks with correspond-
ing vocalizations . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . 40
2.12 Total number of killer whale encounters per date for 2006 and 2007 . . . . 43
2.13 Diurnal distribution of killer whale encounters for 2006 and 2007 . . . . . 44
2.14 Mean ambient noise of environment . . . . . . . . . . . . . . . . . . . . . 46
2.15 Acoustic range of the hydrophone array . . . . . . . . . . . . . . . . . . . . 48
2.16 Interference of signal at receiver due to Lloyd’s Mirror effect . . . . . . . . 49
2.17 Spectrogram showing low energy locations in sidebands of N04 call . . . . 51
3.1 Spectrogram of a typical N04 pulsed call . . . . . . . . . . . . . . . . . . . . 55
3.2 N04 pulsed calls separation into subtypes . . . . . . . . . . . . . . . . . . . . 59
3.3 Schematic of acoustic data points and segments taken along of N04 contours 60
3.4 Spectrogram showing sideband numbering and sideband intervals . . . . . 60
<table>
<thead>
<tr>
<th>Section</th>
<th>Title</th>
<th>Page</th>
</tr>
</thead>
<tbody>
<tr>
<td>3.5</td>
<td>Discriminant analysis of 5 N04 subtypes</td>
<td>62</td>
</tr>
<tr>
<td>3.6</td>
<td>Discriminant analysis of 4 N04 subtypes</td>
<td>63</td>
</tr>
<tr>
<td>3.7</td>
<td>Overall occurrence of N04 subtypes by pod</td>
<td>64</td>
</tr>
<tr>
<td>3.8</td>
<td>Slopes of N04 segments (1-6) for the four N04 subtypes</td>
<td>65</td>
</tr>
<tr>
<td>3.9</td>
<td>N04-2/3 variation of sideband interval (SBI) at Pt5 during foraging and traveling</td>
<td>67</td>
</tr>
<tr>
<td>3.10</td>
<td>Contours of the four N04 subtypes</td>
<td>71</td>
</tr>
<tr>
<td>3.11</td>
<td>SB2 and non-SB2 N04 call production during foraging and traveling behaviors</td>
<td>72</td>
</tr>
<tr>
<td>3.12</td>
<td>SB2 and non-SB2 N04 call production around swimming behavior</td>
<td>72</td>
</tr>
<tr>
<td>4.1</td>
<td>Mean pulsed call rates pre- and post- joining events</td>
<td>88</td>
</tr>
<tr>
<td>4.2</td>
<td>Seven major discrete pulsed call types during pre- and post- joining events</td>
<td>91</td>
</tr>
<tr>
<td>5.1</td>
<td>Matched and mixed pulsed call production across encounters</td>
<td>104</td>
</tr>
<tr>
<td>5.2</td>
<td>Matched and mixed pulsed call production across vocal bouts</td>
<td>106</td>
</tr>
<tr>
<td>5.3</td>
<td>Matched and mixed pulsed call production within pods</td>
<td>107</td>
</tr>
<tr>
<td>5.4</td>
<td>Initiated and first response occurrences by age group</td>
<td>110</td>
</tr>
<tr>
<td>5.5</td>
<td>Number of pulsed call responses in vocal bouts to initiators</td>
<td>111</td>
</tr>
<tr>
<td>6.1</td>
<td>Skull anatomy of an odontocete whale showing a single monkey-lip/dorsal bursa (MLDB)</td>
<td>120</td>
</tr>
<tr>
<td>6.2</td>
<td>Spectrogram of N04 call highlighting 2 frequencies merging into a single frequency</td>
<td>124</td>
</tr>
<tr>
<td>6.3</td>
<td>Spectrogram of N04 call defining sideband and sideband intervals</td>
<td>125</td>
</tr>
<tr>
<td>6.4</td>
<td>Spectrogram illustrating PSD data points along SB7/HFC and LFC locations</td>
<td>127</td>
</tr>
<tr>
<td>6.5</td>
<td>Power spectral densities of 2 frequencies in HFC vicinity merging into a single frequency</td>
<td>128</td>
</tr>
<tr>
<td>6.6</td>
<td>Higher frequency component relationships with sidebands and sideband intervals</td>
<td>130</td>
</tr>
<tr>
<td>6.7</td>
<td>Power spectral density difference when HFC is above and below SB7</td>
<td>131</td>
</tr>
<tr>
<td>6.8</td>
<td>Power spectral density difference between post merge SB7/HFC and LFC for adults and young</td>
<td>133</td>
</tr>
<tr>
<td>6.9</td>
<td>HFC location to SB7 during foraging and traveling</td>
<td>136</td>
</tr>
<tr>
<td>A.1</td>
<td>Photo of temperature probe</td>
<td>150</td>
</tr>
<tr>
<td>A.2</td>
<td>Schematic of temperature probe calibration setup</td>
<td>152</td>
</tr>
<tr>
<td>A.3</td>
<td>Temperature probe calibration 2006</td>
<td>152</td>
</tr>
<tr>
<td>A.4</td>
<td>Temperature probe calibration 2007</td>
<td>153</td>
</tr>
<tr>
<td>A.5</td>
<td>Temperature probe calibration bucket showing thermister locations</td>
<td>154</td>
</tr>
<tr>
<td>A.6</td>
<td>Temperature probe calibration bucket conductivity trial 1</td>
<td>155</td>
</tr>
<tr>
<td>A.7</td>
<td>Temperature probe calibration bucket conductivity trial 2</td>
<td>156</td>
</tr>
</tbody>
</table>
B.1 Photograph of a HTI-96-min hydrophone with built-in pre-amp . . . . . . 158
B.2 Calibration curve for hydrophone 1 . . . . . . . . . . . . . . . . . . . . . 159
B.3 Calibration curve for hydrophone 2 . . . . . . . . . . . . . . . . . . . . . 159
B.4 Calibration curve for hydrophone 3 . . . . . . . . . . . . . . . . . . . . . 160
B.5 Schematic of audio recorder setup . . . . . . . . . . . . . . . . . . . . . . 161
B.6 Noise floors of 3 hydrophone channels . . . . . . . . . . . . . . . . . . . . 162
B.7 Pipe and plate photograph . . . . . . . . . . . . . . . . . . . . . . . . . . 163
B.8 Sound level of pipe/plate system . . . . . . . . . . . . . . . . . . . . . . . 163

D.1 Spectrograms N04 subtypes part 1 . . . . . . . . . . . . . . . . . . . . . . 171
D.2 Spectrograms N04 subtypes part 2 . . . . . . . . . . . . . . . . . . . . . . 172
# List of Tables

1.1 Discrete pulsed call repertoires of A clan members ........................................... 13  
1.2 Northern Resident Community social structure ..................................................... 19

2.1 Vertical visibility of Johnstone Strait ..................................................................... 29  
2.2 Example of individual scan sample data with theodolite recordings ...................... 34  
2.3 Array error with variations in range ....................................................................... 38  
2.4 Age/sex class categories ....................................................................................... 45

3.1 Dunn’s post hoc test’s for N04 slope analysis between subtypes ............................. 66  
3.2 Analyzed N04 acoustic parameters during varying behaviors ............................... 66  
3.3 N04 subtype usage by individuals .......................................................................... 68

4.1 Call type occurrence during pre-joining events for the three A pods ...................... 92  
4.2 Call type occurrence during pre-joining events for the I11 pod .............................. 92  
4.3 Call type occurrence during post-joining events for the three A pods ................. 93  
4.4 Call type occurrence during post-joining events for the I11 pod ......................... 93

5.1 Pulsed call production for mother/offspring groups during separations ............... 103  
5.2 Matched versus mixed calling rates during encounters ........................................... 105  
5.3 Matched versus mixed calling rates during bouts ................................................ 106  
5.4 Matched and mixed calling rates for four pods .................................................... 107

6.1 Analyzed N04 power spectral densities for adults and young .............................. 133  
6.2 Analyzed N04 power spectral densities during foraging and traveling ............... 136

C.1 Symbols in statistical tests ...................................................................................... 169
Acknowledgments

I extend my gratitude to Dr. Richard Stern and the Exploratory Foundational Funding from the Applied Research Laboratory for funding my research assistantship here at Penn State. A special thanks to my main advisor, Dr. David L. Bradley for all his support, patience and insight during this Ph.D. process, especially for the four-star accommodations in the field! Thanks to my other committee members, Dr. Dean E. Capone, Dr. Susan E. Parks, Dr. Jennifer L. Miksis-Olds, Dr. Timothy J. Kane for directing me on scientific theory and concepts. Dr. Capone for his acoustic signal analysis expertise. Dr. Parks and Dr. Miksis-Olds for providing their insight on bioacoustics. Dr. Kane for his input on dispersion and diversifying my committee. To my special signatory, Dr. John K. B. Ford of the Cetacean Research Program at the Pacific Biological Station, Nanaimo, BC, Canada for helping initiate this research and for his scientific feedback of killer whale sounds and behaviors.

I would like to give thanks to a number of individuals who made the field season portion of my research possible. First, Doug Sandilands and Nic Dedeluk of the Robson Bight Marine Warden Program, Cetus Research & Conservation Society for their assistance with on site logistics. My gratitude to Doug for coordinating all the site logistics such as camp accessibility, deploying the hydrophone array, collecting temperature-depth profiles, feedback on the best ways to power my equipment, keeping me supplied with coca cola, and getting me into shape. Thank you Nic for assisting with on-site accommodations, as well as financial and other logistical matters. My gratitude to Jim Dorminy of the Applied Research Laboratory, for assisting me with the cliff-site hydrophone bottom-mounted array design and for prepping my hydrophones and solar panel for this research.

Data collection would not be possible without the dedicated efforts of my field research assistants and marine warden program wardens and volunteers for all of their assistance. Sincerest gratitude to my research assistants, Hella Martens, Dagmar Larsen and Jennifer Keating for helping to collect audio, video, still photos, animal bearings, group composition and animal behavior information. I would also like to thank the marine wardens, Kathy Bortolin, Luke Clarke, Trish Nettleship and Andrea Hunter for boat transport to collect ocean measurements. To all the volunteers I am eternally grateful for
their assistance in spotting the surfacings of the animals, collecting ocean measurements and photography for animal identifications (Vanessa Taverney, Maryke Olivierse, Hannah Spitzhorn, Simon Steffen, Birte Hegemann and Mandy Bunke). Last but not least, Marie Fournier for assisting with animal identifications during and post encounters.

There were other people who were integral in fine-tuning a rigorous data collection design, preparing for acoustic measurements and post-analyzing acoustic data. Dr. Catherine Berchok, Dr. Desray Reeb and Dr Susan Parks for being sounding boards by sharing their data collection wisdom and potential field research pitfalls. Dr. Thomas Gabrielson for assisting me with building measurement tools and allowing me to use his equipment for calibrations. Dr. Catherine Berchok for helping me build the temperature probe, sharing her temperature calibration matlab code and her all around support during this process. Dr. Robert Keolian for introducing me to various acoustic demonstrations on phase shifting and hearing, as well as providing insight on these topics.

Many thanks to additional people who were integral in successfully launching this research. Dr. Whitlow Au of the University of Hawaii for initiating connect between John and myself. Dr. David Bain of the University of Washington for connecting me to his Vancouver theodolite rental shop. Dr. Kathleen Stafford for her wise words and correspondence at the onset of my research seeking endeavors.

To my family, friends and colleagues for their support and patience during this time. To Elaine Berteletti for taking care of Suky and my affairs during my field seasons. To Jean and Larry Sullivan for being the backup caretakers and housing me at the Cape to decompress after field seasons. To my dear friends in Seattle, Erin Horan and Remy Gutierrez who became my package shipping depot for two field seasons without complaint, and provided me with a home base from which to launch and recover from my field season adventures (which was often not an easy transition). To Karen Brooks for helping to acclimate me to the program, directing me to appropriate professors and locating equipment. Ki Won Jung for his friendship and readily locating and lending me equipment. Miguel Horta, Marce Barajas, Yada Juntarapaso and Janice Lingle for their friendship and always Suky sitting when I went to conferences. In addition, thanks to my other friends and fellow students while at Penn State for their assistance, support and general interest in my research: Shawn Johnson, Andrew Barnard, Alexandra Loubeau, Lauren Falco, Mandy Hanford, Megan Ballard, Colin Jemmott, Joy Lyons, John Camin, John Brady and Randy Carbo.
Dedication

To my good friend Dana Wright who introduced me to the world of animal acoustics and my parents, Ann and Donald Grebner, for showing me that will and determination go a long way. I wish you all could be here with me to share in life’s adventures.
Chapter 1

Introduction

1.1 Relevance of this Study

The Northern Resident killer whale population off British Columbia, Canada provides an excellent opportunity to examine individual killer whale vocal variation and how it relates to intra-group behavioral dynamics. Extensive research has been conducted for almost four decades on this population’s life history, group dynamics, individual identity and pod-specific dialects (Bigg, 1982; Bigg et al., 1987, 1983; Ellis et al., 2007; Ford, 1989, 1991), making the Northern Residents one of the more well known whale populations. The ongoing and vast knowledge base for Northern Resident killer whales coupled with their complex social and vocal traditions makes them an ideal candidate for research geared toward localizing individual animal sounds and examining call use during varying behavioral movement patterns of family members. Once there is an understanding of how killer whales use sound to maintain group cohesion, further research can isolate acoustic sources which may disrupt communication (potentially weakening the viability of the population). Group cohesion requires that individuals within the group sustain physical, visual or acoustic contact with other individuals to coordinate spacing or movements (Ford, 1989). Ultimately, appropriate conservation measures to prevent or lessen the degree of signal disruption can be strategically implemented. (Anthony and Blumstein, 2000; Blumstein and Fernandez-Juricic, 2004; Sutherland, 1998; Williams et al., 2006).

The Northern Resident killer whale population has a highly complex social structure, which in an aquatic environment mandates vocal production in order to maintain group cohesion because other forms of communication are not reliable beyond visual range. Killer whales would not be able to rely on most other cues other than vocalizations outside their visual range (which is limited by water quality and light). As odontocetes
evolved they lost their olfactory bulbs or nerves so they can not smell (Berta and Sumich, 1999). Odontocetes do have some taste buds (Berta and Sumich, 1999), but chemical senses would only be near field comparatively speaking for the size and movement of larger animals. Additionally, animals may be able to physically sense changes in water motions made by other killer whales, but those also would be limited by near field touch or vision. Killer whale matrilines tend to remain together for life and over the last four decades no individuals have emigrated from any of the Northern Resident pods (rare for mammalian social groups) (Bigg et al., 1987, 1990; Ellis et al., 2007; Ford et al., 2000). Hence, members within a matriline separate for short periods (minutes, hours, a day) to interact with other pod or non-pod members, but they always rejoin. Discrete pulsed calls (dpcs) are a reasonable candidate for maintaining group cohesion for the following reasons (Andrew, 1962; Ford, 1989, 1991; Miller, 2002, 2006): 1) dpcs are their predominant pulsed call during behaviors when animals are more dispersed; 2) dpcs are stereotyped and group-specific which would make them recognizable to family members; 3) the spectral content of dpcs contain a wealth of information (wide bandwidth, biphonation, high source level, multiple sideband and sideband interval (SBI) information, modulated frequency and amplitudes as well as long durations) which could provide the receiving animal with details of a signaling animal’s identity, pod affiliation, behavioral movement and directionality; and 4) dpcs would be more robust against propagation degradation of the call over greater ranges than highly directional clicks and lower source level, narrow band whistles.

Because killer whale behavior dictates the separation of individuals from groups, their methods of rejoining provide critical understanding of killer whale vocal communication. If they are maintaining contact or rejoining using vocalizations and vocal exchanges then any disruption (e.g. anthropogenic noise, other biotic sounds) of their sounds or counter-calling could be costly and have negative ramifications on population size and viability. For instance, call disruption could potentially isolate mothers from young offspring which could decrease the the chance of offspring survival. Second, disruption of calls could prevent family members from sharing food which would weaken the viability of matrilines and individuals within it who may rely on intra-group support. Young offspring just learning how to successfully capture prey may rely on their mothers, siblings or other matriline members to supplement their diets (Ruiz-Miranda et al., 1999) until they become more proficient predators. In addition, older individuals who engage in allomaternal care of young in turn may benefit from prey catches made by younger, faster offspring. Ultimately, any factor which adversely lowers survival rate of individuals
within a group provides less protection of young in open waters.

The goal of this dissertation is to provide insight into individual killer whale vocal behavior within intra-group dynamics. In this analysis, aspects of call content and vocal usage in a behavioral context will be examined. This is the first study to focus on killer whale vocal usage as it pertains to intra-group dynamics for 1) mother and offspring separations, 2) for all individuals prior to joining events and 3) individual usage of a diverging calls. Intra-group is defined as within the focal group in a given circumstance. For both individuals and small groups, vocalizations were isolated using a triangular hydrophone array and the behavioral movement patterns were captured by a theodolite and video camera. Insight into Northern Resident killer whale intra-group vocal dynamics could potentially aid our understanding of vocal behaviors of many other marine mammal species that rely on vocal exchanges for prey capture, group movement or survival. Understanding correlations of types of killer whale sounds (e.g. pulsed calls) which are produced by other species, would provide insight into how other species within an aquatic environments may use those sounds (e.g. pattern calling, increase call rate) to communicate and coordinate movements. Correlations of call types (e.g. ecolocation clicks, pulsed calls) may be a universal behavior with other species

Furthermore, this study provides behavioral research backing the importance and need to further implement conservation measures (Sutherland, 1998) necessary to protect the welfare and survival of endangered species (e.g. Southern Resident killer whale community, located to the south). The endangered Southern Residents have the same complex social culture and dialect tradition as the threatened Northern Resident Community (Ford, 1989, 1991). Southern Residents forage on the same salmon species as the Northern Residents (Ford and Ellis, 2006; Ford et al., 1998) and also share prey among family members (Ford and Ellis, 2006), contrasting foraging strategies of other known killer whale populations around the world (Nottestad and Axelsen, 1999; Shapiro, 2008; Van Opzeeland et al., 2005). A prey sharing foraging strategy dictates the need for individuals to rejoin for group survival (Anthony and Blumstein, 2000). Increased boat activity seen in this region of the world (Baird, 2001), may be disrupting killer whale vocal communication and adversely affecting the cultural feeding traditions of Northern and Southern Resident killer whales. Though survival decline of the Southern Resident population is due to a number of contributing factors (high PCBs, decreased food supply, acoustic sources), reducing the effects of any factor such as acoustic communication disruption, can increase food intake by individuals and strengthen the population’s viability.
1.2 History of Killer Whales

Adult Killer whales (*Orcinus orca*) of the family Delphinidae, are sexually dimorphic in both dorsal fin and body size (Bigg, 1982; Bigg et al., 1987; Carl, 1945; Wells, 2003). Adult male killer whales grow to an average of 9 m in length and 8-10 tons, while their dorsal fins protrude up to 1.9 m. Adult females are smaller, averaging less than 7 m in length, 4 tons, and dorsal fin heights of 0.4-0.7 m. Newborn calves are approximately 2-2.5 meters in length and weigh 200 kilograms (Bigg et al., 1987). Juveniles tend to have a small fin and body size compared to adult females (Bigg, 1982). The primary means of identifying the gender of younger killer whales is by observing the ventral side of an animal when it rolls, surfaces or jumps. In addition, the sex of younger killer whales can be determined when an individual gives birth to a calf or the dorsal fin begins to ‘sprout’, or grow rapidly, as seen with maturing juvenile males. Physical examination of the genital area or DNA analysis is a less common means of sexual identification of wild killer whales (Bigg et al., 1987). Females mature at 14.1 years (mean) and usually have their first calf between the ages of 11-17 years old (Olesiuk et al., 2005). Males begin to mature at approximately 13.0 years of age (Olesiuk et al., 2005; Robeck and Monfort, 2006) and reach physical maturity by 16-21 years of age (dorsal fin takes 5.5 years to mature) (Olesiuk et al., 2005).

Each killer whale has a unique saddle patch, located on it’s back, posterior to the dorsal fin (Bigg et al., 1983). Identification of individual killer whales is by examination of their saddle patch, size of dorsal fin, along with any nicks or scratches found on these two regions (Bigg et al., 1983). In the Pacific Northeast waters off British Columbia, Canada, photo-identifications of Northern and Southern Resident killer whale saddle patches and dorsal fins have been organized into comprehensive catalogs (Bigg, 1982; Ellis et al., 2007; Ford et al., 1994, 2000). Photo-identification, along with phylogeny trees, have been maintained on these two populations since the late 1970s.

Social interactions of killer whales are highly complex and probably best studied in the Northern and Southern Resident (fish-eating) killer whale populations in the waters off British Columbia and Washington State. There are four populations in this region: 3 fish-eating (Northern Residents, Southern Residents, Offshores) and 1 mammal-eating group (Transients) (Bigg, 1982; Ford, 1989; Ford et al., 2000). Killer whale group associations are further designated into clans (acoustically unique), pods (related individuals) and matrilines (matriarch, her offspring, her daughters’ offspring and their offspring) (Ellis et al., 2007; Ford, 1989; Ford et al., 2000). Matrilineal groups are extremely stable, based on long term studies of fish-eating killer whale social structure in the Northeast Pa-
Specific. Matrilineal killer whales associate regularly and remain with their mothers for life (Bigg, 1982; Bigg et al., 1987, 1990; Ford, 1989, 1991); this is the only known matrilineal society where adult males remain with their matriline (Gouzoules and Gouzoules, 1990; Holekamp et al., 1999; McComb et al., 2000). Killer whale matrilines contain from 2 to 4 generations (Bigg et al., 1987; Olesiuk et al., 2005). Though many other cetacean species do not continuously associate within their familial groups, cetaceans with shorter-term bonds may utilize behavioral and acoustical means for relaying successful communication.

On short time scales (minutes, hours, a single day), individual or small groups of killer whales may disperse to forage or socialize with others and then re-join with family members afterwards. Even if killer whales remain within the immediate vicinity of their matrilineal group, the individual spacing necessary to optimize successful prey capture, usually place killer whales outside the visual range of their family members. Thirty-five years of observations of killer whales in the Northeast Pacific have demonstrated that they repeatedly find each other and maintain these familial associations (Bigg et al., 1990; Ellis et al., 2007; Ford et al., 2000) indicating a strong social culture (Yurk, 2003; Yurk et al., 2002).

Mother and young offspring are tight social groups within killer whale matrilines. Swimming distances of offspring to their mothers increases linearly with age (Bigg et al., 1990). Killer whale behavior has also been examined on the interaction level to determine which animals associate more often with others and the duration of those associations. Though all of a mother’s offspring remain within relatively close distance, a young calf generally swims immediately next to and behind its mother (swimming eschelon), the smallest juvenile usually swims the next closest position and the oldest juvenile swims the farthest away. Adult male offspring will maintain tight associations with their mothers, while adult female offspring will form tighter alliances with her own offspring (Bigg et al., 1990).

Killer whales are allomaternal or allopaternal care-givers as seen with other species (Biben, 1992; Bigg et al., 1990; Fairbanks, 1990; Quiatt, 1979; Ridgway et al., 1995; Wells, 2003). Smaller killer whales, displaced by their mother’s newborn calf, often swim with older females (Bigg et al., 1990; Crance, 2008), while adult males socialize with calves or juveniles, suggesting that ‘uncles’ or ‘big brothers’ may also invest energy in the development of younger relatives (Haenel, 1996).
1.3 Behavioral Movement

Rapid absorption of light in seawater drives the need for marine mammals to emit sounds for intra-species communication and prey detection. Cetacean eyes have adapted some specializations to the aquatic environment. Each eye of dolphins (e.g. killer whales) contains a ‘double pupil’, which provides them with sharp vision both above and below the water’s surface (Herman et al., 1975). These double-slit pupils are also thought to function in focusing or depth perception (Herman et al., 1975; Norris et al., 1994). Despite any visual capabilities or physical traits (i.e. the stark contrast of black and white)) to improve visibility (Berta and Sumich, 1999; Brown et al., 1989), dolphins and other cetaceans are still limited by the attenuation of visible light in seawater due to scattering and absorption. The attenuation of light (and subsequent reduction in visibility) in the ocean increases at an exponential rate (Ross, 2000; Wille, 2005). Visible light consists of multiple wavelengths of light which are perceived as a combination of colors (red, orange, yellow, green, blue and violet) (Johnsen, 2004). Seawater absorbs light faster than in air. When light enters the ocean, the light rays are refracted, and then, scattered or absorbed by suspended particles rapidly in the first few meters (e.g. dissolved particles, water molecules, phytoplankton): the higher density of particles, the higher scatter and absorption of light (Johnsen, 2004; Ross, 2000). Larger wavelengths like red, orange and yellow rays are almost completely absorbed within the first couple of meters. Blue, green and violet light rays, which have shorter wavelengths, can extend into deeper waters, however, at approximately 10 m depth, 85% of visible light is absorbed (Ross, 2000). In the horizontal plane, light attenuates at the same distances as vertical light transmission. Scattering of the light rays by these particles significantly reduces underwater visibility in both the horizontal and vertical planes. As the turbidity of the water increases, visibility can decrease to less than one meter (Ross, 2000). In contrast, sound waves in seawater travel far beyond visual range and provide an efficient means for communication between conspecifics and object detection (e.g. prey) (Simmonds and MacLennan, 2005; Wille, 2005).

Movement is an intrinsic aspect of cetacean behavior largely due to their aquatic environment. All cetaceans must travel to locate temporally and spatially varying food sources. Cetaceans also need to find one another for mating or cooperative foraging, while social whales would also be driven to join for protection and familial interactions. Even if cetaceans are resting in a still position, they are moving by the necessity to breathe and the inherent movement of the water. Therefore, the terminology of movement and behaviors for cetaceans spans from a loosely coupled to a strongly coupled concept.
Furthermore, movement can be described on both the small scale individual behaviors and large scale group or intra-group interactions.

Traditional definitions of killer whale behaviors can be divided into four main categories: traveling, foraging, socializing and resting (Ford, 1989; Osborne, 1986; Osborne and Heimlich, 1981; Saulitis et al., 2000). Each of these behaviors are linked or synonymous to movements. Socializing involves a few individuals interacting physically within close proximity. During socializing, groups slowly progress at about 1 m/sec (Ford, 1989). Killer whale resting is the slowest of the four behavioral movements (less than 1 m/sec) (Barrett-Lennard et al., 1996; Ford, 1989). Killer whales are often seen resting in lines of multiple individuals abreast to one another (Ford, 1989), however, individuals have been seen resting alone for short periods of time, for example, after foraging.

During traveling and foraging behaviors, individuals or small groups tend to disperse beyond visual range and over greater distances than socializing or resting behaviors (Ford, 1989; Miller, 2006). Traveling is exhibited by unidirectional swimming at faster speeds than other behaviors, and synchronous swimming is often seen. Northern Residents travel, on average, 2.88 m/sec (between 1.81 - 5.66 m/sec), though they can sprint up to 12.0 m/sec for short periods (Ford, 1989). Though the definition of foraging varies among different studies, the broader definition means seeking, finding and feeding on prey. This broader definition of foraging is often used in behavioral studies, because without the aid of close boat follows or underwater video cameras it is difficult to determine if an animal is actually eating. Most Northern Resident killer whales selectively forage for the Chinook salmon (Oncorhynchus tshawytscha), which are rich in fat but larger, and less abundant (Ford and Ellis, 2006; Ford et al., 1998). Their second choice is chum (Oncorhynchus keta), which is the next largest salmonid. When Chinook and chum are not available, killer whales will feed on other salmon and a few non-salmon species (Ford and Ellis, 2006). Generally, killer whale movement during foraging is usually multidirectional, generally slower than traveling (up to 1.6 m/sec), and accompanied by diving and other behaviors (Ford, 1989). Successful foraging may dictate slightly wider spacing at the onset of seeking food than other behaviors. Adult males usually forage independently or within close proximity of their mothers and are also often seen foraging closer to the middle of the strait compared to other groups who tend to forage closer to shore (e.g. mothers with offspring) (Ford and Ellis, 2006).

Killer whales have solved the problem of joining with family members after brief separations. Killer whale behaviors and their absolute duration are not uniformly executed by individuals within a matriline or pod. At any given time different individuals in a
group may be traveling, foraging, socializing or resting (Ford, 1989). Even if the entire

group is participating in one behavior, foraging, for instance, one individual may begin
traveling earlier than other matriline members which would inevitably increase inter-
aminal spacing. Scientists have observed that matrilineal members repeatedly find each
other, and they are most likely doing so by using sound (Bigg et al., 1990; Ford, 1989,
1991). Recently researchers discovered that individual Northern Resident killer whales
routinely break up their food and share it with two or three other killer whales which
temporarily join that individual after a kill (Ford and Ellis, 2006). Hence, the joining
of individuals may benefit other family members by increasing group fitness, along with
maintaining overall group movement cohesion.

1.4 Auditory and Vocal Behavior

Hearing is an essential part of vocal development and vocal exchanges between indi-
viduals. Only two studies have examined the hearing of killer whales (Hall and Johnson,
1971; Szymanski et al., 1999). The most recent study examined the auditory brainstem
response (ABR) and behavioral audiograms of two captive adult female killer whales in
the early to mid 1990s (Szymanski et al., 1999). Functional hearing of the killer whales
examined in this study was from 1 to 120 kHz. The mean audiogram constructed from
the two techniques was U-shaped, which is consistent with other mammalian and odon-
tocete species (Richardson, 1995). The most sensitive frequency for these two female
killer whales was 20 kHz at 35 dB re 1µPa. The most sensitive hearing range was from
18-42 kHz (Fig. 1.1). Sound is transmitted to odontocete ears by route of fatty tissues
located in their lower jaws (Brill et al., 1988; Norris and Harvey, 1974).

Odontocetes have two unique features among mammals which may be important
in sound generation, as well as, sound perception: lipid-based tissues (‘acoustic fats’) of
varying sound speeds and asymmetrical skulls (Cranford et al., 1996; Norris, 1968). This
fatty tissue is located in the melon, the lower jaw and around the cochlea complex (Brill
et al., 1988; Ketten, 1994, 2000; Norris and Harvey, 1974) and functions as impedance
matching devices between air passage ways and the seawater (Cranford et al., 1996).
Initially the odontocete sounds were thought to be produced in the larynx (Diercks
et al., 1971; Norris and Harvey, 1974), but recent research on impulsive sounds (clicks)
has suggested that the sound source is nasal in nature. The production of impulsive
sounds is thought to be a pneumatic mechanism where the nasal sacs pass air over
the phonic(monkey)-lip dorsal bursae (MLDB complexes), forcing them to vibrate and
the phonic lips to slap (Cranford, 2000; Cranford et al., 1996). These vibrations travel through the main portion of the melon embedded in the forehead. The melon acts as an acoustic impedance matching device and with the assistance of some cartilaginous structures located behind it, impulsive sounds are focused out from the forehead and into the seawater (Cranford et al., 1996). It is also thought that these two MLDB complexes can slap independently of each other (Cranford, 2000). The bottlenose dolphin right MLDB complex is approximately two times longer compared to their left MLDB complex (Cranford et al., 1996); this is thought to also be similar in killer whales. This pneumatic sound source mechanism is thought to be the same for other impulsive sounds like pulsed calls (Cranford et al., 1996), however the means by which whistles are produced is still unknown.

1.4.1 Types of Vocalizations

Killer whales produce three types of vocalizations: broadband clicks, burst pulse sounds (known as pulsed calls) and narrowband whistles (Ford, 1989, 1991). Northern Resident killer whale clicks are broadband sounds which have bimodal distributions with low peak frequency from 20-30 kHz and high peak frequencies from 40-60 kHz (Au et al., 2004; Cranford et al., 1996). Clicks function in prey capture and navigation. Whistles are tonal in nature and vary in amplitude, frequency and duration, sometimes containing
harmonics (Ford, 1989; Riesz et al., 2006). Peak frequencies of whistles tend to be between 6 to 12 kHz, though they extend to 18 kHz (Ford, 1989). In general, Northern Resident killer whale whistles appear to have a close-range function and are produced most often during socializing (Ford, 1989; Miller, 2006; Nousek et al., 2006; Riesz et al., 2006; Thomsen et al., 2001).

Pulsed calls are rich in content having a large bandwidth, vary in amplitude and pulsed frequency modulation, as well as contain mono- and bi-phonation features (Filatova et al., 2007; Ford, 1991; Miller, 2002, 2007). Pulsed calls are vocals which are compound signals comprised of only a few pulses with short time intervals between pulsed series (Bradbury and Vehrencamp, 1998; Watkins, 1967). The rapidness of the pulses creates sidebands around the fundamental sideband (or carrier frequency) when viewing signals spectrally. Fundamental frequencies of harmonic sounds are the lowest frequency band which contain the most energy, while sideband fundamentals are often produced at a higher frequency with sidebands of lower energy above and below it (Bradbury and Vehrencamp, 1998; Watkins, 1967). Biological filtering and amplitude modulation can often obscure which frequency band is the carrier or the fundamental (Bradbury and Vehrencamp, 1998). The difference between harmonics of some sounds and sidebands due to pulsed sounds is thought to be the result of the sound generation mechanism. Often the sidebands of pulsed sounds appear to be ‘harmonically’ related, however the frequency difference between sidebands results from the pulse repetition rate of the sound generation mechanism (Watkins, 1967). Discriminating between harmonics and sidebands can be challenging and requires understanding of the sound generation mechanism. Northern Resident killer whale pulsed calls can be divided into three categories: discrete, aberrant and variable. Discrete calls are the most abundantly produced pulsed call in Northern Resident foraging and traveling behaviors (94-95% of the time) and their function is thought to maintain group cohesion (Ford, 1989). Aberrant and variable pulsed calls, along with whistles, are more prevalent during closer proximity social contexts (Ford, 1989). Discrete pulsed calls are repeatable (stereotyped) and have been previously described and categorized based on their acoustic attributes (Ford, 1984, 1987, 1989, 1991; Ford and Fisher, 1982, 1983). Aberrant pulsed calls are based on discrete pulsed calls but are distorted or modified, while most variable pulsed calls are not repeatable and cannot be clearly defined into categories (with one exception) (Ford, 1989; Rehn et al., 2007). This study will focus on discrete pulsed calls since they are thought to function in maintaining group cohesion.
1.5 Communication Theory of Vocal Production

Communication is the transfer of information (e.g. vocal, behavior) between a sender and a receiver (Simmons, 2003) usually involving members from the same species, however, not limited to intra-species. The content encoded within communicative vocal production varies from very specific to vague information (Simmons, 2003). Communication serves many functions such as increasing mating opportunities, mother and offspring recognition, maintaining group cohesion (e.g. coordination, spacing), indicating a food source and assessing agonistic relationships (Simmons, 2003; Tyack, 2000). Classic communication is the transfer of information (olfactory, tactile, electrical, visual or acoustic) from one animal (signaler) to another (receiver) (Tyack, 2000). In classic vocal communication, the signaler is presumed to know something, thereby reducing the uncertainty for the receiver so that the receiver can make a timely decision and respond accordingly. For true vocal communication to exist, both the signaler and the receiver must benefit from the signaler’s emitted sound. The benefits of the communication are the increased chance (through trial and error) that the receiver will get the signaler’s information correctly and respond accordingly (Bradbury and Vehrencamp, 1998). Communication in marine mammals encompasses: individual and group recognition (mother and offspring, family), mate attraction and threat or challenge signals.

Functional communication modifies classical communication mentioned above by including manipulation, deception and environmental factors which could alter an intended signal or response (Bradbury and Vehrencamp, 1998; Tyack, 2000). In contrast to classical communication, functional communication does not benefit both the signaler and the receiver. First, a signaler may produce an advertisement call meant to influence the receiver’s decision rather than just communicate information. Second, a receiver may not readily respond to the signaler, rather quietly monitor repeated calls made by the signaler. Third, a signaler may vocalize to mislead the receiver or cause uncertainty. Fourth, receivers may use their environment to assess information (e.g. location, fitness) of the signaler. Fifth, unintended receivers intercept or eavesdrop on the signaler’s vocals intended for a closely related individual or group. And sixth, receivers could also intercept signals not intended for attraction, such as cetaceans lured by fishing boat sounds.

Sound generation and the time to produce vocalizations are costly to signallers (Bradbury and Vehrencamp, 1998; Ryan and Kime, 2003; Tyack, 2000). Likewise, responding vocally, behaviorally or physically to an uncertain signal costs the receiver. The interception of a signal could deprive signallers and receivers of food sources or mating opportu-
nities (Ryan and Kime, 2003; Tyack, 2000). Eavesdroppers could intercept signals, and rob the signaller or intended receiver of a potential food source or mating opportunity, accruing minimal cost but increased benefit to the eavesdropper. Prey could intercept signals by their predators and escape attack (Tyack, 2000). Deception signals could mislead receivers, forcing them to swim kilometers away with no energetic or mating benefit. Hence, the disruption of communication escalates costs. Individual variation encoded within calls would provide a secure means of animal identity and reduce the value of eavesdropping, while group-specific calls may reduce mimicry by unwanted individuals (Boughman and Moss, 2003), especially during instances of food-related calls or food sharing (Boughman and Moss, 2003; Janik, 2000a; Notman and Rendall, 2005).

1.6 Maintaining Group Cohesion

Maintaining group cohesion requires that individuals within a group sustain contact (physical, visual and/or acoustic) with other desired individuals for spacing or coordination of movements (Ford, 1989). Maintaining contact can vary on a temporal scale (brief, long), as well as a group size scale (a few individuals, entire group) depending on species or social dynamics (Bigg et al., 1990; Byrne, 1981; Connor, 2000; Ford, 1989, 1991; Janik, 2000b; Janik and Slater, 1998; Kudo, 1987; Notman and Rendall, 2005; Soltis et al., 2005a). If fish-eating matrilineal killer whales rely on vocalizations to find each other after separations, it is important to learn what vocalizations they are producing, and how they are using them in terms of structure, specific vocal patterns and vocal exchanges. Knowledge of these communicative nuances within a species can provide insight into the species’ vocal capabilities, vocal learning (e.g. mimicry) and culturally transmitted information (Andrew, 1962; Brainard and Doupe, 2000, 2002; Holekamp et al., 1999; Janik, 2000b; Janik and Slater, 1998; Poole et al., 2005; Watwood, 2004).

1.6.1 Discrete Pulsed Calls

Each killer whale pod has its own discrete pulsed call repertoire or dialect comprised of 7-17 calls (Ford, 1989, 1991) (Table 1.1 for the A clan, Fig. 1.2). Pods within a clan share anywhere from one to all calls in their repertoires depending on recent pod relatedness. For instance, the three A pods of the A clan share a large number of the pulsed calls in their repertoires, however they share only a few calls with other A clan pods (e.g. B, C, D, etc.) and no calls with non-clan members (e.g. members of the G or R clans) (Ford, 1989, 1991; Ford and Fisher, 1983). Some of these pulsed calls have
variants within a call, which are traditionally designated by roman numerals (i, ii, iii, iv, v) following the discrete pulsed call name (i.e. N01i and N01iv are both variants of the N01 call). For simplicity in Table 1.1, a call which has multiple variants is denoted by ‘var’ after the call name (e.g. N01var). Pods with only one variant have no roman numerals (e.g. N12). Overall, the A1 pod has 14 pulsed calls in their repertoire, while the A4 pod has 13 and the A5 pod has 12 (Ford, 1989). In this thesis, pulsed calls with single digits will be designated with a 0 preceding the digit (e.g. N01, N04) though they are traditionally seen in the literature written as N1 and N4. Furthermore, the Northern Resident killer whale also exhibit a hierarchy of call production with approximately five pulsed calls in their repertoires being produced 75 – 85% of the time (Ford, 1989)(Fig. 1.3).

<table>
<thead>
<tr>
<th>Call</th>
<th>A1</th>
<th>A4</th>
<th>A5</th>
<th>B1</th>
<th>C1</th>
<th>D1</th>
<th>H1</th>
<th>I1</th>
</tr>
</thead>
<tbody>
<tr>
<td>N01var</td>
<td>x</td>
<td>x</td>
<td>x</td>
<td>x</td>
<td>x</td>
<td>x</td>
<td>x</td>
<td>x</td>
</tr>
<tr>
<td>N02</td>
<td>x</td>
<td>x</td>
<td>x</td>
<td>x</td>
<td>x</td>
<td>x</td>
<td>x</td>
<td>x</td>
</tr>
<tr>
<td>N03</td>
<td>x</td>
<td>x</td>
<td>x</td>
<td>x</td>
<td>x</td>
<td>x</td>
<td>x</td>
<td>x</td>
</tr>
<tr>
<td>N04</td>
<td>x</td>
<td>x</td>
<td>x</td>
<td>x</td>
<td>x</td>
<td>x</td>
<td>x</td>
<td>x</td>
</tr>
<tr>
<td>N05var</td>
<td>x</td>
<td>x</td>
<td>x</td>
<td>x</td>
<td>x</td>
<td>x</td>
<td>x</td>
<td>x</td>
</tr>
<tr>
<td>N07var</td>
<td>x</td>
<td>x</td>
<td>x</td>
<td>x</td>
<td>x</td>
<td>x</td>
<td>x</td>
<td>x</td>
</tr>
<tr>
<td>N08var</td>
<td>x</td>
<td>x</td>
<td>x</td>
<td>x</td>
<td>x</td>
<td>x</td>
<td>x</td>
<td>x</td>
</tr>
<tr>
<td>N09var</td>
<td>x</td>
<td>x</td>
<td>x</td>
<td>x</td>
<td>x</td>
<td>x</td>
<td>x</td>
<td>x</td>
</tr>
<tr>
<td>N10</td>
<td>x</td>
<td>x</td>
<td>x</td>
<td>x</td>
<td>x</td>
<td>x</td>
<td>x</td>
<td>x</td>
</tr>
<tr>
<td>N11var</td>
<td>x</td>
<td>x</td>
<td>x</td>
<td>x</td>
<td>x</td>
<td>x</td>
<td>x</td>
<td>x</td>
</tr>
<tr>
<td>N12</td>
<td>x</td>
<td>x</td>
<td>x</td>
<td>x</td>
<td>x</td>
<td>x</td>
<td>x</td>
<td>x</td>
</tr>
<tr>
<td>N13</td>
<td>x</td>
<td>x</td>
<td>x</td>
<td>x</td>
<td>x</td>
<td>x</td>
<td>x</td>
<td>x</td>
</tr>
<tr>
<td>N16var</td>
<td>x</td>
<td>x</td>
<td>x</td>
<td>x</td>
<td>x</td>
<td>x</td>
<td>x</td>
<td>x</td>
</tr>
<tr>
<td>N17</td>
<td>x</td>
<td>x</td>
<td>x</td>
<td>x</td>
<td>x</td>
<td>x</td>
<td>x</td>
<td>x</td>
</tr>
<tr>
<td>N18</td>
<td>x</td>
<td>x</td>
<td>x</td>
<td>x</td>
<td>x</td>
<td>x</td>
<td>x</td>
<td>x</td>
</tr>
<tr>
<td>N19</td>
<td>x</td>
<td>x</td>
<td>x</td>
<td>x</td>
<td>x</td>
<td>x</td>
<td>x</td>
<td>x</td>
</tr>
<tr>
<td>N20</td>
<td>x</td>
<td>x</td>
<td>x</td>
<td>x</td>
<td>x</td>
<td>x</td>
<td>x</td>
<td>x</td>
</tr>
<tr>
<td>N21</td>
<td>x</td>
<td>x</td>
<td>x</td>
<td>x</td>
<td>x</td>
<td>x</td>
<td>x</td>
<td>x</td>
</tr>
<tr>
<td>N27</td>
<td>x</td>
<td>x</td>
<td>x</td>
<td>x</td>
<td>x</td>
<td>x</td>
<td>x</td>
<td>x</td>
</tr>
</tbody>
</table>

Table 1.1. Discrete pulsed call repertoires of A clan members. Calls are based on an alphanumeric system (Ford, 1984, 1987) where ‘N’ is Northern Residents and the number following is the number of the pulsed call. Some discrete pulsed calls have more than one variant or version and pulsed calls can have between 1-5 variants (designated by ‘var’). For example, N10 has only one version, while N01var has 5 variants. Each blue ‘x’ indicates calls seen at least once during this study. Chart was obtained from Ford (1991).

For some mammals the structure of a single call may encode dual or multiple pieces of behavioral and identity information. For example, the chimpanzee pant hoot call shows distinct structural differences upon arrival to a food site compared to instances where the chimpanzees are re-joining (Notman and Rendall, 2005). A single killer whale pulsed
Figure 1.2. Example of four discrete pulsed calls by the A pods (A clan) and I pods of the G clan (not A clan). The top two calls are N04 (left) and one variant of N09 (right) made by the 3 A pods (Table 1.1). The bottom two calls are a N23i call (left) and an N24 call (right) made by the I11 and I31 pods. Naming of calls is based on an alphanumeric system where ‘N’ stands for Northern Residents, followed by the number of the call, while roman numerals denote variants (Ford, 1984, 1987).

call could transfer multi-layered information based on slight but distinct call structure variations which group members would recognize (Notman and Rendall, 2005). One distinctive feature in killer whale discrete pulsed calls is the presence of ‘two-voices’ or biphonic characteristics (Aubin et al., 2000; Fitch et al., 2002; Miller, 2002; Tyson et al., 2007). The distinctive sidebands consist of a lower frequency component (LFC) and an independently produced higher frequency component (HFC) at approximately 9-12 kHz. The HFC is thought to provide directional information about the signaler to the receivers (Miller, 2002, 2007). Analysis of both the HFC and LFC within pulsed calls may provide receiving animals with the signaler’s 3-D position as seen with Norwegian killer whales during carousel feeding (Shapiro, 2008). In addition, HFCs may also contain individual identity information, either alone or in relation to the LFCs (Crance, 2008; Nousek
Figure 1.3. Northern Resident family tree and predominant discrete pulsed call production. Pods, matrilines, and calls are based on an alphanumerical naming system (Ford, 1984, 1987). Delineated in red are Pods and matrilineal units (MU) groups which were analyzed in this study (e.g. A1 pod, A12 MU). The boxes beneath each MU highlight examples of the top five discrete pulsed calls (dpc) produced by the matrilines as presented in (Ford, 1991); all call proportions were collected during foraging. N4 is Northern Resident is usually the predominant call for the 3 A pods (Ford, 1989, 1991). Some of the dpc proportions were grouped between matriline groups as indicated by the dashed arrows. Source: Ford (1991).
et al., 2006). Another analysis revealed that energy distribution between sidebands may indicate the sex of individuals (Miller, 2007). This study found that adult females calls had greater energy in the first two sidebands of the lower frequency component compared to adult males.

In addition to variations within a call, animals can also increase call complexity by how they use calls within vocal exchanges (Falls et al., 1988; Gerhardt et al., 2000; Janik, 2000a; Krebs et al., 1981; Todt and Hultsch, 1998; Todt and Naguib, 2000). Killer whales produce calls in repetitive (Ford, 1991) or match call-type sequences (Miller et al., 2004), both of which would be identifiable and noticeable to other animals and potentially convey a particular context (behavior, movement). Call exchanges may also be another means of transferring behavioral movement information necessary for foraging, traveling or in transitions between these behaviors. For example, animals not responding to signalers may serve a different meaning or intent than animals actively participating in vocal exchanges (Tyack, 2000). Likewise, matched vocal exchanges may play a different role than mixed (or non-matched) call types (Falls et al., 1988; Gerhardt et al., 2000; Janik, 2000a; Krebs et al., 1981; Todt and Hultsch, 1998; Todt and Naguib, 2000).

1.6.2 Selective Pressures

Vocalizations are essential for cetaceans to mate and sustain their populations, despite the previously mentioned costs of vocal production (Deecke et al., 2005; Lachlan and Slater, 1999). To minimize these costs, animals can repeat a single sound (Ford, 1991) or produce a call which is more simple temporally and spectrally. Most odontocetes produce both whistles and broadband sounds (clicks and pulsed calls), which exhibit variability in signal complexity (Ford, 1989, 1991; Janik and Slater, 1998; Rendall et al., 1999). For instance, whistles and pulsed calls are both amplitude and frequency modulated. However, pulsed calls are broadband, produced at higher amplitudes and have a more complex structure compared to whistles. Whereas killer whales are similar to many odontocetes in that they produce whistles (Ford, 1989; Janik, 2000b; Janik and Slater, 1998), they contrast odontocetes in their copiousness of pulsed call production (Ford, 1989). Killer whales have evolved seemingly more costly vocal type, pulsed calls, to be their predominant mode of communication despite their whistling capabilities. The abundance of pulsed call production by killer whales may be shared by other less studied species who are thought to exhibit similar social networks (e.g. pilot whales) comprised of at least pod, if not matrilineal associations (Amos, 1999; Ottensmeyer and Whitehead, 2003; Whitehead, 1998).
The intricate social culture of killer whales and their need to relocate family members on short-time scales (minutes, hours, a day) is a fundamental driving force for the production of pulsed calls (Bigg et al., 1990; Ford, 1989, 1991). Because multiple pods and clans swim within the same location, having pod-, matriline- and individual-specific acoustic characteristics all within the same call, aids killer whales in maintaining cohesion with familial associations (Ford, 1989, 1991; Nousek et al., 2006). Hence, social complexity and density of different groups within a given area often increases vocal complexity (Green, 1975; Nottebohm, 1969).

An additional parameter which may be important in the selective pressures for pulsed call production by killer whales is animal spacing and distribution. Intrinsic features of discrete pulsed calls may provide necessary long-range distinctiveness which animals can more more easily detect (Brown, 1982), even under increased background noise conditions where more complex signals would tend to be masked (Andrew, 1962; Aubin et al., 2000). Since the salmon that Northern Residents show a preference for are not a schooling fish, individual or small groups may have to space themselves over greater distances to catch prey and sustain their dietary needs. The greater spacing required during foraging would potentially drive their need to produce longer range pulsed calls, while the poor hearing and distribution patterns of their prey, salmon, may allow them to ‘freely’ do so (Barrett-Lennard et al., 1996; Shapiro, 2008; Simon et al., 2007).

1.7 Study Species and Location

Northern Resident killer whale habitat extends from the upper portion of Vancouver Island, British Columbia north to the Queen Charlotte Islands, British Columbia and up to Glacier Bay, Alaska (top graph in Fig. 1.4, region with red striped lines). There are 238 individuals within the Northern Resident Community (Ellis et al., 2007). The Northern Resident are comprised of 3 clans which are acoustically distinct in their discrete pulsed call repertoires (A Clan, G clan, and R clan) (Ford, 1991). There are 16 pods and 35 matrilines (Table 1.2). During the summer months only a portion of the Northern Resident killer whales frequent Johnstone Strait. This region is highlighted in red on the lower map in (Fig. 1.4).
Figure 1.4. Map of the Northern Resident habitat off the northern region of Vancouver Island, British Columbia. Northern Resident killer whales (red) traverse the upper portion of Vancouver Island further north to the Queen Charlotte Islands and up to Glacier Bay Alaska (not shown on map). Though the three fish eating populations each have a habitat (the Offshores west of Vancouver Island, the Southern Residents encompassing the bottom portion of Vancouver Island) there is some overlapping in their ranges. Transient or mammal eating killer whale populations traverse all three fish-eating killer whale habitats. The Northern Resident habitat is highlighted in red on the map. The lower map shows a zoom in to the region where the Northern Residents spend the majority of their time in the summer months (highlighted in red) (maps courtesy of Fisheries and Oceans Canada).
<table>
<thead>
<tr>
<th>Clan</th>
<th>Pod</th>
<th>Matriline</th>
<th>Generations</th>
<th>Individuals</th>
</tr>
</thead>
<tbody>
<tr>
<td>A</td>
<td>A1</td>
<td>A36</td>
<td>1</td>
<td>3</td>
</tr>
<tr>
<td></td>
<td></td>
<td>A12</td>
<td>4</td>
<td>8</td>
</tr>
<tr>
<td></td>
<td></td>
<td>A30</td>
<td>3</td>
<td>9</td>
</tr>
<tr>
<td></td>
<td>A4</td>
<td>A11</td>
<td>4</td>
<td>9</td>
</tr>
<tr>
<td></td>
<td></td>
<td>A24</td>
<td>3</td>
<td>5*</td>
</tr>
<tr>
<td></td>
<td>A5</td>
<td>A8</td>
<td>2</td>
<td>4</td>
</tr>
<tr>
<td></td>
<td></td>
<td>A23</td>
<td>2</td>
<td>3</td>
</tr>
<tr>
<td></td>
<td></td>
<td>A25</td>
<td>2</td>
<td>3</td>
</tr>
<tr>
<td>B1</td>
<td>B7</td>
<td>3</td>
<td>3</td>
<td>6</td>
</tr>
<tr>
<td>C1</td>
<td>C6</td>
<td>4</td>
<td>9</td>
<td></td>
</tr>
<tr>
<td></td>
<td>C10</td>
<td>3</td>
<td>7</td>
<td></td>
</tr>
<tr>
<td>D1</td>
<td>D7</td>
<td>3</td>
<td>8</td>
<td></td>
</tr>
<tr>
<td></td>
<td>D11</td>
<td>3</td>
<td>3</td>
<td></td>
</tr>
<tr>
<td>H1</td>
<td>H3</td>
<td>2</td>
<td>3</td>
<td></td>
</tr>
<tr>
<td></td>
<td>H5</td>
<td>3</td>
<td>5</td>
<td></td>
</tr>
<tr>
<td>I1</td>
<td>I1</td>
<td>4</td>
<td>16</td>
<td></td>
</tr>
<tr>
<td>I2</td>
<td>I22</td>
<td>2</td>
<td>2</td>
<td></td>
</tr>
<tr>
<td>I18</td>
<td>I17</td>
<td>3</td>
<td>10</td>
<td></td>
</tr>
<tr>
<td>I18</td>
<td></td>
<td>3</td>
<td>10</td>
<td></td>
</tr>
<tr>
<td>G</td>
<td>G1</td>
<td>G3</td>
<td>4</td>
<td>12</td>
</tr>
<tr>
<td></td>
<td>G16</td>
<td>1</td>
<td>2</td>
<td></td>
</tr>
<tr>
<td></td>
<td>G17</td>
<td>2</td>
<td>10</td>
<td></td>
</tr>
<tr>
<td></td>
<td>G29</td>
<td>3</td>
<td>4</td>
<td></td>
</tr>
<tr>
<td></td>
<td>G31</td>
<td>2</td>
<td>3</td>
<td></td>
</tr>
<tr>
<td>G12</td>
<td>G2</td>
<td>4</td>
<td>7</td>
<td></td>
</tr>
<tr>
<td></td>
<td>G8</td>
<td>1</td>
<td>1*</td>
<td></td>
</tr>
<tr>
<td></td>
<td>G27</td>
<td>2</td>
<td>4</td>
<td></td>
</tr>
<tr>
<td>I11</td>
<td>I11</td>
<td>3</td>
<td>9</td>
<td></td>
</tr>
<tr>
<td>I15</td>
<td></td>
<td>3</td>
<td>14</td>
<td></td>
</tr>
<tr>
<td>I31</td>
<td>I31</td>
<td>3</td>
<td>12</td>
<td></td>
</tr>
<tr>
<td>R</td>
<td>R1</td>
<td>R2</td>
<td>1</td>
<td>2</td>
</tr>
<tr>
<td></td>
<td>R5</td>
<td>3</td>
<td>22</td>
<td></td>
</tr>
<tr>
<td></td>
<td>R7</td>
<td>3</td>
<td>3</td>
<td></td>
</tr>
<tr>
<td></td>
<td>R17</td>
<td>3</td>
<td>7</td>
<td></td>
</tr>
<tr>
<td>W1</td>
<td>W3</td>
<td>2</td>
<td>3</td>
<td></td>
</tr>
</tbody>
</table>

**Table 1.2.** Northern Resident Community social structure. Northern Residents have 3 clans, 16 pods and 35 matrilines. The asterisks next to the number under the Number of Individuals/Generation columns indicate that genetically one juvenile in that matriline belongs to that family, but socially they are spending more time with another closely related matriline of the same pod (Ellis et al., 2007).
1.8 Thesis Outline

This thesis examines individual vocal variation of killer whales within intra-group behavioral movement dynamics. Chapter 2 is an in depth look at the site location along with the acoustic and environmental data collection methods, processing and post-processing analyses. The data analysis chapters can be divided into two sections: aspects of call content (Chapters 3 and 6) and vocal usage in a social context (Chapters 4 and 5). Chapter 3 examines discrete pulsed call variation (N04 call) and how it relates to behavioral movement patterns, as well as individual usage. Chapter 4 focuses on vocal production and vocal exchange behavior during joining events. Chapter 5 examines vocal behavior when a mother is separated from one of her offspring. Chapter 6 investigates the frequency split at the onset of the N04 call. Finally, Chapter 7 is a summary of the research and offers some suggestions for future work.
2.1 Part I: Johnstone Strait, British Columbia, Canada

2.1.1 Description of Location

Acoustic recordings were collected off the southern coast of West Cracroft Island, British Columbia, while the observation site was positioned approximately 50 m above sea level and the hydrophone array location (Fig. 2.1, see red dot). The area where the hydrophones were bottom-mounted was a protected area due to two small protrusions of the land located on either side of the array. Eagle Point (east of array) was approximately 140 m away while Pizza Point (west of array) was 810 m away (Fig. 2.2). Sounds sometimes appeared faint if the killer whales were swimming very near to shore on the far sides of these Points. Signal energy would be reduced due to reflections of killer whale sounds when contacting the large rock protrusions at these Points. Mostly, approaching killer whales swam far enough out (20-30 m from shore) that their sounds passed by these rock protrusions without interference.

Bathymetry of Johnstone Strait is relatively steep with a 400 m decline over 1000 m out from the array (Fig. 2.2). The water is well mixed and homogeneous, and there is very little kelp in this small cove. The center of the strait is approximately 440 m deep and the Robson Bight Ecological Reserve is located approximately 3 kilometers across the strait. Other marine mammals which frequent the strait are Dall’s porpoise, sea lions, Pacific white-sided dolphins, humpback whales and Transient killer whales. Five species of salmon are usually plentiful, as well as, rock fish.

Ambient noise levels vary and peaked during daylight hours when fishing boats (trawlers, seiners and smaller boats), recreational boats and motoring sailboats were present. Also, tug boats carrying large cargo and giant cruise ships pass through John-
Figure 2.1. Map of Johnstone Strait region which is located on the northeast portion of Vancouver Island, British Columbia, Canada. The red dot in the center of the picture in Johnstone Strait is the approximate location of triangular hydrophone array. Drawing from Thomson (1981).

stone Strait daily. In general, the boat noise was not a major issue and signal-to-noise ratios were high over the acoustic range of this study. Most boats slowed down when the killer whales were in the vicinity, which reduced noise levels. Obviously, signal-to-noise ratios of the killer whale sounds were greatly reduced when very loud boats were present or close to the array. Waves were relatively nonexistent at the shoreline by the array, except when a cruise ship or a near shore, speeding boat passed. In such instances, larger waves were generated and hit the shore for about a minute or two, during which time noise levels were increased at the array.

2.1.2 Oceanography of Johnstone Strait

Johnstone Strait is a relatively narrow passageway rarely greater than 2.5-3 km wide but contains some of the deepest waters midstrait of any of the inland waters located between Vancouver Island and mainland British Columbia (Thomson, 1981) (Fig. 2.1).
Figure 2.2. Map of Pizza and Eagle Points. Eagle Point is located to the east of the array, while Pizza Point was located to the west of the array.

Near the study site, depths at mid-strait waters vary from 444 m to the west of array and from 426-457 m deep to the east. The water column has little to no stratification layers, due to the narrow channels, strong tidal currents and many shallow sills (Thomson, 1981).

Johnstone Strait experiences only subtle changes in temperature and temperature gradients with depth (Thomson, 1981). Surface temperatures of Johnstone Strait rarely reach 10°C during the summer and below 30 m temperatures often become uniform (during winter and spring the entire water column is uniform in temperature) (Thomson, 1981). A previous study showed a weak decreasing temperature gradient with depth from approximately 10°C and falling to about 9°C (readings were recorded in upper Johnstone Strait on the Vancouver Island side, west of the observation site) (Candy and Quinn, 1999). Examination of five CTD (Conductivity, Temperature & Depth sensor probes) analyses collected in Johnstone Strait by both the Ocean Science and Productivity Agency (1 CTD in 2005) and the IOS Offshore Oceanography Agency (4 CTDs
between 1976-1978) (Thomson et al., 1980), showed temperature variations were small scale (10ths or 100ths of a degree) but also gradients varied from positive, negative or a multiple combination of both with increased depth. Three CTDs were collected at basically the same location from 1976-1978 (April 1976, November 1977, January 1978) at times 17:59:00, 16:44:00 and 4:27:00, respectively. Two of the measurements revealed multiple, slight changes in positive and negative temperature gradients (April 1976 and November 1977), the other one showed a positive gradient (December 1978). The February 2005 CTD measurements (11:20:32), which were east of and closer to the location of the three CTDs above, showed a positive temperature gradient, while July 1977 CTD readings (12:09:00) revealed a negative temperature gradient (slightly southwest, close to Robson Bight Ecological Reserve). No trend of gradient with time of day was seen from these five CTDs. Hence, the temperature/depth profile of Johnstone Strait appears uniform with minor shifts in a slightly positive or slightly negative profile.

Based on observations during dredging studies, the seafloor composition is thought to be rocks and coarse sand with little or no fine sand or silt (personal correspondence with
R. E. Thomson). These bottom conditions are also consistent with personal observations seen along beaches and intertidal zones along this southwest region of West Cracroft Island, located near the array.

The salinity profile, like the temperature gradient, is nearly uniform in Johnstone Strait, however, unlike temperature gradients (which vary), the salinity appears consistent year round increasing with depth from 30 ppt to 32 ppt (Thomson, 1981). In the five CTD measurements mentioned above, the salinity gradients, also, always slowly increased with increased depth. Johnstone Strait also tends to be more saline on the western seaward side (Thomson, 1981).

The tidal pattern in Johnston Strait where the hydrophone array was bottom-mounted followed a higher high water level, a lower low water level, a lower high water level and a higher low water level (Thomson, 1981). Flooding refers to rising tides and ebbing is when the tides are falling and in Johnstone Strait tides flood from the west to east, ebb from the east to west (Thomson, 1981). Tidal speed slows down upon entering upper Johnstone Strait from the ocean more to the west, and slows down even more once in the strait (Thomson, 1981). Currents would also be expected to travel slower closer to the coastlines than midstrait due to basic water velocity channel characteristics. Wind speed may also sometimes affect current on surface waters if it is strong enough (Thomson, 1981).
2.1.3 Sound Speed Profiles

A calibrated temperature probe consisting of a 50 kOhm thermistor mini sensor connected to a 150 m of Belden RG-174/U coaxial connected to a multimeter was used to determine the temperature profile of the water (design based on (Berchok, 2004)) (see Appendix A for picture and calibration). Resistance readings (kOhms) were taken in increments of 2 meters to 50 m depth and then every 10 m up to 140 m in 2006 and 110 m in 2007. Due to the limitations of boat access, resistance and depth readings were only taken on two occasions during both field seasons 2006 and 2007. The speed of sound \(c\) of that body of water was calculated from the temperature profile, depth and salinity (Medwin, 1975):

\[
c = 1449.2 + 4.6T - 0.055T^2 + 0.00029T^3 + (1.34 - 0.010T)(S - 35) + 0.016D \quad (2.1)
\]

Where \(T\) is the temperature in degrees Celsius (obtained from the calibration charts of resistance measurements at descending depths taken in the field), \(S\) is the salinity in psu (estimated to be 31 psu) (Candy and Quinn, 1999; Thomson, 1981), and \(D\) is depth in meters. Graphs of the sound speed profiles taken in Johnstone Strait during the summers of 2006 and 2007 are shown (Fig. 2.4). The left graph contains readings from 2006, while the right graph has data from 2007. The little red ‘x’s in the upper left hand corner of the graphs is the depth of the hydrophone array at mid-tide (approximately 8 m) and the blue shaded region is the expected foraging depths of the killer whales (Baird et al., 2005; Candy and Quinn, 1999). In 2006, the July 28 resistance readings were taken on the south side of mid-strait starting at about 10:30 am, the water conditions were turbulent with a Beaufort reading of 3-4, the tide level varied from about 1.0-2.1 m during the collection of data. Readings were initially obtained on the opposite side of midstrait because the usable acoustic range of the array was not yet known. All other temperature depth profiles were taken north of midstrait, the side of the strait where the hydrophone array was located (August 20, 2006, August 7 and 17, 2007). Readings for August 20, 2006 began at 10:50 am, conditions were glassy with a sea state of 0, and the tide level varied from 3.2 to 3.8 m during the course of the measurements. Since the localization of the calls required sound files with high signal-to-noise ratio, only resistance readings were taken on the north side of midstrait during summer 2007. On August 7, readings began at 11:37 am, low, heavy fog but the water was still with a sea state of 1, the tide level fell from about 2.8 to 2.4 m during data collection. On August 17, readings began at 10:40
Temperature depth readings were obtained from thermister calibrations to create the sound speed profiles. Two profiles were conducted for each season in Johnstone Strait (2006 on left, 2007 on right). All profiles were obtained on the north side of the strait (side the array was located), except for readings obtained on July 28, 2006, which were obtained just south of midstrait. The small red star represents the depth of the hydrophone array at mid-tide levels. The blue shaded regions are expected foraging depths for killer whales based on time-depth recorders and Chinook salmon daytime swimming depths (Baird et al., 2005; Candy and Quinn, 1999).

Data retrieval was not instantaneous (data collection took approximately 20-30 minutes for complete profile), readings were more representative of mean resistances. Profiles were averaged for the three data measurements collected north of midstrait and used for any subsequent analysis requiring sound speed information (e.g. transmission loss).

The profiles seen here show a greater variation in velocity change with depth than previously seen. Candy and Quinn (1999) showed only approximately 1° difference over the same depth, while the mean temperature differences in this study were 4° for 2006 and 0.6° for 2007. The 2007 field season is the most consistent with earlier data.
Sound speed of the ocean environment where audio recordings are collected is an important environmental factor to obtain especially when trying to acquire the actual time an animal produces a sound. For example, if the animal is 1 km away pulsing at a frequency of about 2 kHz and the time of arrival of the signal at the first hydrophone is 14:33:12.80 (hh:mm:ss.ss), the sound speed profile needs to be used to estimate the approximate time the animal actually vocalized. If the sound travels 1 km at a sound speed of 1480 m/sec it would take approximately 0.67 sec to reach the front element of the array, which would make the actual time the animal produced the sound to be 14:33:12.13. If an animal is sprinting at top speeds of 12 m/sec (an extreme case) then the animal could have moved ahead by 8 m by the time the signal arrived at the front hydrophone in the array. Generally these killer whales are travelling up to 5.6 m/sec and foraging at an average of 1.6 m/sec which would be a displacement of approximately 3.7 m and 1.0 m, respectively, by the time the sound reaches the front element of the array from the same range. This is less of an issue for a distance of 500 m which under the same frequency and sound speed conditions it would take 0.33 sec for the sound to reach the array, but the animal would only have moved approximately 4 m if swimming 12 m/sec, 1.8 m if swimming 5.6 m/sec, and approximately a half meter if swimming 1.6 m/sec.

2.1.4 Water and Weather Conditions

2.1.4.1 Water Visibility

In summer 2007, a black and white secchi disk was deployed to gain a rough estimation of visibility during a few different weather and water conditions. A secchi disk is a method to measure the water transparency. The depth at which the secchi disk was no longer visible during descent and then the depth which it becomes visible upon ascent are averaged to provide an estimate of the vertical visibility of the water. Readings with their dates, times, weather conditions, tide, sea state and vertical visibility are listed in Table 2.1. Though the vertical visibility can not be an exact indicator of horizontal visibility due to the higher light levels near the surface, it is thought to provide a conservative estimation of their vision capability. The value of this measurement highlights the difference in illumination with depth, so the visual range of killer whales would be reduced in the horizontal at greater depths. Other factors may increase their visibility or awareness of nearby individuals. The white or light gray coloring on their abdomens and behind their dorsal fins, respectively, may increase visual capabilities. In addition,
the killer whales probably sense water displacements produced by nearby swimming animals. In this study, secchi disk measurements during varying weather conditions helped provide a rough estimate of when animals were considered within visual range of one another, especially during instances when animals were merging (e.g. joinings).

<table>
<thead>
<tr>
<th>Date</th>
<th>Time (hh:mm)</th>
<th>Conditions</th>
<th>Tide (m)</th>
<th>Sea State</th>
<th>Visibility (m)</th>
</tr>
</thead>
<tbody>
<tr>
<td>July 27</td>
<td>10:08</td>
<td>sunny, a few clouds</td>
<td>2.8</td>
<td>1</td>
<td>14.2</td>
</tr>
<tr>
<td>August 7</td>
<td>11:29</td>
<td>low, heavy fog</td>
<td>2.6</td>
<td>1</td>
<td>11.4</td>
</tr>
<tr>
<td>August 17</td>
<td>10:27</td>
<td>overcast, some blue</td>
<td>1.6</td>
<td>4</td>
<td>7.1</td>
</tr>
</tbody>
</table>

Table 2.1. Vertical visibility of Johnstone Strait. Listed are measurements taken by a secchi disk. Visibility varied with sea state and sunlight conditions. All measurements were taken in 2007 on the north side of Johnstone Strait near the hydrophone array location.

2.2 Part II: Acoustic Recording System

2.2.1 Sensitivity, Frequency Response, Bandwidth, and Gain

The three elements in the hydrophone array were High Tech, Inc. HTI-96-min hydrophones with built in pre-amps. Sensitivity of two of the elements with built-in pre-amps were -164.1 dB re 1V/uPa, while the sensitivity for the third element was -164.0 dB re 1V/uPa. The frequency response of the hydrophones was flat from 2 Hz to 30 kHz (see Appendix B). Each hydrophone was connected to an external Sound Professional mono microphone pre-amp (SP-PreAmp-10) which provided 31 dB additional gain to the signal for the first two hydrophones and 32 dB to the third.

A four channel portable digital recorder, Edirol R-4, a product by Roland, was used to collect both human voiced information on killer whale behavior and acoustic recordings (also see Appendix B). Channel 1 was the human voice while channels 2, 3 and 4 were connected to the three hydrophones. The sampling frequency was 48.0 kHz using a 16 bit analog-to-digital converter. The analog line input was set to 4-channels simultaneous recording to one 4-channel file. This recording option provided simultaneous sampling of all four channels necessary for post-processing analysis of the sounds. Recording mode was continuous, and recording sessions automatically rolled over to a new file after files reached 2 Gigabytes. The output of each recording was a 4-channel root mean square voltage ($V_{rms}$) .wav file.
2.2.2 Power Supply

There was no electricity at this location on West Cracroft Island where the camp and field observation sites were located. All equipment at the field site was battery powered by 12 V-33/35 Amp scooter batteries. All batteries were re-charged using a Kyocera (KC65T) solar panel module mounted on the roof of the small shack located atop the cliff observation site. At standard test conditions (1000 W/m² and module temperature of 25°C) the maximum power ($P_{max}$) was 65 W, maximum power voltage ($V_{mpp}$) was 17.4 V and maximum power current ($I_{mpp}$) was 3.75 Amps. So it was expected under sunny conditions that a re-charging battery using the KC65T solar panel would supply 3-3.75 Amps to the battery every hour. Four to six 12 V-35 Amp hour batteries were purchased in order to account for high energy consumption days when multiple killer whale encounters occurred accompanied by cloudy days when poor battery re-charge performance was imminent. At least one or two batteries were set aside unused for emergency energy situations.

The Edirol R-4 audio digital recorder was powered directly by a 12 V-33/35 Amp external battery connected to the DC input. The recorder output was 9 Volts at 2.0 Amp DC (a conservatively rounded-up number), so 18 W were required to run the recorder. The expected current draw on the battery was 2 amps/hour and expected daily battery consumption by the recorder was 16 Amp-hours. The expected hours the recorder could run off the 12 V-35 Amp battery was determined to be approximately 17 hours. The actual observed time that the recorder depleted the battery was 52 hours. The audio recorder drew the least energy compared to the other major field equipment (computer and video camera).

Batteries were rotated and a battery was charged by a solar panel daily. The 12 V battery used to power the digital audio recorder was switched daily to power the video camera the following day. Batteries used to power the video camera one day were rotated to be charged by the solar panel the following day. The digital audio recorder always received the newly re-charged battery from the solar panel. Hence, if equipment was being used daily to record encounters, each battery was charged every other day. This rotation of batteries helped to maintain ample battery power during the audio recordings.
2.2.3 Hydrophone Array Setup

A triangular hydrophone array was bottom-mounted in Johnstone Strait, 50°31'22" N and 126°35'53" W, in July and August 2006-2007, to localize sounds emitted by individual or small groups of killer whales (Fig. 2.1, Fig. 2.5, Fig. 2.6). The spacing between hydrophones in the triangular array was 20 m in the horizontal. Each hydrophone was positioned approximately 1.3 m off the seafloor. The hydrophone mounted farthest out was approximately at 6.5 m depth in at the lowest of tides while the two hydrophones closest to shore were approximately 4.5-5 m deep. The closest hydrophone to shore was located 23 m away from the shoreline. The three hydrophones were positioned in an equilateral triangle 20 m apart. Each hydrophone was bottom-mounted and the hydrophone cable was connected to tension wire which was then connected by rope to a smaller cork buoy situated about a meter above the element; an additional buoy rested at the water’s surface. The smaller submersed buoy was used to help keep the hydrophones off the seafloor during lower tides. The electronic cables were deployed up to the cliff observation site located approximately 54 m above the water’s surface at the hydrophone array location.

2.3 Part III: Data Collection, Processing and Analysis

2.3.1 Data Collection

This study was limited to encounters of killer whales who passed between north of midstrait to the cliffside of West Cracroft Island near the hydrophone array. The hydrophone array was located in a shallow cove located between two small points jutting out into the strait, located on the eastern and western ends of the cove (Eagle Point and Pizza Point). Encounters officially began when the killer whales were seen approaching the Cracroft shore side. Depending on the killer whale movement tracks (nearshore, mid-strait) encounters could begin within a few or several hundred meters of either point. At the onset of each encounter, audio recordings, video and theodolite data were collected. An encounter was terminated after all killer whales passed by the observation site and were beyond visual and acoustic range.

Killer whale behaviors (traveling, foraging, socializing and resting) (Ford, 1989) were collected using individual focal follow and scan sampling methods (Altmann, 1974). The definition of foraging encompasses the broader definition which means seeking, finding and feeding on prey. More instantaneous behaviors, or event behaviors, were also
Figure 2.5. Hydrophone array location between Pizza and Eagle Points. Zoomed insert of array and observation site is provided. Array was approximately 140 m from Eagle Point and 810 m from Pizza Point.

Spatial and temporal positioning of individual and small groups of killer whales were obtained from the cliff located above the hydrophone array. A calibrated and leveled Pentax Electronic Theodolite, ETH-010D, with a 30x zoom and 7-10” accuracy, was used to obtain vertical and azimuthal angles needed to calculate distances to the animals. The eye-hole of the theodolite was located approximately 54 m above the waters surface at mid-tide level (50°31’24"N, 126°35’51"W). Vertical and horizontal angles were set to 0°00’00" mode. Theodolite angles were obtained on killer whales located in all areas of the strait, not just those passing in front of the cliff. Tides were obtained from the Fisheries and Oceans Canada website for Alert Bay, British Columbia which is located 25 km west of the hydrophone array setup. In addition, tide levels were marked on a nearby rock and the theodolite was calibrated to the same location every day and for

Examples of event behaviors are spyhops, breaches and fluke slaps.
Figure 2.6. Schematic of a representative bottom-mounted hydrophone array used in summers 2006 and 2007. Hydrophone array was triangular in formation (only one hydrophone shown here); total of 3 elements were bottom-mounted in equilateral triangle (sides equaled 20 m each). Buoys are used to hold the hydrophones off the seafloor during low tide, while weights on the seafloor (not shown) were used to maintain hydrophone positions. Hydrophones were connected to tension wire for protection. Rope was used between the buoys and the tension cable to provide extra slack during low tide states. All tension wire/hydrophone cables were extended up to the top of the cliff observation site.

every encounter. For each theodolite recording other parameters noted were: the time of the animal’s surfacing, direction the animal was facing, its behavior and any other pertinent notes of interest such as identity or proximity to boats. An example of a theodolite recording is shown in Table 2.2. Theodolite recordings were collected on all groups of killer whales in every portion of the strait, before and after designated encounter times. First, obtaining a complete overview of killer whale group composition, location and movement patterns, provided a good assessment of which killer whale groups were present and in which direction they were moving. Second, in case an encounter began cliffside, we had an understanding of the horizontal angle position of all killer whales in the strait. This eliminated any ambiguity about who was vocalizing at a given angle and time. Third, overall observations provided a daily assessment of which group tended to traverse which side of the strait at which times, and if that group previously passed through on the same day.
Table 2.2. Example of individual scan sample data with theodolite recordings. Each scan in an encountered was numbered, the time the animal surfaced and theodolite readings were taken. In addition, matriline, individual gender, orientation and behavior was recorded. Additional notes for this scan said ‘sailboat approaching A12 from Pizza Point’.

A Sony Digital Handycam Digital 8 video camera with a 20-40x zoom was used to capture the surface behaviors, animal associations and the spacing of individuals and small groups of killer whales passing through the strait (Fig. 2.7). The surfacings of the killer whales, orientations, direction of movements and behaviors were recorded visually and orally for future off-site analysis. A Nikon D70s digital camera with a 300 mm zoom lens and telescope were also used for photo-identification of individuals (Fig. 2.8). Pertinent information such as boat traffic, identity, sea state, etc. were recorded. The audio of the video camera was synched to the microphone channel on the digital audio recorder which in turn was synched to the recordings of the three hydrophones.

![_snapshot_of_adult_female](image)

**Figure 2.7.** Snapshot of adult female captured from video camera. The adult female, A43 of the A23 matriline, was foraging slowly west heading toward Pizza Point.

Weather conditions were recorded at various points during the day, and in and around encounters. Humidity and temperature were obtained using an Oregon Scientific Wireless Handheld Weather Forecaster. Wind (miles per hour) was measured using a wind meter. In addition, sea state levels (Beaufort Sea State Scale) and basic weather conditions (sunny, cloudy, rainy) were recorded. All of these weather conditions, provide qualitative
Figure 2.8. Photograph of mother and juvenile captured off Eagle Point. The mother, A52 of the A11 matriline, was foraging for approximately a half hour off Eagle Point. Her young three-year-old juvenile, A81 was seen swimming nearby. At the time of this recording weather conditions had changed to a drizzling rain. A52 has two distinctive nicks in her dorsal fin (left).

or quantitative descriptions of weather conditions which were used to confirm and assess sea state and potential water visibility conditions for that day.

2.3.2 Data Processing

2.3.2.1 Mapping Routes

Horizontal and vertical angles obtained from theodolite readings of the killer whale locations were analyzed in Pythagoras (Williams et al., 2002a,b). Calculated azimuthal distances of animals to the theodolite were adjusted to the appropriate tide height for each reading. Killer whale theodolite and video recordings (along with the time of reading, age/sex class, behavior, orientation, and any additional identification or boat notes) were all plotted onto a bathymetric map of Johnstone Strait (Chart Navigator version 5.073 by Maptech Inc.). Additional surfacings of killer whales which were captured by video or voice notes were also placed on the map. Fig. 2.9 shows the location of the hydrophone array and the cliff-site, along with an example of 2 male killer whale movement tracks based on theodolite and video recordings of animal surfacings during the
encounter. This example is of two males (brothers) from the A36 matriline of the A1 pod.

Figure 2.9. Bathymetric map of 2 male killer whale movement tracks of matriline A36. The movement tracks of the 2 killer whales were obtained from theodolite readings overlaid with video sightings of the animal surfacings (dots under lines). The theodolite was located on the cliff observation site about 54 m above the triangular hydrophone array (dotted purple circle). The two brothers were slowly foraging from East to West. Male1 (green) is slightly ahead of Male2 (red), as seen by the times along the track. The two males joined at about time 14:42:45 (hh:mm:ss) (Map by Maptech, Inc.).

2.3.2.2 Angle of Arrival Analysis

The hydrophone farthest from shore (deepest) was designated yellow, and the other two hydrophones were designated orange (west) and blue (east) (hydrophones 1, 2, and 3 respectively). Calculations for the angle of arrival of sounds were based on an equilateral triangle since the hydrophones were placed 20 m apart in the horizontal in that configuration. Post-processing for the angle of arrival calculations were done in Matlab (The Mathworks, Inc.). Once the arrival times were determined from the waveforms for
all three audio channels, a custom Matlab code displayed the angle of arrival for that sound. Calculations were based on the cartesian coordinate system (Panez, 2004). The distance between two cartesian points is

\[ d = \sqrt{(x_2 - x_1)^2 + (y_2 - y_1)^2} \] (2.2)

Coordinates of the equilateral triangle, were set up as seen in Fig. 2.10, where \( l \) is the distance between hydrophones. For consistency, all distances were converted to seconds. The origin (yellow) is the hydrophone which received the signal first, then based on time of arrivals of the signal at the blue (right) and orange (left) hydrophones, the angle of the arrival was calculated (Fig. 2.10). The slight differences in depth of the hydrophones due to varying bathymetry were examined for their effects on the equilateral calculations. Referring to Fig. 2.10 for \( \theta = 45^\circ \), the angular uncertainty when factoring in differences with distance between elements (0.01-0.09 m) is equal to or less than a 0.25\% uncertainty (0.6\%). Based on the small difference (0.6\% error) from the assumption of 20 m separation lead to the conclusion of a planar array at a nominal depth of 5.5 m from the sea surface at the lowest of tides.

\[ T_r + T_1 = \sqrt{(-L\sin30^\circ - T_r \sin(\theta))^2 + (-L\cos30^\circ - T_r \cos(\theta))^2} \] (2.3)

\[ T_r + T_2 = \sqrt{(L\sin30^\circ - T_r \sin\theta)^2 + (-L\cos30^\circ - T_r \cos\theta)^2} \] (2.4)

\[ \theta = \cos^{-1}((2T_2 T_r + T_2^2 + 2T_1 T_r + T_1^2 - 2L_2)/(2\sqrt{3LT_r})) \] (2.5)

The phase of the array was calibrated in the field using a sound source made from a metal plate and pipe. The bell-shaped pipe was released just under the water’s surface and slid down a 10 m rope until it made contact with the plate (see Appendix B). In lab pre-calibration the sound apparatus generated an impulsive, slightly broadband signal with a peak of 2.1-2.2 kHz. The test sound was generated (and recorded) at approximately twenty positions, each with recorded latitudinal and longitudinal positions, around the array (out to 230 m away) to determine the phase accuracy of the array and subsequent calculations. Close to the array the plate on which the pipe made contact was at the middle of the column, approximately 5 m depth, further out from the array the source depth was 20 m. The mean array error over the varying ranges was calculated to be 0.94 degrees with a standard deviation of 0.58. This error was then used to estimate
Figure 2.10. Equilateral triangular hydrophone array cartesian coordinates. Yellow, orange and blue dots represent the 3 hydrophones in the array. $T_r$ is the range to the hydrophone array converted to time (seconds), $l$ is the distance between hydrophones and $\Theta$ is the angle of arrival.

The error in distance (m) at varying ranges within the acoustic range of this study. For instance, at 100 m range the estimated error was calculated to be 1.64 m $\pm$ 1.01 m, while at 1000 m range (approximate outer boundary of the acoustic range) the error was 16.41 m $\pm$ 10.12 m (Table 2.3).

<table>
<thead>
<tr>
<th>Range (m)</th>
<th>10</th>
<th>50</th>
<th>100</th>
<th>250</th>
<th>500</th>
<th>1000</th>
</tr>
</thead>
<tbody>
<tr>
<td>Error (m)</td>
<td>0.16</td>
<td>0.82</td>
<td>1.64</td>
<td>4.10</td>
<td>8.20</td>
<td>16.41</td>
</tr>
<tr>
<td>Std. Deviation (m)</td>
<td>0.10</td>
<td>0.51</td>
<td>1.01</td>
<td>2.53</td>
<td>5.06</td>
<td>10.12</td>
</tr>
</tbody>
</table>

Table 2.3. Array error with variations in range. The range error (m) and standard deviation (m) are shown with 6 ranges.

Estimated angle of arrival buffer zones were considered when attributing isolated vocalizations to solitary animals or small groups to account for any error (e.g. array error with range). For example, if the waveform of the vocalization arrived at the array...
at a 30° angle than the buffer zone would be defined as 30° +/- 10°. The buffer zones on either side of the localized angle varied some (from 10 azimuthal degrees close to the array about 5 degrees farther away) depending on the distance of the vocalizing animal to the array. This buffer zone takes into account the array error and also any error due to variable depths at which vocalizations were produced (Miller, 1998). Sounds were considered localized if the sound at a given angle could not be produced by any other individual or small group. So if more than one individual (or small group) was at the same angle of arrival of the sound, then the sound was not localized. If only one individual or small group was at the angle of arrival, the sound was attributed to that group. In addition, sprinting speeds of the animals were always considered in attributing calls to individuals or small groups. If any other killer whales could sprint to within the buffer of a vocalizing individual that sound was not considered an isolated individual vocal. For example, at 100 m with a five degree buffer there is about 9-10 m on either side of the animal, but at 600 m it is about 56 m. A nearby animal sprinting at 12 m/sec easily could enter the 5° buffer zone at 100 m but it would take a few seconds to reach the same buffer zone at 600 m. In general, penetration into angle of arrival buffer zones was not an issue, because the killer whale individuals or small groups usually discretely spaced themselves during encounters (100 m apart or more) as previously described (Miller, 1998). On occasion when spatial overlap of buffer zones by different groups occurred, it was brief (up to a minute or two), and the vocalizations were not attributed to either group. After it was determined that no other killer whale or group of killer whales could be in the location of the angle of arrival, localized sounds were then aligned in space and time with the locations of the vocalizing animals.

Sounds are overlaid onto the movement tracks once the sounds were localized and linked to a specific animal or small group (Fig. 2.9). The same example of the movement tracks of the two males shown earlier has been annotated with their corresponding vocalizations and time of occurrence (Fig. 2.11). Click bouts have been denoted by ‘C’, while discrete pulsed calls are noted as N03, N04 and so forth. For instance Male2 (green) slowly swam toward Male1 (red) and produced a N09 call at time 14:40:45 (hh:mm:ss). Within 2 seconds at 14:40:47 Male1 (red) made a N04 call, he was last seen foraging facing in a southeast direction a little more west of Male2. A couple more pulsed calls were made and both animals surfaced within seven seconds of one another around 14:42:43, and swam west together for the remainder of the encounter in silence (Fig. 2.11).
Figure 2.11. Bathymetric map of 2 male killer whale movement tracks with corresponding vocalizations. Overlay of sounds linked to the two killer whales along their movement tracks first seen in Fig. 2.9. At the beginning of the track (right side, east), both males are foraging, separate but both slowly foraging west (toward the left of the picture).

2.3.2.3 Localized Sounds

All three types of sounds were localized (clicks, whistle and pulsed calls). The spectral content of clicks could not be analyzed in this study (due to the bandwidth of the recording system), but they were localized to help validate animal locations and provide insight into what the submerged killer whale was doing vocally. Whistles were difficult to localize by the waveforms since there were no abrupt or discrete increases in amplitude at the onset of the sound and also due to their characteristically lower amplitudes (arrivals were determined by spectrogram analysis). Discrete pulsed calls were initially identified according to Ford’s classifications (Ford, 1987, 1989, 1991). Most pulsed calls contained a start up pulse or exhibited an abrupt increase at the onset of the call. Discrete pulsed calls tended to have these strong onsets more often than the variable or aberrant calls, however, some discrete pulsed calls like N13 and sometimes N47, started with lower,
gradually rising amplitudes which were difficult to accurately localize if the signaler was generally more than 400 or 500m away. In contrast, a call with one ‘start up’ or a series of broadband pulses (or buzz-like component) at the onset of the call were ideal for localization.

2.3.3 Analysis

2.3.3.1 Data Distributions

Only a portion of the Northern Resident killer whale population regularly frequent Johnstone Strait during the summer months. A greater diversity of pods appeared during data collection in 2006 than in 2007. In 2006, pods from all 3 clans visited: A1, A4, A5, B, C, D, I11, I31, R on both sides of the strait. In the 2006 data, C and D pods only traversed the opposite side of the strait during observation hours. The B pod travelled on both sides, but they did not vocalize when they were cliff-side near the array, so encounters with them were not included in this analysis. A few R pod members swam on the cliff-side once while intermixed with A1 pod members, but overall encounter vocalizations were low and only one pulsed call was attributed to them. In 2007, all three A pods of the A clan, C and D pods were farther north and the B pod was eventually spotted on the western upper portion of Vancouver Island in mid August. I11 and I31 pods from the G clan were present in 2007. Additionally, the W pod was present once on the opposite side of the strait and only briefly cliff-side, but were not present during any analyzed encounters.

Killer whales traversed all locations of the strait when passing in the region of the hydrophone array and observation site. The total numbers of encounters during observation hours are displayed for the summer 2006 and summer 2007 field seasons (Fig. 2.12). Encounters usually lasted from 15 minutes to approximately an hour. A total of 58 encounters for both seasons were recorded of killer whales swimming west to east, while in 52 encounters they swam east to west. These distributions are limited to daylight hours due to the necessity to record killer whale locations and contain all instances of when the killer whales entered this region of Johnstone Strait (i.e. distributions include killer whales swimming on both sides of the strait).

During the observation period, the distribution of the total number of encounters by time of day was calculated for both summers 2006 and 2007 (Fig. 2.13). At the beginning of summer 2007 all five species of salmon counts were very low which delayed the first arrival of the killer whales to the region until around July 14th; this was the
latest summer arrival of the Northern Residents since the beginning of record keeping by local researchers conducting annual population assessments. As a consequence, the killer whales often rapidly travelled through the strait and then turned back around and left in the middle of the night. The first data collection began on July 24th. By the end of July they were starting to follow their traditional summer residence patterns in these inland waters.
Figure 2.12. Total number of killer whale encounters per date for 2006 and 2007. Bars represent the number of encounters per date recorded during July and August of 2006 (blue, top) and 2007 (green, bottom). Killer whale encounters occurred from zero to six times a day.
Figure 2.13. Diurnal distribution of killer whale encounters for 2006 and 2007. Encounters were recorded during July and August of 2006 (blue, top) and 2007 (green, bottom). Bars show the daily start and end time of killer whale encounters. Data distribution includes all encounters during these two field seasons, not just the encounters analyzed.
Age/sex class content of pods and matrilines seen in this study varied slightly between years (Table 2.4) (Ellis et al., 2007). This table lists the number of adult males, adult females, juveniles and calves, as well as, the total number of individuals in this group. The numbers do not, necessarily, represent all the individuals seen or individuals who vocalized, it simply provides an age/sex content of matrilines which were present during completed encounters for each year. Though the total number of individuals in each matriline remained constant, of those seen in both 2006 and 2007 (A1, A4, A5 pods and I11 pod (I15 matriline)), a few calves aged into the juvenile category. Killer whales from newborn up to 3 years old were considered calves, while all non-adult individuals from 3 years until late teens were considered juveniles. For example in 2006 the A12 matriline had 1 juvenile and 2 calves (a 2-year-old and a 1-year-old), but by 2007 the former 2-year-old was now categorized as a juvenile.

<table>
<thead>
<tr>
<th>Year</th>
<th>Clan</th>
<th>Pod</th>
<th>Matriline</th>
<th>Adult Males</th>
<th>Adult Females</th>
<th>Juveniles</th>
<th>Calves</th>
<th>Total</th>
</tr>
</thead>
<tbody>
<tr>
<td>2006</td>
<td>A</td>
<td>A1</td>
<td>A36</td>
<td>3</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>3</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>A12</td>
<td>2</td>
<td>3</td>
<td>1</td>
<td>2</td>
<td>8</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>A30</td>
<td>2</td>
<td>3</td>
<td>2</td>
<td>2</td>
<td>9</td>
</tr>
<tr>
<td></td>
<td>A4</td>
<td>A11</td>
<td>1</td>
<td>3</td>
<td>4</td>
<td>2</td>
<td>10</td>
<td></td>
</tr>
<tr>
<td></td>
<td>A24</td>
<td></td>
<td>0</td>
<td>1</td>
<td>3</td>
<td>0</td>
<td>4</td>
<td></td>
</tr>
<tr>
<td></td>
<td>A5</td>
<td>A8</td>
<td>0</td>
<td>2</td>
<td>1</td>
<td>1</td>
<td>4</td>
<td></td>
</tr>
<tr>
<td></td>
<td></td>
<td>A23</td>
<td>1</td>
<td>1</td>
<td>1</td>
<td>0</td>
<td>3</td>
<td></td>
</tr>
<tr>
<td></td>
<td></td>
<td>A25</td>
<td>1</td>
<td>1</td>
<td>0</td>
<td>1</td>
<td>3</td>
<td></td>
</tr>
<tr>
<td></td>
<td>G</td>
<td>I11</td>
<td>I11</td>
<td>3</td>
<td>3</td>
<td>1</td>
<td>2</td>
<td>9</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>A15</td>
<td>1</td>
<td>5</td>
<td>6</td>
<td>2</td>
<td>14</td>
</tr>
<tr>
<td>2007</td>
<td>A</td>
<td>A1</td>
<td>A36</td>
<td>3</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>3</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>A12</td>
<td>2</td>
<td>3</td>
<td>2</td>
<td>1</td>
<td>8</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>A30</td>
<td>2</td>
<td>3</td>
<td>2</td>
<td>2</td>
<td>9</td>
</tr>
<tr>
<td></td>
<td>A4</td>
<td>A11</td>
<td>1</td>
<td>3</td>
<td>6</td>
<td>0</td>
<td>10</td>
<td></td>
</tr>
<tr>
<td></td>
<td>A24</td>
<td></td>
<td>0</td>
<td>1</td>
<td>3</td>
<td>0</td>
<td>4</td>
<td></td>
</tr>
<tr>
<td></td>
<td>A5</td>
<td>A8</td>
<td>0</td>
<td>2</td>
<td>2</td>
<td>0</td>
<td>4</td>
<td></td>
</tr>
<tr>
<td></td>
<td></td>
<td>A23</td>
<td>1</td>
<td>1</td>
<td>1</td>
<td>0</td>
<td>3</td>
<td></td>
</tr>
<tr>
<td></td>
<td></td>
<td>A25</td>
<td>1</td>
<td>1</td>
<td>0</td>
<td>1</td>
<td>3</td>
<td></td>
</tr>
<tr>
<td></td>
<td>G</td>
<td>I11</td>
<td>I11</td>
<td>3</td>
<td>3</td>
<td>2</td>
<td>1</td>
<td>9</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>I15</td>
<td>1</td>
<td>5</td>
<td>8</td>
<td>0</td>
<td>14</td>
</tr>
<tr>
<td></td>
<td></td>
<td>I31</td>
<td>I31</td>
<td>4</td>
<td>3</td>
<td>3</td>
<td>2</td>
<td>12</td>
</tr>
</tbody>
</table>

Table 2.4. Age/sex class categories. Number of individuals in each age/sex class category for cliffside encounters completed for summers 2006 (top) and 2007 (bottom). Numbers are counts of individuals in the group. Not every individual was present during encounters. Pod I31 was not seen in 2006 (Ellis et al., 2007). R pod is not seen here in 2006 due to the contribution of only one pulsed call in one encounter.
2.4 **Part IV: Acoustic Factors**

2.4.1 **Ambient Noise of Environment**

Signal-to-noise ratios were generally high for signals analyzed in this study, and long sustained, increased ambient noise levels were rarely a factor on the time scales of these encounters. Anthropogenic ambient noise levels were temporarily increased when a boat passed. Occasionally, there was a Beaufort Sea State of 3 or 4 which increased noise levels, and in one instance it began raining during an encounter. Whether the encounter was deemed of high quality to localize the killer whale sounds, generally, depended on if the killer whales were swimming near the array which would increase the signal-to-noise ratio of the signal. Mean ambient noise for encounters examined in this study is shown in orange in Fig. 2.14. A representative N04 call (blue) and recorder noise from the three hydrophone channels are also shown in red, green and black (see Appendix B).

![Figure 2.14. Mean ambient noise of environment. A mean of the ambient noise (orange) was taken from encounters examined in this study. Also shown is a representative N04 call (blue) and recording noise from the three hydrophone channels (red, black, green).](image)
2.4.2 Transmission Loss

Signal-to-noise ratios of the killer whale sounds were high, due to the limited ranges of this study. Sounds analyzed during encounters were generally produced 1 km away or less, except in rare instances when both the killer whales were oriented toward the array and current complimented the orientation of the vocalizing animal. A trace of the general acoustic range approximately 1 km out from the hydrophone array bottom-mounted in Johnstone Strait is shown in red in Fig. 2.15. Generally during encounters animals swam from within a couple meters of the array to approximately 600-800 m away. Animals spend the majority of their time from 5 m to approximately 60 m depth (Baird et al., 2005). This range is similar for the range at which Norwegian killer whales mostly vocalized (Shapiro, 2008). For this study, signals are expected to be direct path due to the sound speed profile (Fig. 2.4) and the short propagation range (predominant swimming depths highlighted in blue). Geometrical spherical spreading of the sound over these short ranges and a transmission loss of $20 \log_{10}(R)$ is expected. Transmission loss was used to estimate source levels, since the hydrophones were calibrated and accurate distances of the animals were known.

2.4.3 Lloyd’s Mirror Interference Effect

Lloyd’s mirror interference effects on the amplitude of a signal can occur in calm (low) sea state levels and with lower frequency sounds (Malme, 1995; Urick, 1983). Lloyd’s mirror effects are influenced by the range, depth and frequency of a transmitted sound. In the nearfield of a source, Lloyd’s mirror is not expected to play a role, for the direct propagation path predominates, so spherical spreading is assumed when calculating the transmission loss of the signal ($\text{TL} = 20 \cdot \log_{10}(R)$, where $R$ equals the range). Before the sound reaches the farfield, there is an intermediate range known as the interference region (Urick, 1983). In this interference zone, Lloyd’s mirror effects can occur (assuming surface roughness is minimal). Fig. 2.16 shows the direct and reflected propagation paths from the source ($S$) arriving at the receiver ($R$) at depth $z$; $S'$ is the source image (reflected arrival), $z_o$ is the source depth and $r$ is equal to the horizontal range from the source to the receiver. The effect of both the direct and the reflected paths arriving simultaneously at the receiver could potentially result in constructive and destructive summations of the combined waveforms of the signal, thereby altering the transmission loss. For example, a perfectly reflected wave (i.e. a perfectly glassy sea surface) would return a reflection coefficient of equal to -1. which has the same magnitude but opposite phase of the direct
Figure 2.15. Acoustic range of the hydrophone array. A trace of the general acoustic range approximately 1 km out from the hydrophone array bottom-mounted in Johnstone Strait is shown in red. Generally during encounters animals swam within a couple meters of the array to approximately 600-800 m away from it.

path wave. In less glassy sea states, the reflection coefficient would be less than unity (Kinsler et al., 2000; Urick, 1983). Hence, the fluctuations in amplitudes at the receiver would vary depending on the roughness of the sea surface and the degree of phase shift of the reflected wave compared to the direct wave.

The frequency of the signal must be considered when determining the range of Lloyd’s mirror effects on marine mammal sounds within the interference zone. The interference zone is comprised of maxima and minima which extend to the range \((l)\) equals the reference distance \((l_o)\). The reference distance \((l_o)\) of the interference zone can be calculated as

\[
l_o = \frac{4 \cdot z_o \cdot z}{\lambda}
\]

where \(z_o\) is the depth of the source, \(z\) is the depth of the receiver and \(\lambda = c/f\), where
c is the sound speed and f is the frequency of the source Urick (1983). The maxima and minima positions are given by:

\[ I = \frac{I_o}{l^2} \cdot 2(1 - \cos(\pi \frac{l}{l_o})) \]  

(2.7)

where \( I_o \) is the free-field intensity. The intensity, I, will be zero at the nulls when \( l/l_o \) is equal to 1/2, 1/4, 1/6 and 1/8 and I will be approximately 6 dB greater than \( I_o \) when \( l/l_o \) equals 1, 1/3, 1/5, 1/7 (Urick, 1983). These calculations assume single frequency. For larger cetaceans who produce lower frequency (more tonal) sounds (with durations of the tens of seconds), signal intensity loss within a single call would be anticipated at the minima as calculated above. For instance, a large whale producing a 20 Hz signal for approximately 15 seconds could easily swim through the ranges of the maxima and minima in the interference zone which would alter the true intensity at points along a call (Berchok, 2004). Intensity changes within a call could potentially alter the TL term which is needed to correct for the attenuation in source level measurements (Malme, 1995). Assuming similar \( z_s \) and \( z_r \), smaller cetaceans could have a greater \( l_o \), due to the higher frequency of their sounds and usually shorter durations (e.g. 1 second). Therefore, assuming a killer whale pulsed call is 1.5 seconds in duration and at a frequency of 2 kHz. For a 10 m source and receiver depth, the \( l_o \) would equal approximately 530 m. Examining the ranges where the intensity is at a minima (1/2, 1/4, 1/6 and 1/8), the ranges would be 265 m, 132 m, 88 m and 66 m, respectively. Even if a killer whale was sprinting at 12 m/sec, it would not be able to swim through multiple positions of

\[ \text{Figure 2.16. Interference of signal at receiver due to Lloyd’s Mirror effect. This schematic shows the direct and reflected propagation paths from the source (S) arriving at the receiver (R) at depth z; S’ is the source image, } z_o \text{ is the source depth and } r \text{ is equal to the horizontal range from the source to the receiver.} \]
minimum intensities during the duration of a 1.5 second signal.

Lloyd’s Mirror interference on higher frequency (short duration) sounds would effect the signal if a moving animal is emitting a series of vocalizations over a span of tens of seconds. During the duration and range that the call sequence takes place, a decrease in a signal’s amplitude envelope would be expected (e.g. for one of ten calls) for single frequency sounds due to the animal passing through the range of a minima.

The effects of Lloyd’s Mirror interference was examined on one isolated animal moving in a relatively direct path. Since killer whale pulsed calls are broadband, spectrograms were examined for inconsistencies in amplitude along the same call type as the swimmer vocalized at various ranges from the hydrophone array. An encounter with the individual A12 was chosen because it was swimming in a relatively straight path and produced multiple N04 calls during the encounter at different ranges with respect to the location of the array. A spectrogram of one N04 call that A12 produced when she was located approximately 285 m from the array has been provided to highlight locations of lower energies within the sidebands of the N04 call (Fig. 2.17). The red circles indicate lower energy regions which could potentially be nulls due to Lloyd’s Mirror interference effect. Frequencies were determined at these low energy locations, $z_o$ was estimated to be 10 m, $z$ was 7-8 m and $c$ was assumed to be 1480 m/sec. In this spectrogram, locations of lower energy were examined at each of these lower energy locations to determine if these regions would exhibit nulls when $l/l_o$ is equal to 1/2, 1/4, 1/6 and 1/8. Nulls from each of the ten N04 calls produced by this one individual at the various ranges from the array were examined and compared. Results indicated that most of the nulls in the sidebands (1-3 nulls, if present) of the N04 calls for this analysis did not appear to be due to Lloyd’s Mirror effect.
Figure 2.17. Spectrogram showing low energy locations in sidebands of N04 call. Sidebands of N04 calls produced by the individual, A12, were examined at regions of low energy (red circles) to determine if these nulls in the signal were due to Lloyd's Mirror interference effects. The reference distance \((l_o)\) of the interference zone was determined by the frequencies of these nulls, \(z_o\) was estimated to be 10 m, \(z\) was 7-8 m and \(c\) was 1480 m/sec. Ten spectrograms in total were examined and compared as at different A12 source locations to the array.
Discrete Pulsed Call Variation

3.1 Introduction

Vocal communication is strongly influenced by the environment in which the sound is emitted. Though sound generally propagates farther in seawater than in air, there are a number of environmental factors which can attenuate or mask a signal as it travels from one location to another (Malme, 1995; Richardson, 1995; Urick, 1983). As sounds propagate they are subject to a loss of signal based on a number of physical properties attributed to the water column, sea surface and seafloor topography. Sounds are also subject to masking by abiotic (wind, rain, etc.), biotic (other animal sounds) and anthropogenic sounds which can decrease the signal-to-noise ratio of the aquatic environment (Brumm, 2004). It is beneficial for dispersed animals trying to communicate to produce sounds which are robust to signal degradation and complete masking within their environment (Bradbury and Vehrencamp, 1998). Animals can increase the amplitude of their sounds which would increase the propagation potential of the sound (Miller, 2006; Scheifele et al., 2005). In addition, they can adjust the frequency information within their calls or increase call rates to avoid being completely masked during noisy circumstances or adjust to optimal propagation conditions (Buckstaff, 2004; Foote et al., 2008; Jensen and Kuperman, 1983; Lesage et al., 1999; Parks et al., 2007).

Vocalizations are also an important means to locate other affiliated group members (or mates) (Deecke et al., 2005; Lachlan and Slater, 1999; Seyfarth and Cheney, 2003b), especially for species which traverse visually poor environments where group affiliates are readily masked by foliage, terrain or low light (Boinski, 1993; Byrne, 1981; Ford, 1989, 1991; Kudo, 1987; Miller et al., 2004; Poole et al., 1988; Seyfarth and Cheney, 2003b). Some of the spectral features of killer whale pulsed calls are a result of their anatomical
sound generation system (Cranford, 2000; Cranford et al., 1996). However, like many species, the spectral content of killer whale pulsed calls have the potential to contain an abundance of information (signaler’s arousal and energetic exertion, direction, individual and group identity), including contextual cues (movement change, behavior, prey capture, prey abundance, etc.) (Bradbury and Vehrencamp, 1998; Falls, 1982; Janik, 2000a; Marler and Hobbett, 1975; Miller, 2002; Notman and Rendall, 2005; Rendall et al., 1996; Sayigh et al., 1998; Seyfarth and Cheney, 2003b; Sousa-Lima et al., 2002). Discrete pulsed calls have a large bandwidth comprised of multiple sidebands, pulsed repetition rate information, modulated frequency and amplitude information, ‘two-voiced’ or biphonatic capabilities as seen in the higher frequency and lower frequency components, as well as some potential nonlinear features which may play a role in some pulsed call distinctiveness or excitedness (Filatova et al., 2007; Ford, 1989, 1991; Miller, 2002, 2006, 2007; Tyson et al., 2007). The ability of killer whales to encode multiple pieces of information into these calls would perhaps be the least costly tactic to transfer essential identity and behavioral information, while maintaining cohesion and group trajectory. Northern Resident killer whales routinely break apart their food and share it with two or three other killer whales which temporarily join that individual after a kill (Ford and Ellis, 2006). Hence, the joining of individuals may benefit other family members by increasing group fitness, along with maintaining overall group movement. The social culture of killer whales and their need to relocate family members on short-time scales (minutes, hours, a day) is a fundamental driving force for killer whales to similarly use vocalizations to initiate and sustain contact (Bigg et al., 1990; Ford, 1989, 1991; Miller et al., 2004; Yurk et al., 2002).

Animals can increase and diversify vocal complexity and call content by altering internal features within a call (Byrne, 1981; Notman and Rendall, 2005). Animals may vary acoustic parameters within a call to convey a contextual circumstance. For instance, structural variations within a single chimpanzee pant-hoot call, may serve variable intents to announce the arrival at a food site or elicit contact for re-joinings (Notman and Rendall, 2005). Similarly, Guinea baboons vary wahoo barks which occur during group feeding, cohesion, splittings and re-joinings (Byrne, 1981). Nightingales retain very large vocal repertoires, which have a hierarchical ordering beginning with the context groupings of sounds and ends at the element level within a song’s structure (Todt and Hultsch, 1998). Variations in acoustic features may also convey excitation or arousal states to receivers. Some animals appear to respond to the emotional expression of others (Seyfarth and Cheney, 2003a), though they may not be capable of assessing the
signaler’s mental state (Cheney et al., 1995). Variations in spectral content due to excitation is thought to be physiological and determined by how the animal’s sound generation mechanism adjusts under emotional heightened states. Hence, excitement or arousal can be considered any deviation from the norm, whether excitation is due to an amiable social event or a non-friendly combative circumstance. Baboons produce loud tonal-sounding, harmonic barks repeatedly when they are separated from other affiliates, however, their barks become more harsh or strident when predators have been detected (Fischer et al., 2001). Likewise, African elephant calls become lower in frequency and more strident in structure when animals are in the presence of a dominant animal (Soltis et al., 2005b). In addition, variations of acoustic features within a call may also follow a graded pattern of arousal (high or low urgency) depending on the species and the contextual circumstance (e.g. suricates/mongoose, humans) (Manser, 2001; Owren et al., 1997; Scherer, 1989; Seyfarth and Cheney, 2003b).

This analysis focused on the spectral content of a single discrete pulsed call (N04) produced by three pods (A1, A4, and A5) (Ford, 1989, 1991) and its usage during varying behavioral circumstances. An example of a typical N04 call has been provided in Fig. 3.1. Analysis began with examination of time-frequency slopes along the contour of the N04 call and the eventual parsing of the N04 call into four subtypes which will be discussed in detail. The main acoustic parameter, time-frequency slopes, was chosen based on observations of spectrograms of N04 calls. The second section of this analysis examined the distribution of energy along the duration of the N04 calls. The goal was to determine if the spectral content of the N04 call varied and whether usage was uniform across behavioral circumstances. Encoding multiple pieces of information in the spectral envelope of a call would increase signal complexity, and convey more specific or pronounced information to intended receivers. Usage patterns examined were a) acoustic attributes within N04 calls between subtypes; b) individual usage of subtypes; c) acoustic parameters within N04 subtypes during different behavioral contexts; d) N04 sideband energy between sidebands; and e) N04 parameters in varying social circumstances.

The N04 call was chosen for analysis because: N04 is a commonly used discrete pulsed call by the three A pods; N04 possesses acoustic characteristics which would be well-suited for long range propagation (Miller, 2006); increased production of N04 calls was observed prior to animals joining compared to after the animals had joined (Chapter 4); and matched calling of N04 calls was common during mother/offspring separations (Chapter 5). Research has shown that the Northern Resident killer whale N04 calls produced by signalers possess at least some distinctive acoustic parameters which could
convey reliable information to receivers (Nousek et al., 2006). The high frequency component of pulsed calls is thought to indicate the signaler’s directionality (Miller, 2002, 2007), while group-specific and identity information may lie within the higher and lower frequency components (Crance, 2008; Nousek et al., 2006). Discrete pulsed calls, like the N04 call, also appear to encode some gender-specific acoustic cues (Miller, 2007). In this thesis, the N04 call has been observed in a few circumstances where animals are dispersed beyond visual range from one another. It is expected that a prominent discrete pulsed call in a killer whale’s repertoire, like the N04 call, would contain acoustic parameters which would announce not only an animal’s identity or group affiliation, but also provide information on the signaler’s behavioral movement patterns. Though the N04 call is only one of many pulsed calls Northern Resident killer whales, it should have universal spectral features and nuances which would transcend to other pulsed calls. For instance, other pulsed calls may undergo frequency modulations during similar behavioral circumstances or the energy distributions of the N04 call may parallel those of other calls which would suggest some environmental influence. Having behavioral movement cues within

![Figure 3.1. Spectrogram of a typical N04 pulsed call. This call is representative of an N04 call produced approximately 20 years ago (Ford, 1987). The N04 call has a characteristic upsweep then downsweep at the start of the call, a uniform middle section and a terminal component. Figure from Ford (1987).](image)
a call would alert receiving animals’ to the signaler’s behavioral state, prey catch, desire to move to the next foraging sight, change in trajectory or desire to join with other group members (Bradbury and Vehrencamp, 1998; Falls, 1982; Marler and Hobbett, 1975; Rendall et al., 1996; Sayigh et al., 1998; Sousa-Lima et al., 2002). Furthermore, transmitting clear and reliable acoustic cues within a call would assist individuals (who produce group-specific vocals) to make the most accurate and advantageous behavioral or vocal response in order to orchestrate food sharing or maintain group cohesion (Ford and Ellis, 2006; Tyack, 2000).

3.2 N04 Subtypes and Acoustic Parameter Variation

N04 calls were initially separated into subtypes based on distinctive acoustic parameters located at the onset (hump), middle and end (tail) of the call. Fig. 3.2 shows five initial versions of the N04 calls that were produced by the three A clan pods. Signal parsing began by examining varying acoustic slope trends (Hz/sec), however, data analysis was not limited to these parameters. Initially in this analysis, the subtypes were named N04, followed by the subtype designator -1, -2, -3, -4 and -5 (e.g. N04-1, N04-2, etc.). For example, subtype N04-1 has a very distinctive, relatively narrow hump at the onset of the call which reaches well above 3 kHz for the second sideband (SB2) (second sideband from the bottom of the spectrogram), while the N04-2 subtype has a very broad hump (in duration), which is much flatter and lower in frequency (rarely above 3 kHz) than N04-1. The N04-2 is often much longer in total duration than N04-1, N04-5 and has an elongated descending frequency-time slope just post-hump compared to N04-1, which often descends rapidly to the middle section. Slope (Hz/sec) and other acoustic data (discussed in detail below) were then collected at the 6 segments and 7 points along each call (Fig. 3.3). Analysis frequency resolution was 23 Hz. Separation of the N04 subtype was then put through a discriminant analysis test to validate the parsing.

Before all the acoustic data were obtained from the N04 calls, the relative power spectral densities were examined at the 6 segments along the N04s to determine which sideband had the predominant energy over all the 6 segments (Fig. 3.3). For instance, if the second sideband had the most energy for 4 of the 6 segments then the spectral data information was collected on the second sideband (second from the bottom) (Fig. 3.4). Once the analysis sideband was determined, data (frequency, time and source levels) were obtained at 7 different data points located from the start to the end of the calls. Sideband Intervals (SBI), defined as the frequency difference between sidebands which is thought to
be representative of the repetition rate of the sound generation mechanism (Ford, 1989, 1991; Watkins, 1967) (Fig. 3.4), were also calculated. In addition, slopes and change in time were calculated for each of the 6 segments along the N04 subtypes. Total duration, maximum source level, frequency at maximum source level, and width of the hump (sec) at the call onset were also determined. Frequency and time information, as well as relative power spectral densities, were obtained from spectrograms using SpectraPLUS (Pioneer Hills Software). Source levels were calculated from power spectral densities in Matlab (The MathWorks, Inc.). Sounds were adjusted for acquisition bandwidth, the Hanning window, gain and transmission loss.

Slopes (Hz/sec) were then compared within segments using a Kruskal-Wallis test to validate variations within a slope between subtypes (see Appendix C for description and symbols). A non-parametric test was chosen since normality assumptions (particularly the skewness and kurtosis requirements) were not met. Dunn's post-hoc tests were run since the data distributions of the N04 subtypes varied in sample size (see Appendix C). All analyses were run in SPSS (Statistical Package for the Social Sciences, Inc.) and Matlab code. Post hoc tests (Qs) were calculated by taking the difference of the rank sums of each subtype in each segment and dividing them by the standard error (Jones, 2002) (Q values were then compared to the critical values).

Scatterplots of all acoustic parameters (frequency, change in time, slopes, SBIs, source level, hump-width, total duration, maximum source level, frequency at maximum source level) were then analyzed for variations with behaviors. Behaviors when N04 calls were produced were divided into two different analyses. First, N04 calls were grouped as being produced during foraging or traveling behaviors (other traditional behaviors were not included). Traveling is exhibited by unidirectional swimming at faster speeds than other behaviors, and synchronous swimming is often seen. Northern Residents travel, on average, 2.88 m/sec (between 1.81 - 5.66 m/sec), though they can sprint up to 12.0 m/sec for short periods (Ford, 1989). In this study, foraging means seeking, finding and feeding on prey. Foraging is usually multidirectional, generally slower than traveling (up to 1.6 m/sec), and accompanied by diving and other percussive behaviors (Ford, 1989; Osborne, 1986). Second, the surface swimming patterns of the animals were also examined within ninety seconds of the N04 call. All movements were categorized as either straight movement, single change in direction (‘turn’) or multiple changes in direction (‘multi-turn’). Straight swimming is a relatively direct movement path without major diversions. A single change in movement direction or turn, was approximately 30 degrees azimuthal or greater. Multiple changes in direction (‘multi-turns’) were defined as the
animal changing its direction (again, $30^\circ$ or more) multiple times. Scatterplots of the behaviors within each group (for each subtype) had to be staggered by approximately half the data to be considered eligible for analysis (i.e. the data for behaviors only overlapped each other by half or more). A Mann-Whitney U-test was used to analyze the data (see Appendix C) (McCrum-Gardner, 2008).
Figure 3.2. N04 pulsed calls separation into subtypes. N04 calls were initially divided into 5 subtypes based on slope trends (Hz/sec) within the first section of the call (hump), middle and tail of calls. Though N04 calls were originally subdivided based on slope information, while other acoustic data was collected and analyzed at the 7 points and 6 segments along the N04 calls.
Figure 3.3. Schematic of acoustic data points and segments taken along of N04 contours. Data obtained along the 7 contour points of the N04 call include frequency, duration, sideband interval and source levels. Slopes and time were calculated for each of the 6 segments along the N04 subtypes. In addition, total duration, maximum source level, frequency at maximum source level, and width of the hump at the call onset were also obtained.

Figure 3.4. Spectrogram showing sideband numbering and sideband intervals. This spectrogram of a N04 call (e.g. N04-2), which shows sideband numbering in white and sideband intervals in red. For example, SB1 is the first sideband or the lowest frequency sideband, SB2 is the sideband which is the second from the bottom, etc. Sideband interval (SBI) is the frequency difference between sidebands and is thought to represent the repetition rate of the sound generation mechanism. SBIs varies over the duration of the call, however, SBI measurements between sidebands is consistent between a given point (Pt) (SBI at Pt4 and Pt6 is shown).
3.2.1 Results

In this analysis, 199 calls qualified and were examined for the acoustic parameters (slope, time, frequency, etc.) collected at the six segments and seven inflection points along the N04 call (Fig. 3.3). The N04 call was divided initially into 5 subtypes based on frequency slope (Hz/sec) information along the contour of the calls. Call subtypes were then validated in a stepwise discriminant canonical analysis (Fig. 3.5) (also see Appendix C for description). Stepwise discriminant analysis is used to determine which variables differentiate between two or more groups. Function 1 was driven by slope segments along segments 3, 4 and 1 respectively, while Function 2 was driven by segment 6; 92.5% of the variance was explained by these two functions. Due to overlap, the original call subtypes N04-2 and N04-3 were combined and denoted as N04-2/3. An additional discriminant analysis was then re-run with the four subtypes indicated that 97% of the variance was explained by these same two functions (Fig. 3.6) (additional examples of N04 subtypes are shown in Appendix D). The distribution of the four N04 subtype overall occurrence and occurrence by pod are shown in Fig. 3.7, in the top and bottom graph respectively. N04 subtype usage appears to vary among pods. Subtypes 1 and 2/3 were produced by all pods (Fig. 3.7, bottom graph), while subtypes 4 and 5 were produced almost exclusively the A1 and A5 pods, respectively. All matrilines in these A pods contributed to the N04 subtypes seen here.
3.2.1.1 Acoustic Parameter Variation

The six slope segments along the N04 call were examined to see if they varied by subtypes (Fig. 3.3). The null hypothesis ($H_0$) was that pulsed call production was uniform within slope segments between N04 subtypes. Analysis of the six slope segments indicated that there were variations in slopes between the four N04 subtypes ($\alpha = 0.05, df = 198, X_{0.05,4-1}^2 = 7.815, p << 0.0001, H_0$ rejected). In Fig. 3.8, each graph represents results for each of the six slope segments (highlighted in the internal box with the red segment), while the x-axis represents the four different N04 subtypes. Though all the graphs were scaled to the same y-axis, all segments exhibited slope variations between subtypes. Dunn’s post-hoc tests were conducted to examine variations between subtypes within a segment which were influencing the significance found from the Kruskal-Wallis test (Table 3.1). Significant levels above a critical Q value of 4.10 are indicated with an asterisk (*). For some examples, at the onset of the call (Seg1), the N04-1 subtype had the sharpest positive slope and differed from all the other subtypes (-2/3, 4 and 5). N04-1 differed from all subtypes except N04-4 in Seg4, while only N04-4 and N04-5 differed from one another in Seg5. In the tail region (Seg6), N04-4 and N04-5 were distinctly

![Discriminant analysis of 5 N04 subtypes.](image)

**Figure 3.5.** Discriminant analysis of 5 N04 subtypes. A discriminant canonical analysis was run to validate the 5 subtypes seen in this study (denoted by numbers 1-5). Results indicate that 3 subtypes distinctly separated out (subtypes 1, 4 and 5), while N04-2 and N04-3 showed considerable overlap. Centroids of the data for each subtype is indicated by the black diamond and corresponding subtype number. Function 1 was driven by slope (Hz/sec) segments 3, 4 and 1 respectfully, while, function 2 was strongly influenced by segment 6; 92.5% of the variance was explained by these two functions.
Figure 3.6. Discriminant analysis of 4 N04 subtypes. A discriminant canonical analysis was run to validate the 4 subtypes seen in this study (denoted by numbers 1, 2/3, 4 and 5). The combination of subtype N04-2 and N04-3 were combined into subtype 2/3 for consistency. Centroids of the data for each subtype is indicated by the black diamond and corresponding subtype number. Function 1 was driven by slope (Hz/sec) segments 3, 4 and 1 respectfully, while, function 2 was strongly influenced by segment 6; 97% of the variance was explained by these two functions.

different from one another again, while also mostly varying from the other subtypes.

The scatterplots of the four subtypes along all 7 points and 6 segments were then examined for each of the nine acoustic parameters during varying behavioral contexts (behavior and overall swimming patterns) around the time the signaler produced the N04 call. If the criterion of data distributions was met (data in scatterplots had to be overlapped by less than 50%), statistical tests were run. For the tests, the null hypothesis ($H_o$) was that pulsed call production within a N04 subtype was uniform across behaviors or movements. Due to the spread of variations seen at the segments and points in this study for the nine acoustic parameters (Table 3.2), only one analysis was run for foraging versus traveling behaviors for sideband interval at point 5 (SBI5) for the N04-2/3 subtype (Fig. 3.9, Fig. 3.4). Of all the acoustic parameters analyzed, the SBI showed the least variability resulting in low and consistent standard deviations. In this analysis, the SBI trend for foraging ($\mu = 1122$ Hz, $n=25$) was equivalent for traveling ($\mu = 1081$ Hz, $n=52$) (Mann-Whitney U =483.0, $n=77$, $p=0.069$, $H_o$ not rejected).

N04 subtype usage was examined for matrilines and individuals (Table 3.3). Pods, matrilines (Mat), individuals (Indiv), total number of N04 calls produced (N), number of encounters occurred (No.Enc), number of subtypes produced (No.Subtypes), subtypes
produced (Subtypes), and occurrence of more than two subtypes by that individual in one encounter (2N04sub1Enc). A total of 27 individuals were isolated producing N04 calls from 3 pods and 8 matrilines. Of the 199 N04 calls analyzed, 111 were produced by individuals, the other 88 were produced by small groups (two or more animals swimming close together). A total of 16 of the individuals produced 2 or more subtypes, while 11 individuals produced two subtypes during a single encounter.

Figure 3.7. Overall occurrence of N04 subtypes and N04 subtypes by pod. The top graph depicts usage of four N04 subtypes. N04 subtype usage appeared to vary among pods (bottom graph). All three pods produced subtypes 1 and 2/3, subtype 4 was almost predominantly produced by the A1 pod and subtype 5 was mostly produced by the A5 pod. A1/A5 calls occurred when members from the A1 and A5 pods were swimming together.
Figure 3.8. Slopes of N04 segments (1-6) for the four N04 subtypes. Each graph represents variations in slopes (Hz/sec) within a given segment (1-6) for each of the four N04 subtypes on the x-axis (1, 2/3, 4, 5). Segments on the N04 call are illustrated in the little box in red within each graph (Fig. 3.3). Bars on the slope data represent the 95% confidence interval around the mean slope (Hz/sec).
Table 3.1. Dunn’s post hoc test’s for N04 slope analysis between subtypes. A post hoc test was performed for each slope segment (n=6) between the four N04 subtypes (Fig. 3.3, Fig. 3.8). In the first column the ‘1-2/3’ indicates comparison of N04-1 and N04-2/3 for the 6 different slope segments along the N04 call, while 2/3-5 is comparison of N04-2/3 and N04-5 subtypes. The * indicates values greater than the more conservative critical Q value of 4.10 for determining significance.

<table>
<thead>
<tr>
<th>Subtype Post Hoc (Q)</th>
<th>Seg1</th>
<th>Seg2</th>
<th>Seg3</th>
<th>Seg4</th>
<th>Seg5</th>
<th>Seg6</th>
</tr>
</thead>
<tbody>
<tr>
<td>1-2/3</td>
<td>5.4009*</td>
<td>3.9365</td>
<td>7.7428*</td>
<td>8.3184*</td>
<td>0.6306</td>
<td>1.4691</td>
</tr>
<tr>
<td>1-4</td>
<td>7.8007*</td>
<td>4.7773*</td>
<td>6.6846*</td>
<td>3.5503</td>
<td>2.5913</td>
<td>4.9641*</td>
</tr>
<tr>
<td>1-5</td>
<td>4.5906*</td>
<td>4.3237*</td>
<td>6.7797*</td>
<td>7.6108*</td>
<td>2.7918</td>
<td>5.5649*</td>
</tr>
<tr>
<td>2/3-4</td>
<td>3.7316</td>
<td>1.7579</td>
<td>0.5854</td>
<td>3.2168</td>
<td>3.2733</td>
<td>6.4895*</td>
</tr>
<tr>
<td>2/3-5</td>
<td>0.2458</td>
<td>1.2171</td>
<td>0.5632</td>
<td>0.9523</td>
<td>2.4234</td>
<td>4.6488*</td>
</tr>
<tr>
<td>4-5</td>
<td>2.9755</td>
<td>0.4827</td>
<td>0.0290</td>
<td>3.5364</td>
<td>4.8120*</td>
<td>9.4102*</td>
</tr>
</tbody>
</table>

Table 3.2. Analyzed N04 acoustic parameters during varying behaviors. Acoustic parameters were compared to see if data distributions in scatterplots overlapped by half or less. As indicated in this table as ‘no sig’, all other acoustic parameters did not meet the scatterplot overlap criteria, so no statistical tests were conducted. Only one test was run for SBI5 as seen in Fig. 3.9, however no significance was found.

<table>
<thead>
<tr>
<th>Parameter</th>
<th>Points</th>
<th>Segments</th>
<th>Forg/Trav</th>
<th>Movement</th>
</tr>
</thead>
<tbody>
<tr>
<td>Frequency (Hz)</td>
<td>1-7</td>
<td>-</td>
<td>no sig</td>
<td>no sig</td>
</tr>
<tr>
<td>SBIs (Hz)</td>
<td>1-7</td>
<td>-</td>
<td>no sig</td>
<td>no sig</td>
</tr>
<tr>
<td>Frequency at Max SL (Hz)</td>
<td>-</td>
<td>-</td>
<td>no sig</td>
<td>no sig</td>
</tr>
<tr>
<td>Slopes (Hz/sec)</td>
<td>-</td>
<td>1-6</td>
<td>no sig</td>
<td>no sig</td>
</tr>
<tr>
<td>Duration (sec)</td>
<td>-</td>
<td>1-6</td>
<td>no sig</td>
<td>no sig</td>
</tr>
<tr>
<td>Hump Width (sec)</td>
<td>2 and 4</td>
<td>-</td>
<td>no sig</td>
<td>no sig</td>
</tr>
<tr>
<td>Total Duration (sec)</td>
<td>1 and 7</td>
<td>-</td>
<td>no sig</td>
<td>no sig</td>
</tr>
<tr>
<td>SL (dB)</td>
<td>1-7</td>
<td>-</td>
<td>no sig</td>
<td>no sig</td>
</tr>
<tr>
<td>Maximum SL (dB)</td>
<td>-</td>
<td>-</td>
<td>no sig</td>
<td>no sig</td>
</tr>
</tbody>
</table>
Figure 3.9. N04-2/3 variation of sideband interval (SBI) at Pt5 during foraging and traveling (Fig. 3.3). The SBI trend during foraging ($\mu = 1122$ Hz, n=25) was equivalent to traveling ($\mu = 1081$ Hz, n=52). The red circle on the N04 call in the internal box indicates the location of Pt5 where data was taken. Since this is a SBI measurement it would be the difference in frequencies (Hz) for two adjacent sidebands at Pt5 (Fig. 3.4). Bars on the SBI data represent the 95% confidence interval around the mean SBI (Hz) (Mann-Whitney U, p=0.069).
<table>
<thead>
<tr>
<th>Pod</th>
<th>Mat</th>
<th>Indiv</th>
<th>N</th>
<th>No.Enc</th>
<th>No.Subtypes</th>
<th>Subtypes</th>
<th>2N04sub1Enc</th>
</tr>
</thead>
<tbody>
<tr>
<td>A1</td>
<td>A36</td>
<td>A32</td>
<td>1</td>
<td>1</td>
<td>1</td>
<td>1</td>
<td>-</td>
</tr>
<tr>
<td></td>
<td></td>
<td>A46</td>
<td>7</td>
<td>2</td>
<td>2</td>
<td>1,2/3</td>
<td>Y</td>
</tr>
<tr>
<td>A12</td>
<td>A12</td>
<td>A12</td>
<td>11</td>
<td>3</td>
<td>3</td>
<td>1,2/3,5</td>
<td>Y</td>
</tr>
<tr>
<td></td>
<td>A33</td>
<td>5</td>
<td>2</td>
<td>3</td>
<td>2</td>
<td>2/3,4,5</td>
<td>Y</td>
</tr>
<tr>
<td></td>
<td>A34</td>
<td>4</td>
<td>3</td>
<td>2</td>
<td>4,5</td>
<td>N</td>
<td></td>
</tr>
<tr>
<td></td>
<td>A55</td>
<td>9</td>
<td>4</td>
<td>3</td>
<td>1,2/3,4</td>
<td>Y</td>
<td></td>
</tr>
<tr>
<td></td>
<td>A62</td>
<td>2</td>
<td>1</td>
<td>1</td>
<td>4</td>
<td>-</td>
<td></td>
</tr>
<tr>
<td></td>
<td>A67</td>
<td>4</td>
<td>2</td>
<td>3</td>
<td>1,2/3,4</td>
<td>Y</td>
<td></td>
</tr>
<tr>
<td></td>
<td>A80</td>
<td>4</td>
<td>2</td>
<td>1</td>
<td>4</td>
<td>-</td>
<td></td>
</tr>
<tr>
<td></td>
<td>A83</td>
<td>4</td>
<td>1</td>
<td>2</td>
<td>2/3,4</td>
<td>Y</td>
<td></td>
</tr>
<tr>
<td>A30</td>
<td>A30</td>
<td>8</td>
<td>1</td>
<td>2</td>
<td>1,2/3</td>
<td>Y</td>
<td></td>
</tr>
<tr>
<td></td>
<td>A54</td>
<td>1</td>
<td>1</td>
<td>1</td>
<td>1</td>
<td>-</td>
<td></td>
</tr>
<tr>
<td>A4</td>
<td>A11</td>
<td>A11</td>
<td>4</td>
<td>2</td>
<td>2</td>
<td>1,2/3</td>
<td>N</td>
</tr>
<tr>
<td></td>
<td>A52</td>
<td>1</td>
<td>1</td>
<td>1</td>
<td>1</td>
<td>-</td>
<td></td>
</tr>
<tr>
<td></td>
<td>A70</td>
<td>6</td>
<td>2</td>
<td>2</td>
<td>1,2/3</td>
<td>N</td>
<td></td>
</tr>
<tr>
<td></td>
<td>A81</td>
<td>2</td>
<td>2</td>
<td>2</td>
<td>1,2/3</td>
<td>N</td>
<td></td>
</tr>
<tr>
<td>A4</td>
<td>A24</td>
<td>A24</td>
<td>7</td>
<td>2</td>
<td>2</td>
<td>1,2/3</td>
<td>Y</td>
</tr>
<tr>
<td></td>
<td>A64</td>
<td>3</td>
<td>1</td>
<td>2</td>
<td>1,2/3</td>
<td>Y</td>
<td></td>
</tr>
<tr>
<td></td>
<td>A71</td>
<td>5</td>
<td>2</td>
<td>1</td>
<td>2/3</td>
<td>-</td>
<td></td>
</tr>
<tr>
<td></td>
<td>A78</td>
<td>4</td>
<td>1</td>
<td>2</td>
<td>1,2/3</td>
<td>Y</td>
<td></td>
</tr>
<tr>
<td>A5</td>
<td>A8</td>
<td>A28</td>
<td>4</td>
<td>1</td>
<td>2</td>
<td>2,5</td>
<td>Y</td>
</tr>
<tr>
<td></td>
<td>A66</td>
<td>2</td>
<td>2</td>
<td>1</td>
<td>5</td>
<td>-</td>
<td></td>
</tr>
<tr>
<td></td>
<td>A23</td>
<td>A43</td>
<td>3</td>
<td>1</td>
<td>1</td>
<td>5</td>
<td>-</td>
</tr>
<tr>
<td></td>
<td>A60</td>
<td>1</td>
<td>1</td>
<td>1</td>
<td>5</td>
<td>-</td>
<td></td>
</tr>
<tr>
<td></td>
<td>A69</td>
<td>6</td>
<td>1</td>
<td>1</td>
<td>5</td>
<td>-</td>
<td></td>
</tr>
<tr>
<td>A25</td>
<td>A51</td>
<td>2</td>
<td>2</td>
<td>2</td>
<td>1,5</td>
<td>N</td>
<td></td>
</tr>
<tr>
<td></td>
<td>A61</td>
<td>1</td>
<td>1</td>
<td>1</td>
<td>5</td>
<td>-</td>
<td></td>
</tr>
</tbody>
</table>

3 Pods 8 Mats 27 Indiv 111 N04s 11(1),16(2-3) 11Y,5N

Table 3.3. N04 subtype usage by individuals. Pod, matriline (Mat), individuals (Indiv), total number of N04 calls produced (N), number of encounters occurred (No.Enc), number of subtypes produced (No.Subtypes), subtypes produced (Subtypes), and occurrence of more than two subtypes by that individual in one encounter (2N04sub1Enc). Bottom line highlights totals for number of individuals 27, 3 pods, 8 matrilines, 111 N04 calls (of the 199) were produced by individuals, 16 of the individuals produced 2-3 subtypes, 11 individuals produced 2 or more subtypes in 1 encounter (Y=yes, N=no).
3.3 Predominant Sideband Energy and Its Usage

N04 subtypes were examined to see which sidebands had the most overall energy. As previously mentioned, the most overall energy was determined to be the most number of segments which had predominant sideband energy compared to other sidebands. A binomial test was used to compare across all N04 calls if having more energy in the second sideband (SB2) occurred more often than in all other sidebands (non-SB2) combined (see Appendix C). Post hoc power of these binomial tests were calculated by a binomial or normal approximation based on the sample size and if the probability of the successes was near zero or one (Jones, 2002). Power is the strength of the statistical test and equals $1 - \beta$ (see Appendix C).

3.3.1 Results

The predominant energy in each sideband varied within a call as well as between calls (Fig. 3.10). Frequency-time contours were based on points taken at 7 locations along the call (Fig. 3.3). The lowest sideband in the spectrogram was defined as SB1 and then next up from the bottom is sideband 2 (SB2), etc. In Fig. 3.10 each contour represents the frequency-time data taken for only one N04 subtype call for all calls ($n=199$). In contrast to a typical spectrogram of a single killer whale call which displays one pulsed call with multiple sidebands, the contours seen here represent one contour for a single N04 call displayed at the sideband, which had the most energy across call segments (either SB1, SB2, SB3 or SB4). The null hypothesis ($H_0$) was that predominant energy for N04 calls was uniform between sidebands. Predominant sideband energy for all N04 calls was in the second sideband (SB2) ($\alpha = 0.05, n=199, p << 0.0001$, power $= 0.99$, $H_0$ rejected). In Fig. 3.10, for the N04-1 and N04-5 subtypes, most of the calls had energy predominantly in the second sideband (SB2) with only a few calls in each subtype having more energy in non-sideband 2 (non-SB2). Non-SB2 calls are defined as all calls which had predominant energy in either the first (SB1), third (SB3) or fourth sidebands (SB4). For example, N04-1 had five calls (non-SB2) which had more overall energy in SB1 ($n=3$) and SB3 ($n=2$). N04-5 had four calls in each SB1 and SB3, while the N04-2 calls were produced three times at SB1 and six times at SB3. In contrast, N04-2/3 and N04-4 subtype production varied in which sideband had the most energy. Only one call in one subtype (N04-2/3) had the most energy across segments in the fourth sideband (SB4).

Overall N04 calls were relatively equivalent across behaviors with N04 calls being produced 45.2% during foraging and 50.8% during traveling behaviors. In this study,
straight swimming was the predominant movement behavior (60.3%) where N04 calls occurred, (single) turns were the next most abundance at 30.6%, followed by multiple turns at 9.1%.

N04 SB2 and non-SB2 call usage was examined for variations in behaviors (foraging and traveling) and swimming patterns (turn, straight, multi-turn). For both analyses, the null hypothesis ($H_0$) was that N04 SB2 and non-SB2 usage was uniform. A Fisher’s Exact test indicated that N04 SB2 and non-SB2 were not equivalent between behaviors ($\alpha = 0.05, n = 191, p = 0.0379, H_0$ rejected) (Fig. 3.11) (see Appendix C). Nine N04 calls were not included in this analysis for they occurred during behaviors other than foraging and traveling. In addition, N04 SB2 usage occurred most often with straight swimming behavior (Fig. 3.12). These results indicate that SB2 is used more often during straight path traveling, than non-SB2 N04 calls.
Figure 3.10. Contours of the four N04 subtypes. Frequency-time information was taken at the 7 points along the contours of N04 calls on the sideband which had the most energy relative to other sidebands. In this figure, the sidebands shown represent sidebands where the energy was predominant (they do not represent the traditional sidebands of killer whale pulsed calls as seen in a single spectrogram). Sideband numbers are displayed in the upper righthand graph for the N04-1 call. For instance, nearly all the times the N04-1 subtype was produced the predominant energy was in the second sideband of the signal. In contrast, the N04-2/3 call more often occurred in the 2nd and 3rd sidebands and the N04-4 was more commonly produced in the 2nd and first sideband.
Figure 3.11. SB2 and non-SB2 N04 call production during foraging and traveling behaviors. N04 SB2 and non-SB2 call usage varied between foraging and traveling behaviors, with a slight trend of SB2 being produced during traveling.

Figure 3.12. SB2 and non-SB2 N04 call production around swimming behavior. N04 SB2 usage more often occurred while the signaler’s were swimming in a straight path.
3.4 Social Circumstances

3.4.1 Pre-joining Events

Pre-joining event N04 call usage was examined during variable behavior and swimming patterns, since it was one of the predominant pulsed calls prior to joinings. Three minutes was chosen for that was the maximum time it took for animals to join other individuals (see Chapter 4 for more in depth description). Joining is defined as the point when individuals and/or small groups converge within two body lengths of one another and proceed swimming together. Pre-joining event calls were examined during the three minutes prior to the actual joinings of the animals. Binomial tests were run to determine if N04 usage during behaviors and swimming movements were greater or less than the expected based on overall data distributions. Post-hoc power of these binomial tests was calculated by a binomial or normal approximation based on the sample size and if the probability of the successes was near zero or one (Jones, 2002).

3.4.1.1 Results

N04 call usage was examined within three minutes prior to joining events for behaviors (foraging versus traveling) and for movement course (turn versus all other, direct versus all other). For the behavior analysis, the null hypothesis ($H_0$) was that N04 usage during behaviors was uniform during pre-joining events. A binomial test revealed that N04 usage during foraging ($n=26$) were greater than what would be anticipated by a 50/50 chance (which is equivalent to a presence or absent of a behavior) ($\alpha = 0.05, n = 33, p = 0.0013, power = 0.95, H_0$ rejected). Three N04 calls were excluded during the behavior analysis since they were not produced during either foraging or traveling behaviors. For the swimming movement analysis, the first null hypothesis ($H_0$) was that N04 usage around turns was equivalent to the overall expected proportion of turn occurrences (0.306). A binomial test revealed that N04 usage during turns ($n=23$) were greater than what would be anticipated by a 30.6% chance ($\alpha = 0.05, n = 36, p < 0.0001, power = 0.99, H_0$ rejected). The second null hypothesis ($H_0$) was that N04 usage during straight swimming was equivalent to the overall expected proportion of 0.603. A binomial test revealed that N04 usage during direct course movement ($n=8$) were less than what would be anticipated by a 60.3% chance ($\alpha = 0.05, n = 36, p < 0.0001, power = 0.99, H_0$ rejected). Results here will be further explored in Chapter 4.
3.4.2 Mother and Offspring Separations

A comparison of energy in the sidebands to movement behaviors was examined when a mother and offspring are separated and when they were together. As in above, behaviors were divided into two groups, the first being foraging and traveling, and the second being turn, straight and multi-turn swimming movement. As in Chapter 5, a mother was considered separated from an offspring if the offspring was beyond visual range (greater than two body lengths), though usually beyond a hundred meters (see Chapter 5 for a more in-depth description). In this analysis, mother and offspring who were separated had to be within acoustic range of one another. Offspring (or non-adult animals) were considered together with their mothers if they were swimming nearby and sounds could not be accurately attributed to solo animals. Fisher’s Exact test was used for two-columns comparisons of behavior (foraging versus traveling), while the Freeman-Halton extension of the Fisher Exact probability test was used for a two-columns by three-columns contingency tests on swimming movements (see Appendix C).

3.4.2.1 Results

A comparison of energy in the sidebands to movement behaviors was examined when a mother and offspring were separated and when they were together. Calls were divided into N04 calls that had the most energy in the second sideband (SB2) and those N04 calls that possessed more energy in all other sidebands (non-SB2). The null hypotheses (\(H_0\)) for both the SB2 and non-SB2 analyses was that N04 call production during foraging and traveling were uniform when a mother was with her offspring and when she was separated from an offspring. A Fisher’s Exact showed that non-SB2 N04 call production during foraging and traveling were not equivalent when a mother was separated from an offspring and when she is with all of her offspring (\(n = 30, p = 0.0043, H_0\) was rejected). Non-SB2 N04 production was greater during foraging when mothers were separated from an offspring, while N04 call occurrence was low when mothers were together with offspring. In contrast, there was no difference found in SB2 N04 call production between foraging and traveling when a mother was separated or with her offspring (\(n = 82, p = 0.8206, H_0\) was not rejected). Based on these results, non-SB2 N04 calls may indicate a higher level of anxiety or arousal. For directional movement, the null hypotheses (\(H_0\)) for both the SB2 and non-SB2 N04 call production were uniform across movements when a mother was with her offspring and when she was separated from an offspring. Non-SB2 N04 call usage varied between directional movement tracks when a mother was separated from an offspring and when she was with all her offspring (\(n = 31, p = 0.0128, H_0\) was
rejected). However, N04 usage during SB2 N04 calls was uniform when a mother was with or without her offspring \((n = 89, p = 0.4371, H_o \text{ was not rejected})\). In the non-SB2 analysis, mothers with offspring either did not make or did not produce N04 calls around the time of single turns (as they did with the SB2 analysis). Results here will be further explored in Chapter 5.

3.5 Discussion

The potentially vast spectral information within killer whale discrete pulsed calls make them ideal candidates for cohesion calls based on distinctive acoustic parameters which would be recognizable to other individuals and would better withstand propagation conditions and signal masking (Andrew, 1962; Jensen and Kuperman, 1983; Miller, 2006; Richardson, 1995). This study investigated a commonly produced discrete pulsed call, N04, which was often observed during multiple killer whale group behaviors in other studies (Ford, 1989, 1991; Miller, 2002, 2006; Weib et al., 2007). The results presented here show that N04 calls are highly variable within their distinct and discrete spectral framework. N04 calls were divided into subtypes for the analysis based on repetitive and distinctive slope characteristics found throughout the call. Some forms of the N04 call were very distinctive in the hump region or start of the call, while others were more unique in the tail. Variability of data of other spectral parameters along the six segments and seven points was high, except in middle portion of the call. The ability for dolphins to discriminate between frequencies within a frequency modulated (FM) sound is extremely high and comparable to that of humans (Fay, 1974). Dolphins discriminate best between the frequencies of 2 to 55 kHz and can detect changes in frequency as little as 0.2 – 0.4% (Au, 2003; Jacobs, 1972; Thompson and Herman, 1975; Tyack and Clark, 2000). Hence, these killer whales should be able to differentiate between small shifts in frequency at least if the trend has a longer duration. Having acoustic cues within group-specific vocalizations would assist receivers in accurately assessing the signaler’s intent, whether that cue be to move to the next location or announce a prey capture. It is conceivable that some N04 subtypes are naturally more structured than others, so that differences in acoustic trends are more distinguishable than they would be in more variable N04 subtypes. Whether killer whales are able to differentiate more subtle slope trends within a single discrete call above and beyond individual information differences still remains to be seen. In addition, can any subtle differences that may convey information beyond pod affiliation and identity still exist if a call (e.g. N04) is undergoing a structural shift
or divergence as previously described (Deecke et al., 2000).

This study reveals that individual killer whales produced multiple subtypes of the N04 call, indicating that divergence in the N04 call is not the result of matrilineal or individual differences (Miller, 2000; Nousek et al., 2006), but rather may indicate the gradual evolution of a new stereotyped call (Deecke et al., 2000). Previously, acoustic parameters of pulsed calls were found to be more similar for the A1 pod between the A36 and A30 matrilines than either matriline was to the A12 matriline (Miller, 2000). In addition, research suggested a divergence of acoustic features in the N04 calls between the A12 and A30 matrilines over a period of thirteen years (Deecke et al., 2000). Individuals from the A12 matriline produced three to four different N04 subtypes (1, 2/3, 4, 5) while animals from the A36 and A30 matrilines only produced two subtypes (1 2/3). Potential subtypes which may indicate a gradual evolution of the N04 call would be subtypes 1, 4, and 5, while subtype 2/3 may be an intermediate stage. A12 matriline almost exclusively produced the N04-4 subtype, while the A5 pod mostly produced the N04-5 subtype. The N04-1 subtype may indicate an evolution of the call because it distinctly differs from all other three subtypes in the hump region of the call. The creation of new sounds by killer whales may arise from the divergence of an existing call type through physical characteristics of the environment, population dynamics or through vocal learning (Boughman and Wilkinson, 1998; Cleveland and Snowden, 1982; Cocroft and Ryan, 1995; Fuisz and de Kort, 2007). Adaptations of some acoustic parameters may accentuate the call or optimize transmission within the environment (Cleveland and Snowden, 1982; Jensen and Kuperman, 1983). The segments of the Northern Resident N04 call may be diverging at different rates as seen with anurans (Cocroft and Ryan, 1995). Vocal learning may also play a role in the shift of these sounds (Boughman and Wilkinson, 1998; Deecke et al., 2000). Adapting minor changes in animal calls is one way to increase repertoire size and vocal diversity (Snowdon, 1979). In addition, multiple usage of N04 subtypes by individuals within matrilines may serve some functional purpose and warrants further investigation.

Time-frequency slope variability of the N04 call within the middle region of the call (i.e. Seg5) was low compared to the other segments of the call. Pre-analysis observations of the N04 call produced from varying locations in Johnstone Strait revealed a tendency for the front and tail regions of the N04 call to degrade at longer ranges from the hydrophone array. The regions of the call which remained intact were from approximately Seg4 through Seg5 (Fig. 3.3). In this analysis, the middle segments of the call (Seg5) exhibited the least variability. It is conceivable that the N04 pulsed call and other
pulsed calls have portions which are less variable and would better withstand long-range propagation on which conspecifics could determine pod affiliations. Killer whales may also be able to adapt certain segments of their calls to frequencies more optimal to their local environment. Though this can not be examined here, optimal frequencies for the habitat can be found by collecting propagation conditions for Johnstone Strait. The longer duration of segment 5 compared to the other sections would also provide a reliable cue for detectability over range compared to shorter signals. Another possibility is that Seg5 may be produced at a frequency that is optimal for propagation conditions in Johnstone Strait, which would make it robust over distance. Hence, the middle uniform portion of the call may encode less information than the frequency modulated segments, but its uniformity in frequency may serve its own vital purpose if the frequency is optimal for the habitat. Once animals are within closer range, they would be able to detect more subtle information cues of individuals (size, gender, sound generation mechanisms etc.), arousal states or contextual circumstances located in others portions of the call (Deecke et al., 1999; Nousek et al., 2006). Many Northern Resident killer whale calls contain both uniform and frequency modulated segments, so observations here may be universal. Investigation in signal content should not be limited to focusing on variable acoustic parameters which are thought to encode more information, for consistent parameters may serve their own physical and biological importance to the animals.

Killer whales produce many of the pulsed calls in their dialects during most behaviors, though call proportions or usage has been seen to differ between varying behaviors or contextual circumstances (Ford, 1989; Shapiro, 2008). The use of context-specific vocalizations have yet to be found in killer whales, and there are several reasons why this may be. The first reason may be that resident killer whales have pod-specific vocalizations. The need to identify pod (or matriline) members to maintain group cohesion may be the first and most essential subdivision (or tier) in terms of overall group viability. Additionally, individuals may use pod-specific dialects to determine non-membership. Though no aggression has been documented between pod or matriline members or even between ecotypes (Ford et al., 2000), it is hypothesized that pod members use dialectal differences to choose mates outside their natal pods or clans. (Ford, 1989, 1991). Hence, maintaining the overall distinctive acoustic envelope of individual discrete pulsed calls in their repertoires would be essential. Second, since killer whales are at the top of the food web, risk of predation is minimal. Therefore, having a context-specific call, like alarm calls for many species, would not be necessary (Manser, 2001; Owren et al., 1997). That is not to say that some of the vocalizations that are unique to a single pod
are not context-specific, they are just produced so infrequently it is difficult to examine
them. Third, killer whales may be able to aurally resolve small-scale variations in a
call’s spectral envelope at least within closer ranges (e.g. differences in individual sound
generation mechanisms, arousal or contextual circumstances). Thus, the N04 call would
be a distinctive call over greater ranges which would be recognizable to pod or matriline
members to locate one another. However, within closer proximity of a kilometer or so,
more subtle individual, excitement or behavioral information may be reliably received.
Possessing fine scale acoustic variations that are aurally resolvable would assist animals
in maintaining contact (e.g. mother and offspring) and coordinating movements (e.g.
joinings). Most studies are limited in their design and data collection capabilities. Con-
tinued research and cumulative information on individual animal vocalizations coupled
with fine-scale behavioral observations would assist in targeting more subtle call usage
or variations in call structure during different behavioral movements if they exist (Miller,
2000; Shapiro, 2008). Not being able to identify the specific intent of a call does not
mean the call is devoid of information or that the rich content of a call (from the receivers
perspective) should be overlooked (Seyfarth and Cheney, 2003b).

The level of information transferred in a signal (either a specific call or variations
within a call) appears to vary among species and probably depends on several factors
such as group dynamics and predatory circumstances. Sound generation and the time
to produce vocalizations are costly to both signalers and receivers (Tyack, 2000). In
classical communication, the signaler is presumed to know something, which reduces
the receiver’s uncertainty so that the receiver can make a timely decision and respond
accordingly (Tyack, 2000). Vocalizing animals can relay information on their location,
direction of travel, identity, and often behavioral context or intent (Boinski, 1993; Janik,
2000b; Janik and Slater, 1998; Kudo, 1987; Notman and Rendall, 2005; Smolker et al.,
1993; Soltis et al., 2005a; Wilkinson and Boughman, 1998). Some calls like baboon ‘move’
grunts have a distinct intent, while infant grunts, which occur during varying behaviors,
are less informative and are thought to convey a friendly interaction (Cheney et al.,
1995). The Northern Resident killer whale N04 call is produced during several different
behavioral contexts. In this study, N04 was produced often during pre-joining events and
mother and offspring separations (see Chapters 4 and 5, respectively), both of which may
require discrete pulsed calls to maintain cohesion or coordinate movements (Ford, 1989,
1991; Miller, 2006). Even though the N04 call may not be used in a specific call context,
like dolphin bray calls (Janik, 2000b), it may be used in a more general context for
movement. Unlike the baboon ‘move’ calls which are highly informative, killer whales
may be able to extract enough information from signals to assess and coordinate their group’s movement (trajectory (swimming path), behavior, speed, etc.). For a prey-sharing population consisting of lifelong associations at the matrilineal level, exhibiting contextual cues within a call would assist family members in successfully locating one another in a timely manner so that food can be dispersed. The usage of N04 calls during both foraging and travelling implies no costs associated with prey alert, though fish may be able to detect particle velocity when killer whales are near. Additional costs for animals would be physical energetics of vocal production, the time committed to vocalizing when they are actively foraging or resting, risks of eavesdroppers being alert to prey location and lack of coordination of movements in situations such as joining for prey sharing (Deecke et al., 2005).

Knowledge of what was learned in the N04 acoustic parameter analysis can be applied to other calls from other pods. On a structural level, other calls can be examined to determine if calls have stable sections and less stable sections. Segments with little variability may maintain the stable characteristics of the signals which animals can recognize over long distances. Do calls produced by pods contain these stable segments and are these segments distinctly different from one another when isolated on their own? Are animals varying slope information regularly in some portion of the calls and not others? In an earlier study, the N04 call was found to diverge over a decade between the A12 and A30 matrilines, while the N09 remained stable (Deecke et al., 2000). Understanding both the stable and variable segments of a call and how the call varies with time, speaks to not only the evolutionary divergence of the call but potentially some functional context. Showing that multiple pods or matrilines all exhibit the same trends in vocal variability and stability, would further provide insight into how killer whale vocal repertoires evolve and how they may be using those calls.

Killer whales varying the energy distribution within a pulsed call may be due to different arousal states or to adapt to optimal frequency for propagation conditions (Jensen and Kuperman, 1983; Manser, 2001; Rendall, 2003; Scherer, 1989; Seyfarth and Cheney, 2003b). Some N04 subtypes had energy predominantly in SB2, while other subtypes varied the energy more among other sidebands (non-SB2). Some potential influences on energy distributions of sidebands could be age/sex class (and size) of individuals (Miller, 2007), while in other instances it may be due to some sort of arousal or varying level of urgency (Manser, 2001; Rendall, 2003; Scherer, 1989; Seyfarth and Cheney, 2003b). Examination of all N04 calls in this study indicated that SB2 and non-SB2 N04 calls varied between foraging and traveling behaviors. Call usage with SB2 N04 calls occurred slightly
more often during traveling. Interpreting whether animals are at a heightened arousal or level of urgency is difficult to assess, especially when behavioral observations are limited to animal surfacings. If SB2 is usually the more predominant sideband in terms of energy for the N04 call then any deviations from this norm could potentially be an increase in arousal or change urgency level. In terms of prey capture and prey-sharing, there may be excitement associated in a catch by either the signaler or the responding animal which would most likely result in acoustic feature differences within a call. Likewise, for socially tight mother/offspring groups there may be a heightened or shifted energy within the sidebands of vocalizations when they are separated compared to when they are together. Announcing excitation and urgency, however indirectly, would make the call more distinctive and more likely to elicit a response from conspecifics. In contrast, low arousal behavioral contexts, may be produced at lower frequency, common sidebands (like the baboon ‘move’ grunt) (Cheney et al., 1995). This analysis only touched on frequency differences in the N04 spectral content which may indicate changes in arousal. Though the predation of killer whales is low, killer whales have formed lifelong family groups which depend on the vitality of their individual members. Like the baboons, which exhibited a more strident, unstable internal call structures when separated from group members (Fischer et al., 2001), killer whales may also exhibit excitation or urgency when they are beyond visual range of family members. Arousal urgency may be graded with respect to age of the animal, with younger family members exhibiting greater variations in spectral content with excitation compared to older individuals. Further investigation on vocalizations at the individual level and how they are used contextually is essential to understanding and targeting these potential vocal nuances.

Another reason energy may be predominant in the SB2 and not SB1 may be due to filtering during sound production and in some species the lowest frequency band may be residual (Bradbury and Vehrencamp, 1998). The usage of SB2 may be the best suited frequency to pass through filters, the size and shape of the monkey-lip dorsal bursae may also play a role (Cranford et al., 1996). An argument supporting the use of SB2 over SB1 is that killer whale hearing at 2 kHz (location of SB2) is approximately 30 dB more sensitive than it is at 1 kHz (approximate location of SB1) (Szymanski et al., 1999). Producing sounds in a more sensitive hearing range would assist both signaler and receiver in effective communication.

An alternative hypothesis would be that animals have some control of the energy distribution in their calls. If killer whales are capable of selectively altering the energy distributions between sidebands within their calls, they may be able to distribute energy
in the frequency most suited to the current environment. Shallow water conditions are known to have optimal frequencies (Jensen and Kuperman, 1983). Animals are known to adapt vocalizations for long ranges, so it is feasible they could adjust energy distributions to more optimal conditions (O’Connell-Rodwell et al., 2000). This study is limited to a fixed location, so this analysis can not be conducted. However, obtaining vocalizations from the same animals and propagation conditions in a different region (e.g. off Queen Charlotte Islands, which is more open ocean), would provide insight toward whether killer whales can adjust the energy distributions in their sounds to better suit local propagation conditions.

In summary, this study reveals that individual killer whales produced multiple subtypes of the N04 call, indicating that divergence in the N04 call is not the result of matrilineal or individual differences (Miller, 2000; Nousek et al., 2006), but rather may indicate the gradual evolution of a new stereotyped call (Deecke et al., 2000). These findings indicate that the N04 call possesses distinct structural features that vary within its acoustic envelope. In two of the N04 subtypes (1, 2/3), variations in slope parameters of the N04 call were shared by the 3 A pods, while subtypes 4 and 5 may be more group-specific variants. The N04 call contained surprising internal variability with respects to behavior. An alternative hypothesis would be that measured variability is not biologically relevant or the key parameters in the call were not identified, to allow for correlation with behavior. Further research on the spectral content of calls produced by individual animals and their spectral resolution capabilities, would help to identify parameters that would be relevant and distinctive to the animals. Understanding of what does not degrade the signal would provide animals with confidence about which signal characteristics would most successfully be transmitted to receivers. Acoustic parameters more suitable for long range propagation would be higher intensity signals, lower frequency sounds, ample duration and using directivity to avoid boundary layer interactions (Kinsler et al., 2000; Miller, 2006; Urick, 1983). The N04 is a high amplitude signal that contains directionality cues (Miller, 2002, 2006, 2007); it was also found in this study to have predominant energy in its second to lowest sideband (SB2). Segment 5 of the N04 call was most consistent in time-frequency information between subtypes and was still visible on spectrograms outside the acoustic range of this study (from approximately 2-3 km away). Since shallow water propagation has optimal frequencies (Jensen and Kuperman, 1983), it is also conceivable that killer whales may adjust the energy distributions within their call to increase the efficiency of transmission (O’Connell-Rodwell et al., 2000).
Chapter 4

Intra-Group Joining Events

4.1 Introduction

Vocal communication plays an important role in the coordination and movement of many mammalian species in order to maintain overall group or intra-group (small groups within a larger group) cohesion. Specifically, vocalizations can coordinate group trajectory, changes in direction, progression to the next foraging site, spatial distributions needed for successful foraging, rapid group movement, and separations and re-joinings of individuals or small groups (Boinski, 1993; Ford, 1989, 1991; Janik and Slater, 1998; Kudo, 1987; Miller et al., 2004; Notman and Rendall, 2005; Poole et al., 1988; Shultz et al., 2003; Soltis et al., 2005a; Waser, 1977; Wilkinson and Boughman, 1998). Some species have one call which serve a single function. For example, wild mandrill baboon 2PG calls organize overall group coordination while ‘crow’ calls are used to maintain contact and join subgroups which had separated from the larger group during feeding (Kudo, 1987). White-faced Capuchin monkeys produce trills to initiate and redirect group movement, while ‘huh’ vocals were more abundant when individuals were within a food patch (Boinski, 1993). Some mammals produce specific food-associated vocalizations such as the greater spear-nosed bat and the cotton-top tamarins (Roush and Snowdon, 2001; Wilkinson and Boughman, 1998). Likewise, wild bottlenose dolphins produce bray calls when the dolphins feed on salmonids (Janik, 2000a). In contrast, structural variations within a single chimpanzee pant-hoot call, may serve variable intents to announce the arrival at a food site or elicit contact for re-joinings (Notman and Rendall, 2005). Similarly, Guinea baboons vary wahoo barks during group feeding, cohesion, splittings and re-joinings (Byrne, 1981). For some species, direct linkage of calls to usage are still being investigated but some vocalizations appear to elicit con-
tact of individuals spaced far beyond visual range. Antiphonal calling made by African elephants may facilitate contact with associated individuals or family members (Soltis et al., 2005a). Long-distance calls by Diana monkeys were followed by a decrease in inter-animal spacing and increase in traveling behavior (Shultz et al., 2003). While bottlenose dolphin signature whistles, which are thought to function as cohesion calls, were produced more often during separations (Janik and Slater, 1998; Smolker et al., 1993), and rarely, after animals had re-joined (Janik and Slater, 1998).

Individuals vocalizing to elicit contact or coordinate group movements also varies by species. For example, African elephant antiphonal calls are produced between affiliated females over varying ranges and also during reunions (Soltis et al., 2005a). The 2PG call is produced by only a few dominant male mandrill baboons to coordinate overall group trajectory, while crowing sounds are produced by female and juvenile groups during foraging dispersals and before their subsequent re-joinings (Kudo, 1987). In contrast, both adult female and adult male Capuchin monkeys appeared to direct group trajectory by producing several trill sounds while positioning themselves at the group’s leading edge (Boinski, 1993). Leading edge adult monkeys usually trilled several times over a few minutes before successfully changing the movement of all individuals in the group (Boinski, 1993). Furthermore, rhesus monkey infant contact calling behavior varied depending on their physical proximity to their mothers (Kalin et al., 1992). While cooing calls were more abundant when infants were isolated from their mothers, the production of infant ‘girn’ calls increased when mothers and infants were united.

There is a benefit for animals to recognize not only the contact call but also individuals or social affiliates producing that call (Boughman and Moss, 2003; McComb et al., 2000). It would be costly if an animal traveled long distances to the location of where a contact call was produced just to find it was produced by a copycat or unwanted individual (Boughman and Moss, 2003; Tyack, 2000). Hence, individual identity features in calls help aid animals in correctly identifying affiliated animals. Also, many animals preferentially exchange vocals with affiliated animals and not animals they only occasionally encounter. Female African elephants have been seen to travel long distances in response to an affiliate’s call, even ones they have not seen in years (McComb et al., 2000); they are also more than two times as likely to respond to affiliated group members than non-affiliated group members (Soltis et al., 2005a). The search for and consumption of food is another instance where correctly identifying and responding to contact or cohesion calls would be beneficial for animals (Boinski, 1993; Janik, 2000a; Roush and Snowdon, 2001).
Most of the aforementioned species reside in visually poor environments where group affiliates are visually masked by foliage, terrain or low light. Consequently, similarities exist between the continuously changing movement patterns of these species to those of killer whales, despite notable differences in habitat or group social dynamics (Boinski, 1993; Byrne, 1981; Ford, 1989, 1991; Kudo, 1987; Miller et al., 2004; Poole et al., 1988). Moreover, many of these mammalian group-living species must disperse into smaller sub-units spaced beyond visual range to increase foraging success and overall group viability (Boinski, 1993; Byrne, 1981; Kudo, 1987). Killer whale matrilines are socially cohesive units within pods where affiliations are lifelong (Bigg et al., 1990; Ford, 1989, 1991). The social bonds of sharing species that disperse would also be a fundamental driving force for killer whales to use vocalizations to initiate and sustain contact to maintain overall group fitness (Bigg et al., 1990; Ford, 1989, 1991; Ford and Ellis, 2006; Miller et al., 2004; Yurk et al., 2002), order to rejoin.

Northern Residents killer whales, located in coastal waters of British Columbia, have longterm vocal traditions with each pod having its own dialect comprised of discrete pulsed calls (Ford, 1989, 1991; Yurk et al., 2002). The population dynamics within this region (unrelated and related individuals, fish-eating and mammal-eating communities) have most likely increased the complexity of call structure, as well as, the diversity and size of group-specific repertoires (Ford, 1989, 1991). Discrete pulsed calls (dpcs) are a reasonable candidate for maintaining group cohesion for the following reasons (Andrew, 1962; Ford, 1989, 1991; Miller, 2002, 2006): 1) dpcs are killer whales’ predominant pulsed vocalization during longer range behaviors; 2) dpcs are stereotyped and group-specific which would make them recognizable to family members; 3) the spectral content of dpcs contain a wealth of information (wide bandwidth, bi-phonation, high source level, multiple sideband and sideband interval information, modulated frequency and amplitudes as well as ample durations) which could provide the receiving animal with details of a signaling animal’s identity, pod affiliation, behavioral movement and directionality; and 4) dpcs would be more robust against propagation degradation of the call over greater ranges than highly directional clicks and lower source level, narrow band whistles.

This analysis focused on a movement pattern which can be considered a key portion of maintaining group cohesion: joining events. Call production prior to and after joining, call types, vocal exchange type and who initiated contact are explored. The goal of this study was to determine if killer whale calling behavior varied pre- and post- joining events. This analysis examined if a) discrete pulsed call rates vary between pre- and post-joining events of individuals and small groups (post-joining events would be after the
individuals have joined); b) vocalizations pre-joining are one-way signaling or two-way vocal exchanges between joining individuals; c) the initiator of pulsed calls are consistent over different group sizes; d) call type production varied during joining events and e) N04 usage during different behaviors prior to animals joining. It would be expected that pulsed call production would be greater prior to than after joining events for a number of reasons (Janik and Slater, 1998; Smolker et al., 1993). First, if food sharing is one driving force for the physical intra-group joining events which are occurring (Ford and Ellis, 2006), some vocal (or behavioral) indicator would be expected which would announce an abundant food supply or successful catch (Boinski, 1993; Janik, 2000b; Roush and Snowdon, 2001; Wilkinson and Boughman, 1998). Second, after joining the need to make contact would be minimized because animals would be in physical or visual contact of one another (Janik and Slater, 1998). Third, after joining individuals may be focusing energy on consuming prey or reacquainting with one another socially after separations where tactile or visual cues may predominate over vocalizations. And finally, after joining opting for lower amplitude, shorter distance pulsed calls or whistles would be more efficient and possibly customary behavior when animals are within close proximity to one another.

Although this analysis can not identify who catches the prey or which joining events result in prey shares or some other group motivator (Ford, 1989, 1991; Ford and Ellis, 2006; Miller et al., 2004), it can examine the type of vocal exchanges and who is initiating contact prior to joining events. It would be expected that two-way exchanges would occur more often than one-way signaling for both parties would be relaying and receiving useful identity and behavioral information. For example, each party involved in a joining event would, at least, be able to assess the other’s location and trajectory (especially with repeated exchanges) so that joinings can be successfully orchestrated. The social culture of killer whales provides a strong driving force for individuals to locate one another (Ford, 1989, 1991; Yurk et al., 2002). Vocal exchanges between individuals of a prey sharing population would benefit both the signaler and the receiver. In addition, some instances such as abrupt changes in direction may warrant a two-way vocal exchange compared to just one individual vocalizing. Vocal initiators may be strong indicators of social motivation or roles which individuals may have within group behavioral dynamics. Individuals, or solo swimming animals, would be expected to initiate pulsed call prior to joining events compared to small groups for a few reasons. First, solitary individuals would need to maintain social contact more than individuals in small groups, who are already swimming with affiliate(s). Second, animals in small groups, such as mother and
offspring, may be involved in social behaviors necessary for offspring development and, therefore, may be temporarily distracted. For instance, a mother may be nursing a calf or socializing along with multiple offspring. In this instance, close proximity vocalizations (whistles and low amplitude pulsed calls) may be abundant (Ford, 1989; Riesch et al., 2006), while longer range, higher amplitude pulsed calls to non-mother groups might be minimized to focus their energy on the present intra-group behavior. In either case, actively foraging individuals or small groups may be temporarily preoccupied and not produce vocalizations until the actual prey catch. Consequently, if prey sharing is one motivation for joinings, the killer whale(s) capturing the prey are the most likely candidates to be announcing the catch to others. For example, vocal contact can be a direct announcement of a catch or food source by using food-specific sounds (Janik, 2000b; Roush and Snowdon, 2001; Wilkinson and Boughman, 1998), identity cues encoded within non-specific vocals (Boughman and Moss, 2003; Nousek et al., 2006) or a transfer of information like echolocation on which others could eavesdrop (Boughman and Moss, 2003; Gregg et al., 2007; Tyack, 2000). Since only a couple of individuals were observed swimming to the individual who captured the prey (Ford and Ellis, 2006), and salmon are not a schooling fish, announcement of a catch, and subsequent prey sharing, may strategically be reserved for select animals to sustain overall group viability. In addition, joinings due to food sharing, may require some two-way exchange so the individual or small group who captured the prey would know whether or not to consume the catch or wait to share it with family members.

4.2 Calling Exchange Behavior

4.2.1 Call Rates

Joining events were defined as two or more individuals or small groups (2 or more individuals) converging at the same location who then proceeded to swim together. This analysis includes obvious joinings (change in direction, speed) of killer whales, as well as more subtle convergings. Pulsed call production was examined for three minutes pre- and post-join events. Post-joining events are when the animals have joined and they swim together for at least three minutes. A three minute window was chosen because that was the amount of time it physically took the killer whales farthest from a joining event to reach their destination. Only join events that met both the three minute pre- and post-joining durations were analyzed. Additionally, due to the fixed locale of this study, only small group joining events (e.g. a few individuals within a matriline or pod)
were examined. Sometimes encounters had multiple joining events, but, for this analysis, only one event was examined during an encounter for each group of joining individuals. Individuals or small groups of animals were considered joined once they were within two adult body lengths (approximately 20-25 m) because they were within visual range or could see fresh fluke movements in the water. All individuals (adult males, adult females, juveniles and calves) were considered in this analysis. The rate of pulsed call production (calls/minute) was calculated for each pre- and post- join event. Due to the dependency of the pre- and post- categories around a single event, a paired t-test ($\alpha = 0.05$, two-sided) was conducted on all joinings (see Appendix C for description and symbols). Data were square-root transformed to meet normality assumptions and variances were examined for equality. The power ($1 - \beta$) for the t-test was also calculated (see Appendix C).

4.2.1.1 Results

Forty-three joining events with pulsed calls were examined in this analysis. A total of 35% (15/43) of events contained only discrete pulsed calls in the three minutes prior to joinings, while only 7% (3/43) had no discrete pulsed calls. The remaining 58% of pre-join events were discrete pulsed calls with at least 1 or more click bouts, whistles or non-stereotyped pulsed calls. Mean discrete pulsed call proportions over the total number of events was 68% of all vocals prior to and 35% after joining events. The occurrence of click bouts rates had a mean of 28% prior to joinings and 12% post-joinings. While whistle and non-discrete pulsed call mean proportions over the total number of events combined was 3.7% during pre-joinings and 4.8% during post-joinings. Animals were completely silent for 47% (20/43) of events following joinings (i.e. during the three minute post-join period). Presence and absence of these three different vocal types (pulsed calls, click bouts and whistles was also examined) were compared between pre- and post-joinings. Pulsed calls were present more often during pre-joinings (40/43) than post joinings (18/43) ($\text{sign test, df = 43, p } < < 0.0001$) (see Appendix C); click bouts were present in 27/43 pr-join events and 13/43 post-joinings ($\text{sign test, df = 43, p = 0.007}$); and whistles were present 13/43 prior and 5/43 post ($\text{sign test, df = 43, p = 0.039}$). All individuals (adult males, adult females, juveniles and calves) were involved in the joining events seen in this study.

Rates of call occurrences were calculated per minute for each joining events. The null hypothesis ($H_0$) was that pulsed call production was uniform during pre- and post-joining events. Pulsed call rates were found to be greater pre- compared to post- joining
events as seen in the paired t-test results ($\mu = 0.77369, \sigma = 0.86359, \alpha = 0.05, df = 42, t = 5.875, p << 0.0001$), $H_0$ was rejected) (Fig. 4.1). Bars surrounding the mean represent the 95% confidence intervals. The power ($1 - \beta$) of the t-test was calculated to be 0.99. The mean of pre-joining pulsed call rates was 1.2708 calls/min compared to 0.4971 calls/min for post-joinings, which is approximately 2.1 calls/min compared to 0.64 calls/min, respectively, prior to the square-root transformation.

4.2.2 Vocal Exchanges

Call exchanges were examined to determine if calling during pre-joining events was one-way signaling or two-way vocal exchanges. Calls were considered one way signals if only one individual or small group involved in a joining produced a discrete pulsed call prior to re-joinings. Likewise, a two-way vocal exchange was one in which both joining individuals produced discrete pulsed calls in the three minute interval prior to joining events. In addition, killer whales that initiated pulsed calls during pre-joining events were grouped into two categories for analysis: solitary or small group. Solitary individuals were individuals which are travelling alone at a distance large enough to distinguish from other individuals, usually greater than 100 m. Small groups who swam together during an encounter, usually 2-25 m apart. Isolated vocalizations of individuals within a small
group could not be localized due to the inter-animal spacing, so all calls were attributed to that small group. A binomial test was used to examine whether individuals or small groups initiated calls more often. Post hoc power of these binomial tests were calculated by a binomial or normal approximation based on the sample size and if the probability of the successes was near zero or one (Jones, 2002).

4.2.2.1 Results

A total of 39 of the 43 join events had discrete pulsed calls during pre-joining events (the one event with many N03 calls was not included). The null hypothesis ($H_0$) was one-way signaling was equal to two-way vocal exchanges during pre-joining periods. A binomial test revealed that two-way exchanges (29 events) were greater than what would be anticipated by a 50/50 chance ($\alpha = 0.05, n = 39, p = 0.0034, power = 0.88, H_0$ was rejected). In one-way signaling ($n=10$), the $9/10$ of the cases involved intra-matriline joinings.

This study also examined whether solitary swimming animals or small groups initiated calls prior joining. The only events analyzed were pre-joining events with pulsed calls which involved a solitary animal and a small group, which constituted 23 of 43 events previously examined. The other 20 events involved either two single animals or two groups changing, so they were not included. The null hypothesis ($H_0$) was that solitary animals and small groups uniformly initiated pulsed call contact during pre-joining events. In a binomial test, solitary animals were found to initiate pulsed calls more often than small groups ($\alpha = 0.05, n = 23, p = 0.035, power = .61, H_0$ was rejected) by a ratio of approximately 3:1. All types of individuals initiated calls.

4.3 Call Type Usage

This analysis examined which call types were used during the three minutes pre- and three minutes post-joining events. For the analysis only calls which were seen in a minimum of five joining events were considered. A minimum of five joining events was chosen to obtain a stronger mean; most of the other calls were only seen in a one or two events. The means of the call type rates (call type/minute) were calculated and compared using a paired t-test ($\alpha = 0.05$, two-sided). Data were square-root transformed to meet normality assumptions and variances were examined for equality. The power for the t-test was also calculated.

The proportion of call type production during pre- and post-joining events were
examined using a one-way goodness-of-fit test. Two tests were conducted, one with the shared calls of the three A pods (A1, A4, A5) and one for calls made by the I11 pod. The test proportions of call type production were considered uniform in the one-way goodness-of-fit tests. Since it is not known which contexts are driving the hierarchy of call production as seen in previous studies (Ford, 1989; Weib et al., 2007), and call rates vary with behavioral conditions or excitement (Ford, 1989), equivalent test proportions were chosen (i.e. each observed value was compared to a single expected value).

4.3.1 Results

Twenty-two discrete pulsed call types were recorded during the three minutes pre- or post-join events. Only seven of the twenty-two calls observed qualified for the analysis criterion of five or more join events (e.g. N03, N04, N05, N09, N23, N24, N25). The mean call type rates (call type/min) were compared using a paired t-test (n=7), to determine if there was variation in call type usage. The null hypothesis ($H_0$) was that individual discrete pulsed calls were uniform pre- and post-joining events. One outlier was removed from this analysis due to the over abundance of N03 calls within a single event (thirty N03 calls). The outlier was approximately 2-3 times greater than any call type occurrence in any joining event and was removed based on Chauvenet’s Criterion (Coleman and Steele Jr, 1999). Chauvenet’s Criterion defines an acceptable data scatter, based on probability, which provides guidelines for reasonable data point elimination. The analysis showed that mean call type rates varied between pre- and post-joining events for most of the call types ($\mu = 0.48563, \sigma = 0.14076, \alpha = 0.05, df = 6, t = 9.128, p < 0.0001, power = 0.99, H_0$ was rejected) (Fig. 4.2). All potential long range calls (N04, N05, N09, N23, N24, N25) exhibited an increase in production prior to joinings, while the one short range pulsed call, N03, showed no difference between pre- and post-joinings. Additionally, Fig. 4.2 also indicates that killer whales are not exclusively using a specific call type(s) prior to joining events.

The abundance of discrete pulsed call types seen during the 43 encounters was examined using a one-way goodness-of-fit test to determine if call type usage differed from expected during pre-joining events (see Appendix C). The call types which the 3 A pods (A1, A4, A5) share are presented first (total of 128 calls in 29 joining events), then the calls made by the I11 pod (total of 87 calls in 10 joining events). These tallies include all discrete pulsed calls which occurred during pre-joining events. For the A pod analysis, the N02 and N07 calls were included as their own entities since they often vary in call rate across behaviors (Ford, 1989). In addition, all other calls produced at
Figure 4.2. Seven major discrete pulsed call types during pre- and post-joining events. Mean of seven predominant discrete pulsed calls present during pre- and post-joining events. All seven calls occurred in five or more join events. Bars represent 95% confidence intervals. The rate of most of the calls, were greater during pre- than post-joinings. However, there does not appear to be any specific pulsed call, which predominated during pre-joinings.

low rates were included for each analysis under ‘Other’ category. The null hypothesis ($H_0$) for both tests was that call production was equivalent across call types (Table 4.1). The goodness-of-fit test for the 3 A pod calls revealed a disproportional increase in N09 calls (86%) and N04 calls (113%) during pre-joining events, and less than expected abundance of N03 and N07 calls ($\chi^2 = 58.93, df = 6, \chi^2_{0.05,7-1} = 12.592, p < 0.0001, H_0$ was rejected). The goodness-of-fit test for the I11 pod calls revealed a disproportional increase in N25 calls (70%), while N24 call was lower than anticipated ($-59\%$) ($\chi^2 = 16.1, df = 3, \chi^2_{0.05,4-1} = 7.815, p = .0001, H_0$ was rejected) (Table 4.2). Standardized residual values greater than 2 were considered high. All three calls (N04, N09 and N25), which were elevated prior to joinings, were produced throughout three minute interval prior to joinings, starting from approximately the three minute point to immediately before joinings (10-30 seconds). In the events when N09 calls were present, 91% (15.5/17) of those events showed that N09s were produced prior to joinings, while only two events had N09 calls after animals had joined (9%) (1.5/17) (ratios were assigned when a call (e.g. N09) was produced in both pre- and post- of a single joining event with
each call given a count of 0.5 instead of 1). In the events when N04 calls were present, 79% (13.5/17) of those events showed that N04s were produced prior to joinings, while events with N04 calls were 21% (3.5/17). In the events when N25 calls were present, 71% (5/7) of those events showed that N25s were produced prior to joinings, while events with N25 calls occurred 29% (2/7) post-joining. The N25 call occurred more often in post-joining events compared to the N09 call.

<table>
<thead>
<tr>
<th>Call Type</th>
<th>Observed</th>
<th>Expected</th>
<th>Expected Prop.</th>
<th>Deviation (%)</th>
<th>Std. Residuals</th>
</tr>
</thead>
<tbody>
<tr>
<td>N02</td>
<td>4</td>
<td>18.28</td>
<td>0.1428</td>
<td>-78.12</td>
<td>-3.34</td>
</tr>
<tr>
<td>N03</td>
<td>10</td>
<td>18.28</td>
<td>0.1428</td>
<td>-45.3</td>
<td>-1.94</td>
</tr>
<tr>
<td>N04</td>
<td>39</td>
<td>18.28</td>
<td>0.1428</td>
<td>+113.11</td>
<td>+4.84*</td>
</tr>
<tr>
<td>N05</td>
<td>16</td>
<td>18.28</td>
<td>0.1428</td>
<td>-7</td>
<td>-0.3</td>
</tr>
<tr>
<td>N07</td>
<td>7</td>
<td>18.28</td>
<td>0.1428</td>
<td>-61.71</td>
<td>-2.64</td>
</tr>
<tr>
<td>N09</td>
<td>34</td>
<td>18.28</td>
<td>0.1428</td>
<td>+85.79</td>
<td>+3.67*</td>
</tr>
<tr>
<td>Other</td>
<td>17</td>
<td>18.28</td>
<td>0.1428</td>
<td>-7</td>
<td>-0.3</td>
</tr>
</tbody>
</table>

Table 4.1. Call type occurrence during pre-joining events for the three A pods. This table only represents call types that are shared by the three A pods. Both the N09 (+85.79%) and N04 (+113.11%) calls were higher expected based on the goodness-of-fit test (high residual values were values over 2). The observed value, expected value, expected proportion, deviation (%) and standardized residuals (std. resid.) of the test have been provided. The ‘Other’ category is a tally of the remaining calls shared by all 3 A pods observed in this study (N08, N10, N11, N12).

<table>
<thead>
<tr>
<th>Call Type</th>
<th>Observed</th>
<th>Expected</th>
<th>Expected Prop.</th>
<th>Deviation (%)</th>
<th>Std. Residuals</th>
</tr>
</thead>
<tbody>
<tr>
<td>N23</td>
<td>26</td>
<td>21.75</td>
<td>0.25</td>
<td>+19.54</td>
<td>+0.91</td>
</tr>
<tr>
<td>N24</td>
<td>9</td>
<td>21.75</td>
<td>0.25</td>
<td>-58.62</td>
<td>-2.73</td>
</tr>
<tr>
<td>N25</td>
<td>37</td>
<td>21.75</td>
<td>0.25</td>
<td>+70.11</td>
<td>+3.27*</td>
</tr>
<tr>
<td>Other</td>
<td>15</td>
<td>21.75</td>
<td>0.25</td>
<td>-31.03</td>
<td>-1.45</td>
</tr>
</tbody>
</table>

Table 4.2. Call type occurrence during pre-joining events for the I11 pod. The N25 call was significantly higher (+70.11%) than anticipated based on the goodness-of-fit test (high residual values were values over 2). The observed value, expected value, expected proportion, deviation (%) and standardized residuals (std. resid.) of the test have been provided. The ‘Other’ category is a tally of the other I15 calls produced at low rates during pre-joinings (N26, N30, N41, N46).

For completeness, the same analyses as above were run on post-joining pulsed call production for the same pods, despite low sample sizes and expected values. The null hypothesis (\( H_0 \)) for both tests was that call production was equivalent across call types. The goodness-of-fit test for three A pods revealed there was no difference found between call type usage after animals had joined (\( \chi^2_{0.05,7-1} = 12.592, p = 0.0983, H_0 \) not rejected) (Table 4.3). Likewise, the goodness-of-fit test for the I11 pod post-joining calls showed no variation (\( \chi^2 = 6.29, df = 3, \chi^2_{0.05,4-1} = 7.815, p = 0.101, H_0 \) not rejected) (Table 4.4).
Table 4.3. Call type occurrence during post-joining events for the three A pods. This table only represents call types that are shared by the three A pods. Both the N09 (+85.79%) and N04 (+113.11%) calls were higher expected based on the goodness-of-fit test (high residual values were values over 2). The observed value, expected value, expected proportion, deviation (%) and standardized residuals (std. resid.) of the test have been provided. The ‘Other’ category is a tally of the remaining calls shared by all 3 A pods observed in this study (N08, N10, N11, N12).

Table 4.4. Call type occurrence during post-joining events for the I11 pod. The N25 call was significantly higher (+70.11%) than anticipated based on the goodness-of-fit test (high residual were values over 2). The observed value, expected value, expected proportion, deviation (%) and standardized residuals (std. resid.) of the test have been provided. The ‘Other’ category is a tally of the other I15 calls produced at low rates during pre-joinings (N26, N30, N41, N46).
4.3.1.1 N04 Usage During Behavioral Movements

N04 call usage was analyzed and discussed at the end of Chapter 3 and will be reexamined in this chapter for completeness. In Chapter 3 a binomial test revealed that N04 usage during foraging ($n=26$) was greater than what would be anticipated by a 50/50 chance ($\alpha = 0.05$, $n = 33$, $p = 0.0013$, $power = 0.95$, $H_0$ rejected). A binomial test revealed that N04 usage during single turns ($n=23$) was greater than what would be anticipated by a 30.6% chance ($\alpha = 0.05$, $n = 36$, $p < 0.0001$, $power = 0.99$, $H_0$ rejected) and that usage during direct course movement ($n=8$) were less than what would be anticipated by a 60.3% chance ($\alpha = 0.05$, $n = 36$, $p < 0.0001$, $power = 0.99$, $H_0$ rejected).

4.4 Discussion

Killer whale discrete pulsed calls have been hypothesized to maintain group cohesion (Ford, 1989, 1991), but specific usage of these calls in relation to animal movements (trajectory, orientation, joinings, etc.) is not well known (Miller, 2006; Shapiro, 2008). This study investigated pulsed call usage by individuals and small groups involved in joining events (pre- and post-). The results presented here (increased pulsed call rates and two-way vocal exchanges) strengthen the hypothesis that discrete pulsed calls play an important role in intra-group cohesion of a few individuals. Furthermore, not only were pulsed call rates lower after animals had joined, animals were silent in approximately 47% of all events after joinings. Joining events are a complex movement coordination which may be dependent or require multiple factors in order to be successfully executed. Joinings may require the ability of receivers to accurately localize signaling animals, a certain ‘social state’ of the animals (e.g. willingness to join), as well as the ‘physical states’ of animals (doing something (e.g. foraging)). These results are supported by previous studies on bottlenose dolphins which examined whistle production during separations and after joining. The first study found that whistle production increased when a mother and calf swam beyond visual range of one another (Smolker et al., 1993). The second study found that signature whistles, hypothesized to be cohesion calls, increased in abundance during separations and were greatly reduced after the animals had joined (Janik and Slater, 1998).

Sound generation and the time to produce vocalizations are costly to both signalers and receivers (Tyack, 2000) for it may disrupt either from the task at hand (foraging, traveling, etc.). Receiving animals can respond to the signalers to counter-exchange
information or choose to remain silent. In this study, two-way vocal exchanges were found in 74% of the pre-joining events where discrete pulsed calls were present. In addition, (two-way) vocal exchanges between solitary animals and small groups suggest that solitary individuals are more than often the primary initiators of pulsed calls prior to joinings. Two-way exchanges would provide joining individuals with the locations of one another which could be continuously updated with repeated calling over time. In contrast, with one-way signalling, only the receiver would know where the signaler was located (which occurred in 26% of pre-joining events). The inter-animal spacing and the time it takes for individuals and small groups to join, may play a role in whether animals need to counter-call or if only one animal needs to vocalize. For instance, if animals are within close proximity when the signaler initially vocalizes, the receiver would know this and could swim toward the signaler in a timely manner (a behavioral instead of vocal response). In some instances, the signaler may be cognizant of whether the receiver is behind or in front of them, so the receiver upon hearing the signaler may slow down their pace in order to join. Additionally, nearly all of the one-way signaling seen were intra-matriline joining events. Since these smaller intra-group joinings occur multiple times daily, animals who are closely related and very recently swimming together would not need two-way exchanges to rejoin one another. An alternative hypothesis would be that the receivers do not want the solitary animal to join with them, so they do not initiate contact. However, since many of the animals joining are related or associate regularly over long time scales (decades) this scenario does not seem likely (Bigg et al., 1990).

In a previous study, a few individuals were observed swimming toward the individual who had captured the prey; the prey was then broken up and shared between those individuals (Ford and Ellis, 2006). Though it is not known how the other killer whales knew to join the individual who had captured the prey, it is likely that some sort of vocalization was produced (in either one-way or two-way exchanges).

In this analysis, no single call type was correlated to joining events, which is consistent with previous studies that found multiple discrete pulsed calls produced during a single behavioral context (Ford, 1989; Miller, 2002; Shapiro, 2008). There are two major ways that two communicating animals can find one another: signal content (e.g. amplitude) and directionality (hearing or transmission). Most of the call types analyzed in this study exhibited a distinct difference in call rates prior to joinings (N04, N05, N09, N23, N24, N25), except for N03. Discrete pulsed calls may be divided into long- or short-range vocals depending on source levels and estimated active spaces (range over which a signal can be detected based on source levels and assumed transmission loss) (Miller,
The N04, N09 and N05 calls seen here are examples of calls thought to be used in longer range communication (Miller, 2006). Though the N23, N24 and N25 calls have not been examined, the source levels of these vocals suggest that all or most are suitable when animals are dispersed over greater ranges. In contrast, the lower source level and estimated active space of the N03 call makes this call more suitable during close range vocal exchanges (Miller, 2006). Calls with greater estimated active spaces (e.g. N04, N09, etc.) may be more costly to generate (Tyack, 2000) than lower amplitude sounds (e.g. N03), but would comparatively remain more robust in noisier conditions (Miller, 2006). This in turn, would increase the reliability and efficiency of vocal exchanges in order to maintain contact. Animals may also adjust their acoustic behavior (e.g. change in vocal or source levels) according to their relative proximity to other individuals. For instance (and potential future research), a signaler may produce a very high amplitude sound initially (not knowing where other individuals are), but may adjust the source level of that sound once the signaler is aware of the receiver’s location. In turn, the receiver who may be within only a 100 m of a loudly vocalizing signaler, may respond with a lower source level compared to that of the initial call of the signaler. In the same scenario, animals might change which vocalization they use, especially if their repertoires have vocalizations which have lower and higher amplitudes with varying active space. Thus, animals that are separated by a large distance may opt for higher source level signals, but as they approach other individuals, they may vary call types depending on the context.

The call type usage varied during pre-joining events, with some calls being more predominant than others. Only three calls showed an increased production from the expected values, the N04 and N09 calls for the three A pods and the N25 call for the I11 pod. All three calls (N04, N09 and N25) were produced throughout the three minute period prior to joinings. The proportion of killer whale pulsed call production appears to vary with situational contexts (Ford, 1989). In a previous study, the proportion of N12 calls were found to increase when Northern Resident killer whales are beach rubbing, while N11 calls were elevated during large aggregations and N03 calls predominated during resting (Ford, 1989). In a previous study, the proportion of N12 calls were found to increase when Northern Resident killer whales are beach rubbing, while N11 calls were elevated during large aggregations and N03 calls predominated during resting (Ford, 1989). Similarly, the N04 and N09 calls are predominant vocalizations during foraging and traveling behaviors (Ford, 1989, 1991), as also seen in this study. There may be some movements that are innate to these two behaviors (e.g. separations, joinings, inter-animal spacings, changes in speed or trajectory), which actually drives the abundance of these vocalizations. In Chapter 3, results revealed that during both N04 usage during foraging and movements patterns involving single turns were elevated.
Hence, the distributions necessary to successfully forage and the inevitable variations in inter-animal spacings which occur during behavioral transitions, may dictate longer range vocals, like the N04 call, which are more distinctive (a separately modulated high frequency component) and reliable (greater estimated active spaces) for vocal exchanges and locating conspecifics.

In conclusion, these findings indicate that discrete pulsed calls play an important role in the vocal exchanges between killer whales prior to joining events. Since joinings may rely on a number of factors in order to be successfully execute (localization, ‘social state’, ‘physical state’). This study also revealed that a specific call was not correlated to pre-joining events, but that the proportion of some calls were elevated during this time. In Chapter 3, analysis of N04 production revealed that pre-joining N04 usage during foraging was greater than expected by chance. In addition, N04 usage was greater around the time animals were turning and less during straight path swimming. Further research examining vocalizations and exchanges during other behavioral movements are warranted to obtain a more comprehensive understanding of how killer whales are maintaining group cohesion both on the intra-group and overall group levels. Though other vocalizations were not examined in this study, killer whales, like other odontocetes, are capable of eavesdropping (Gregg et al., 2007; Tyack, 2000). Receivers would most likely be able to locate a signaler producing clicks or whistles. The exchange of pulsed calls (one-way or two-way) by killer whales may actively provide animals with the signaler’s (and receiver’s) intent so that specific cohesive movements can be coordinated between individuals. Orchestrating movements would not necessarily require a specific vocalization as long as animals could successfully transmit and receive information. One-way signalling was also seen during pre-joinings involving individuals of the same matriline. Hence, closely related individuals who are constantly rejoining on a minutely or hourly basis may not need two-way exchanges because of familiarity with the individuals and regular or expected movements.
Chapter 5

Mother and Offspring Separations

5.1 Introduction

The stability of killer whale matrilines within pods provides an excellent opportunity for vocal development and learning (Bigg et al., 1990; Ford, 1989, 1991). Killer whale mother and offspring groups are socially tight units within matrilines where offspring often spend the majority of their day within close proximity to their mother. Physical swimming distances between offspring and their mothers increases linearly with age (Bigg et al., 1990) with newborn calves swimming at their mothers’ sides while the oldest offspring swims the farthest away. Young and sub-adult killer whale offspring, like other animals, are thought to learn the vocal and behavioral skills they will need later on as adults (Bowles et al., 1988; Brainard and Doupe, 2000; Caldwell and Caldwell, 1979; Fripp et al., 2005). Therefore, young killer whales would not only need to identify their mothers’ vocalizations, they would also need to recognize and successfully produce their pod’s repertoire.

It is in the early stages of a mammal’s life that it is introduced to group vocalizations and behavioral skills (Bowles et al., 1988; Brainard and Doupe, 2000, 2002; Caldwell and Caldwell, 1979; Caldwell et al., 1990; Dahlheim and Awbrey, 1982; Fripp et al., 2005; McCowan and Reiss, 1995; Tyack, 1997; Tyack and Sayigh, 1997) which they will later need as an adult to maintain group cohesion (Ford, 1989, 1991). Social vocal learning is thought to occur when a novel sound is produced or a signal is associated with a new context (Janik and Slater, 2000). For other toothed whale species, such as bottlenose dolphins, calves and adults are thought to develop their unique whistle within the first year of life (Caldwell et al., 1990). Bottlenose dolphin calves imitate whistles common to their environment (Caldwell and Caldwell, 1979; Miksis et al., 2002; Tyack, 1997)
and calf signature whistles may be modelled on those of community members (diagonal learning transmission which is, for example, the learning from older community members to young) (Fripp et al., 2005). In the waters off Sarasota, male bottlenose dolphin calves produce similar signature whistles to their mothers, an example of vertical learning transmission (learning from parent to young) (Sayigh et al., 1995). Also, dolphin whistles in bond pairs appear to converge over time by horizontal learning (i.e. learning between conspecifics) (Watwood, 2004; Wells, 2003).

Since killer whales and bottlenose dolphins belong to the same family, Delphinidae, it is highly likely that killer whales are also capable of vocal learning. Mimicry is one form of vocal learning which has been observed in captive killer whales emulating man-made sounds (van Heel et al., 1982), wild killer whales occasionally copying the vocals of other non-clan members (Ford, 1991), as well as inter-species vocal imitation (Caldwell and Caldwell, 1972; Payne and Payne, 1985; Tyack, 1986). Captive killer whale calves produce some calls within the early stages of life (Dahlheim and Awbrey, 1982) as early as the first year (Bowles et al., 1988; Lane, 1996). In a study on wild Northern Resident killer whales, group-specific pulsed call production increased the first two weeks after a calf’s birth which was thought to assist the calf in recognizing its group affiliation (Weib et al., 2006).

Killer whales may also be capable of horizontal learning. The spectral structure of the N04 pulsed call examined for both the A12 and A30 matrilines of the A1 pod, underwent a horizontal transmission over the span of thirteen years (Deecke et al., 2000). The call shift appears not to be due to an error which was copied, because both matrilines equally shifted the call in a similar converging pattern (Deecke et al., 2000). In fact, younger animals exhibit a greater plasticity earlier in life, but may have a ‘learning window’ as they age (Brainard and Doupe, 2000; Crance, 2008). A young captive Icelandic killer whale shifted its repertoire to match that of an older British Columbia juvenile killer whale soon after the two were housed together in the same pool; the older juvenile never mimicked any of the the younger Icelandic killer whale’s vocalizations (Bain, 1986). In a later study, a young, captive, juvenile male killer whale shifted some of his vocalizations (previously resembling his mother’s) to that of two unrelated males (an older juvenile male and adult male) (Crance, 2008). This young male had been displaced from its mother’s side by the birth of a new calf. At this point it is not known if the younger male, who exhibited the greatest vocal plasticity compared to the four older killer whales in the pool, will revert back to his mother’s repertoire or will maintain a mixed repertoire. There are some indications that the adult male in that study unsuccessfully tried to
mimic the young juvenile male, indicating a potential ‘learning window’ in killer whale vocal development (Crance, 2008).

Similar to other animals, young killer whales are thought to be born with a crude template of their sounds (Boughman and Moss, 2003; Brainard and Doupe, 2000, 2002; Konishi, 1965; Marler, 1976). Auditory feedback, memorization, and repeated practice of sounds allow animals to improve motor skills and solidify the vocal template they will use as adults (Boughman and Moss, 2003; Todt and Hultsch, 1998). On a cognitive level, young killer whales would need to learn many skills potentially important for killer whale communication and survival: call function (behavioral movement, prey capture (Todt and Hultsch, 1998); identifying vocalizing animals (discriminating between related and non-related individuals); determine location information or (ranging) of other vocalizing animals (Boughman and Moss, 2003; Miller et al., 2004; Smolker et al., 1993); practice participating in vocal exchanges (who initiates, who responds, when to respond, when not to respond) (Smolker et al., 1993; Todt and Naguib, 2000); the timing of responses (Todt and Hultsch, 1998); and other complex pattern-specific vocal responses or exchanges (call sequences, call-type matching) (Falls et al., 1988; Gerhardt et al., 2000; Janik, 2000b; Krebs et al., 1981; Miller et al., 2004; Sugiura, 1998; Todt and Naguib, 2000). Though killer whales have pod-specific repertoires, they share some or many of those discrete pulsed calls with other pods. Hence, young killer whales are similar to many bird species in that they would need to develop vocalizations which belong to their group (matriline and pod) (Ford, 1991), yet also distinguish between their own groups’ calls and those of non-family members (Todt and Naguib, 2000). In addition, since many young animals often experience greater vocal plasticity at an early age (Brainard and Doupe, 2000; Crance, 2008; Tyack, 1986), they would need to decipher which of the non-matrilines or non-pod mimicked sounds to maintain in their adult vocal repertoire.

One type of pattern-specific vocal exchange behaviors is matched calling, which requires vocal flexibility and auditory vocal feedback (Boughman and Moss, 2003; Miller et al., 2004; Sugiura, 1998; Todt and Naguib, 2000), and is hypothesized to be necessary for vocal learning (Sugiura, 1998). However, understanding its function can be difficult and species/context specific (Boughman and Moss, 2003; Todt and Naguib, 2000). Match call-types occur when one individual produces the same call type as a previous animal, usually within a relatively short time period (Burt et al., 2002; Falls et al., 1988; Miller et al., 2004; Todt and Naguib, 2000); in some instances this could be matching of acoustic features of calls as seen with Japanese macaques (Sugiura, 1998). Call sequences between individuals which contain unlike calls are known as non-matched or
(mixed) vocalizations (Falls et al., 1988). Match call-types or songs have been seen for many song bird species, some frog species, bottlenose dolphins, humpback whales and killer whales (Falls et al., 1988; Ford, 1989; Gerhardt et al., 2000; Janik, 2000b; Krebs et al., 1981; Miller et al., 2004; Payne and Payne, 1985; Sugiura, 1998; Todt and Naguib, 2000). Depending on the species, behavioral context during match call-type sequences or exchanges vary. Whereas matched call sequences have occurred during aggression displays of quacking frogs, great tit birds and song sparrows (Burt et al., 2001; Gerhardt et al., 2000; Krebs et al., 1981), they have also been recorded during non-aggressive vocal exchanges of affiliated animals (Sugiura, 1998). In comparison, matched calling is thought to function in animal identification for some species (Cheney et al., 1995; Todt and Naguib, 2000), while in others it is hypothesized to be a means for reporting positions, coordinating movements and directions (Cheney et al., 1995; Krebs et al., 1981; Kudo, 1987; Miller, 2002). The rapidity of match calls within sequences may provide the actual arousal level of the context. For instance, rapid matching has been associated with high arousal while delayed matching has indicated that signalling animals are relatively relaxed (Todt, 1981; Todt and Naguib, 2000).

This study examined vocal behavior when a mother is separated from at least one of her offspring (juvenile(s) and/or calf). It does not include adult male offspring, adult females or motherless juveniles. The aim of this study was to determine if the rate of call patterns were uniform across encounters, bouts and pods and if vocal exchange behavior was uniform amongst mother/offspring groups during separations. This analysis examined if a) matched and mixed call rates differed by encounters and bouts, b) matched and mixed call rates differed by pod, and c) mother and offspring both initiate and respond to calls. Matching call-types might benefit and strengthen mother/offspring vocal exchanges because matched sequences are conspicuous compared to mixed (or non-matched) call production (Todt and Naguib, 2000), and may aid mother/offspring groups to accentuate their vocalizations amongst other members of the matriline or pod. Varying their vocal production when separated may aid mother and offspring in maintaining intra-group cohesion and facilitate certain behavioral movement patterns which may be essential and unique to this traditionally socially tight group. Initiated calls and responses would be expected to be uniform between mothers and offspring. In other marine species such as fur seals, mothers are responsible for initiating vocal contact when returning to pups after foraging, while pups have distinctive response vocals which mothers are able to recognize (Carrier et al., 2002). Due to predation risks, humpback whale mothers may remain within close proximity to their calves and vocal production...
may occur more often by mothers than calves (Zoidis et al., 2008). In contrast, dolphin calves and mothers were found to whistle at high rates when separated (Smolker et al., 1993).

5.2 Call Production During Encounters and Bouts

Matched and mixed pulsed call production was examined during encounters and within call bouts when a mother was separated from one of her offspring. Encounters occurred when a group of killer whales (including mothers with offspring) entered the acoustic range of the hydrophone array until when they swam out of range. Call bouts were defined as short vocal exchanges between individuals in the separated mother and offspring groups. In each circumstance (encounter or bout) the analysis focused on call rate, call rate per number of individuals and call rate per number of pods present. In this analysis match call-types occurred when one individual produced the same call type as a previous animal in the group, usually within a relatively short time period of seconds or tens of seconds. An example of a matched vocal exchange was when the mother produced an N04 call, and then her offspring followed with an N04 call. An example of a mixed call-type would be if the juvenile produced an N04 call and the mother then produced a N09 call. A 90 second time window was given from the onset of a vocal bout until its termination. Vocal bouts were terminated when the animals stopped vocalizing, the animals joined, or there was a change in group composition or predominant behavior. In ambiguous longer vocal bouts, the response window was extended to 2 minutes, so as not to start a new event. Most vocal bouts by mothers and offspring during separations were complete by two minutes before lapsing into silence. Additionally, in multiple pod situations, matched and mixed call classifications could only be made for groups or individuals present which share the same call in their repertoires. Variations in call rates of matched and mixed categories for both the encounter and bout analysis were calculated using a Wilcoxon Signed Ranks tests in SPSS to test the null hypotheses (see Appendix C for definition and symbols). Matched and mixed calling rates were also examined for each pod and compared using the Wilcoxon Signed Ranks test.

5.2.1 Results

Multiple recordings of mother/offspring separations were obtained for all pods seen in this study, except for one pod (I31), that was only seen once (Table 2.4). Of the forty encounters examined in this study 32 had at least one to a couple instances when a mother
was separated from one of her offspring. A total of 578 pulsed calls were attributed to individuals or small groups during mother/offspring separations. A total of five pods, ten matrilines and fifteen mother/offspring groups contributed to the vocal analysis when mothers were separated from one of her offspring (Table 5.1). Some mother/offspring groups were seen both years when separations occurred, some were only seen in one of the years (e.g. A62, A11, I12, I31 (names of mothers)). One mother/offspring group, A54, was seen both years but only produced pulsed calls in 2006 when there was a separation of mother and offspring, in 2007 only clicks were localized from them. Five mother/offspring groups in the five pods listed in Table 5.1 were never seen when a mother was separated from an offspring, or they were not seen at all. The distribution of juveniles (juv) and calves (calf) varied due to the aging of the calves into juveniles (turning three years old). One juvenile of each I27 and I31 mothers were or became mature juveniles during this study, indicated by an asterisk (*).

<table>
<thead>
<tr>
<th>Clan/ Line</th>
<th>Matriline</th>
<th>Mother</th>
<th>2006</th>
<th>2007</th>
<th>Total PCs</th>
<th>Total ENCs</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td></td>
<td>Juv</td>
<td>Calf</td>
<td>PCs</td>
<td></td>
</tr>
<tr>
<td>2006</td>
<td></td>
<td></td>
<td>Juv</td>
<td>Calf</td>
<td>PCs</td>
<td></td>
</tr>
<tr>
<td>A</td>
<td>A1</td>
<td>A12</td>
<td>1</td>
<td>1</td>
<td>46</td>
<td>85</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>2</td>
<td>0</td>
<td>39</td>
<td></td>
</tr>
<tr>
<td>A62</td>
<td></td>
<td></td>
<td>0</td>
<td>1</td>
<td>12</td>
<td>12</td>
</tr>
<tr>
<td>A30</td>
<td>A54</td>
<td></td>
<td>1</td>
<td>1</td>
<td>21</td>
<td>21</td>
</tr>
<tr>
<td>A4</td>
<td>A11</td>
<td>A35</td>
<td>2</td>
<td>0</td>
<td>38</td>
<td>38</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>2</td>
<td>0</td>
<td>-</td>
<td></td>
</tr>
<tr>
<td>A24</td>
<td>A24</td>
<td></td>
<td>3</td>
<td>0</td>
<td>8</td>
<td>9</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>3</td>
<td>0</td>
<td>90</td>
<td>98</td>
</tr>
<tr>
<td>A5</td>
<td>A8</td>
<td>A52</td>
<td>1</td>
<td>1</td>
<td>7</td>
<td>12</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>2</td>
<td>0</td>
<td>34</td>
<td>41</td>
</tr>
<tr>
<td>A23</td>
<td>A43</td>
<td></td>
<td>1</td>
<td>0</td>
<td>2</td>
<td>25</td>
</tr>
<tr>
<td>A25</td>
<td>A51</td>
<td></td>
<td>0</td>
<td>1</td>
<td>10</td>
<td>14</td>
</tr>
<tr>
<td>G</td>
<td>I11</td>
<td>I12</td>
<td>1</td>
<td>1</td>
<td>-</td>
<td>4</td>
</tr>
<tr>
<td></td>
<td>I15</td>
<td>I27</td>
<td>2*</td>
<td>1</td>
<td>63</td>
<td>41</td>
</tr>
<tr>
<td></td>
<td>I14</td>
<td>I4</td>
<td>2</td>
<td>0</td>
<td>4</td>
<td>58</td>
</tr>
<tr>
<td></td>
<td>I15</td>
<td>I51</td>
<td>0</td>
<td>1</td>
<td>2</td>
<td>6</td>
</tr>
<tr>
<td></td>
<td>I31</td>
<td>I35</td>
<td>2</td>
<td>0</td>
<td>-</td>
<td>6</td>
</tr>
<tr>
<td>Totals</td>
<td></td>
<td></td>
<td>226</td>
<td>352</td>
<td>578</td>
<td></td>
</tr>
</tbody>
</table>

Table 5.1. Pulsed call production for mother/offspring groups during separations. This table illustrates the number of juveniles and calves of each mother (e.g. A62) for each field season (2006 and 2007). The number of pulsed calls produced by each mother and her offspring is listed along with total pulsed call counts by matriline and year. This table only represents pulsed call production when a mother was separated from an offspring. The ‘0’ under the PCs columns indicate that the mother group was seen in that year when separated but they did not produce any PCs, while ‘-’ indicates that mother/offspring was not seen separated in that year. * represents a juvenile in the group was or became mature juvenile during study.

Matched call-type production was compared to mixed pulsed call productions during mother and offspring separations. Twenty-nine of the thirty-two encounter where mother/offspring separations occurred had more than one pulsed call and could be ex-
Figure 5.1. Matched and mixed pulsed call production across encounters. Matched call rates are indicated in blue and mixed (or non-matched) call rates are in green. Circles indicate the means, while bars represent the 95% confidence intervals for both call patterns. The mean rate of matched call production was greater than mixed call production during encounters (Wilcoxon Rank Sum test, \( p = 0.038 \)).

amined in the matched/mixed call analysis. The null hypothesis \( (H_0) \) was that matched and mixed call rate production was equivalent during encounters. This analysis choose the most conservative option of a 50/50 chance, though the probability of mixed calling would be much greater than matched calling. When a mother was separated from at least one of her offspring, matched pulsed call rates were greater than mixed pulsed call production \( (df = 29, z = 2.072, p = 0.038, H_0 \text{ rejected}) \) (Fig. 5.1, Table 5.2). A large variability was seen between encounters for overall number of calls produced, which may explain some of the overlap. Call rates within encounters per individual and per number of pods were also examined. The first null hypotheses \( (H_0) \) was that matched and mixed call rate production was equivalent per individual within an encounter. A Wilcoxon Signed Ranks test revealed there was no difference in call rate per individual \( (df = 29, z = -1.913, p = 0.056, H_0 \text{ not rejected}) \) (Table 5.2). The second null hypotheses \( (H_0) \) was that matched and mixed call rate production was equivalent per number of pods within an encounter. The Wilcoxon Signed Ranks test showed that there was no difference in mother/offspring call rates when including the number of pods present \( (df = 29, z = -1.890, p = 0.059, H_0 \text{ not rejected}) \).

Call rates per bout were also analyzed to define more fine-tuned small group vocal behavior information within encounters. Since this analysis is a subset of the encounter
data it is being presented here. Call rates/bout, call rates/bout/individual and call rates/bout/number pods present were also examined. Overall mean bout lengths were 48.7 seconds. Call rates over all were 5.87 calls/bout, 3.59 matched calls/bout and 2.28 mixed calls/bout. A plot of matched and mixed call rates per bout shows a great deal of overlap in the 95% confidence intervals. An example of the mean call rates/bouts and confidence intervals have been provided (Fig. 5.2, Table 5.3) \((df = 93, z = -2.679, p = 0.007, H_o rejected)\). Call rate per bout per individual and per pod were also investigated. Call rates/bout/(number of individuals) was 0.031 calls/bout/individual overall, 0.018 for matched calls and 0.013 for mixed calls. Call rates/bout/(number of pods) was 0.182 overall, 0.112 for matched all rates and 0.075 for mixed calls.

<table>
<thead>
<tr>
<th>Call Rates</th>
<th>n</th>
<th>z</th>
<th>p</th>
</tr>
</thead>
<tbody>
<tr>
<td>Encounters</td>
<td>29</td>
<td>2.072</td>
<td>0.038</td>
</tr>
<tr>
<td>Encounters/Individual</td>
<td>29</td>
<td>-1.913</td>
<td>0.056</td>
</tr>
<tr>
<td>Encounters/Pod</td>
<td>29</td>
<td>-1.890</td>
<td>0.059</td>
</tr>
</tbody>
</table>

Table 5.2. Matched versus mixed calling rates during encounters. Matched calling rates were greater than mixed calling rates during encounters. No significance was found for either encounters per number of individuals or number of pods. All hypotheses were tested for uniformity between call patterns using Wilcoxon Signed Ranks test. Call rates were calls/min. Also shown in the table is number of samples (n), z-statistic (z) and probability (p).
Figure 5.2. Matched and mixed pulsed call production across vocal bouts. Matched call rates are indicated in blue and mixed (or non-matched) call rates are in green. Circles indicate the means, while bars represent the 95% confidence intervals for both call patterns. The mean rate of matched call production was greater than mixed call production during vocal bouts (Wilcoxon Signed Ranks test, p=0.007).

Table 5.3. Matched versus mixed calling rates during bouts. Matched calling rates were greater than mixed calling rates during vocal bouts. Significance for greater matched calling was found in all instances. All hypotheses were tested for uniformity between call patterns using Wilcoxon Signed Ranks test. Call rates were calls/min. Also shown in the table is number of samples (n), z-statistic (z), probability (p) and whether the null hypothesis ($H_0$) was rejected or not.

<table>
<thead>
<tr>
<th>Call Rates</th>
<th>n</th>
<th>z</th>
<th>p</th>
</tr>
</thead>
<tbody>
<tr>
<td>Bouts</td>
<td>93</td>
<td>-2.679</td>
<td>0.007</td>
</tr>
<tr>
<td>Bouts/Individual</td>
<td>93</td>
<td>-2.397</td>
<td>0.017</td>
</tr>
<tr>
<td>Bouts/Pod</td>
<td>93</td>
<td>-2.486</td>
<td>0.013</td>
</tr>
</tbody>
</table>
Figure 5.3. Matched and mixed pulsed call production within pods. Matched calls rates are indicated in blue and mixed (or non-matched) call rates are in green. Circles indicate the means, while bars represent the 95% confidence intervals for both call patterns. The mean rate of matched call production compared to mixed call production were equivalent for the 3 A pods however matched calls were greater for the I11 pod (Wilcoxon Signed Ranks test, p=0.001).

Vocal bouts were also examined for pods A1, A4, A5 and I11 to determine if there was a difference in matched and mixed call rates between pods. The null hypothesis ($H_0$) was that matched and mixed call rates per bout were equivalent within pods. The mean rates of matched call production compared to mixed call production were equivalent for the three A pods however matched calls were greater than mixed call rates for the I11 pod (Wilcoxon Signed Ranks test, p=0.001) (Fig. 5.3, Table 5.4).

<table>
<thead>
<tr>
<th>Pod</th>
<th>Call Pattern</th>
<th>N</th>
<th>Mean</th>
<th>Std. Deviation</th>
<th>p value</th>
</tr>
</thead>
<tbody>
<tr>
<td>A1</td>
<td>Matched</td>
<td>24</td>
<td>0.09926</td>
<td>0.1275</td>
<td>0.702</td>
</tr>
<tr>
<td></td>
<td>Mixed</td>
<td></td>
<td>0.15728</td>
<td>0.3208</td>
<td></td>
</tr>
<tr>
<td>A4</td>
<td>Matched</td>
<td>21</td>
<td>0.08571</td>
<td>0.1002</td>
<td>0.687</td>
</tr>
<tr>
<td></td>
<td>Mixed</td>
<td></td>
<td>0.07701</td>
<td>0.0765</td>
<td></td>
</tr>
<tr>
<td>A5</td>
<td>Matched</td>
<td>12</td>
<td>0.09975</td>
<td>0.0926</td>
<td>0.131</td>
</tr>
<tr>
<td></td>
<td>Mixed</td>
<td></td>
<td>0.10870</td>
<td>0.2830</td>
<td></td>
</tr>
<tr>
<td>I11</td>
<td>Matched</td>
<td>34</td>
<td>0.22770</td>
<td>0.6799</td>
<td>0.001*</td>
</tr>
<tr>
<td></td>
<td>Mixed</td>
<td></td>
<td>0.05961</td>
<td>0.1076</td>
<td></td>
</tr>
</tbody>
</table>

Table 5.4. Matched and mixed calling rates for four pods. This table only represents matched and mixed calls by 4 of the 5 pods seen in this study (A1, A4, A5 (of the A clan) and I11 (of the G clan)). Mean call rates per bout for both matched an mixed calling for each pod is shown along with sample size, std. deviation and significance. Only the I11 pod showed a significant difference between call patterns (Wilcoxon Signed Ranks test, p=0.001)
5.3 Initiated and Response Call Production

In the mother/offspring separations, offspring were divided into three categories: calves (up to and including 2 years old), immature juveniles (3- to 12-year-olds) and mature juveniles (13-years or more) (Olesiuk et al., 2005). The only females included in this analysis were females with present day young offspring (with either calves, immature and/or mature juveniles). Vocalizations with confounding group compositions were excluded. For instance, if a non-mother/offspring individual (e.g. adult male) was swimming with the mother or separated juvenile, those vocalizations and events were not included.

Initiated pulsed calls and first responses to them were examined across individuals when a mother was separated from one of her offspring. Since mothers often have more than one offspring, calls were also tallied for small groups when a mother is with an offspring or when multiple offspring swam together. Initiated calls were considered the first call when a mother became separated from at least one of her offspring, often proceeded by a period of silence. The definition for vocal bouts is the same as previously described. Within the analysis window there were initiated calls, first responses to those initiated calls, and also repeated vocal exchange of pulsed calls after the initiated and first response calls. In this analysis, in order to balance response to initiated call production, only first responses were examined. Initiated and first response calls of individuals were analyzed using a Freeman-Halton extension of the Fisher Exact probability test, which uses 2 x 3 contingency tables to examine categorical data with sample sizes much less than 300.

Call usage during first responses were also examined to determine if a single call was being produced or matched for first responses. Binomial tests were run. Age groups of animals initiating and responding to calls was also examined. Matched and mixed responses to initiated calls was examined between offspring and mothers for any bias using a sign test. In addition, variations in call usage between mothers and offspring were examined for first response calls using a sign test.

5.3.1 Results

All age groups initiated and responded to pulsed calls when a mother was separated from one of her offspring. Mothers often have more than one offspring, so mothers were often seen swimming with one or two offspring while being separated from another one. In some instances, a mother was separated from multiple offspring. Multiples often had
individuals from different age groups. The number of occurrences of initiated calls to first response calls for each age group is seen in Fig. 5.4. Red bars denote initiated calls, while the gray bars represent first response call occurrences. Solo animals are designated as solid bars (upto2, 3to12yr, 13yrplus and Mother) in the two graphs, while grouped animals are denoted with the multiple colored bars (MultipleOff (2 or more offspring) and MotherPlus (mother and some offspring)). Only data in the graph on the left were used in the statistical analysis.

The number of times mother and offspring initiated pulsed calls when separated compared to how often they responded differed ($\chi^2 = 12.9969, df = 2; \chi_{0.05,3-1}^2 = 5.992, p = 0.0015$, $H_0$ rejected). The null hypothesis ($H_0$) was that mother and offspring uniformly initiate and respond to pulsed calls when separated. Mother and calves initiated calls more often than they responded to calls, while juveniles responded as much as they initiated calls. This statistical analysis was only conducted on solo individuals (calves, immature juveniles and mothers). Mature juveniles were eliminated because data was from only one individual. Examination of the abundance of no response to initiated calls was compared to the number of response calls in each bout in this analysis (Fig. 5.5). Zero or no response was the most common 42.4% (n=36), followed by one vocal response call bouts (22.4%), then 2 call response bouts (12.9%) and so forth. A total of 78% of the thirty-six no responses were due to mothers not responding to offspring. In 79% of the 78% no responses by mothers, the mothers were foraging. In addition, 56% of the thirty-six no response bouts ended in a joining event.

Call usage varied during first responses, with no single call being the first response to an initiated call. The N04 call was the most often produced for the A pods for first responses. The null hypotheses ($H_0$) was that first response calls matched initiated call types 50% of the time. A binomial test revealed that there was no bias toward matching for first responses to initiated calls ($\text{binomial test}, \mu = 0.52, df = 83, p = 0.826$, $H_0$ not rejected). In addition, matched and mixed first responses to initiated calls did not vary by pod.

All ages and age groups of killer whales responded to initiated calls and no noticeable difference in rates were seen between groups. The null hypotheses ($H_0$) was that matched calling was equivalent between mothers and offspring for first response calls. Examination of matched and mixed first responses to initiated calls indicated no bias for offspring or mothers to match calls in vocal bouts ($\text{sigin test}, df = 15, p = 0.146$, $H_0$ not rejected). The null hypotheses ($H_0$) was that call type usage was equivalent between mothers and offspring for first responses. No difference was found in specific pulsed call usage for first
responses of mother versus offspring (sign test, df = 83, p = 0.077, $H_0$ not rejected).

**Figure 5.4.** Initiated and first response occurrences by age group. Initiated calls are indicated by red bars for individual (2 years and below, 3 to 12 year-olds, mother) and by striped red bars for small groups (13 years or older, multiple offspring, mother with offspring), while gray bars represent the first response to initiated calls. First response calls are highlighted in gray and grey striped for the same groupings. Mothers and calves initiated calls more often than they responded ($\chi^2 = 12.9969, df=2; \chi_{0.05,3−1}^2 = 5.992, p=0.0015$).
Figure 5.5. Number of pulsed call responses in vocal bouts to initiator. No responses (vocal) to an initiator during mother and offspring separations occurred most often (designated by '0'). The only responses shown here are for isolated individuals only. When animals did respond a one call response was the most common, followed by a two call response, and so forth.

5.4 Predominant Sideband Energy in N04 Calls

Predominant sideband usage for the N04 call was previously discussed in Chapter 3, however it will be repeated here also for completeness. Calls were divided into N04 calls that had the most energy in the second sideband (SB2) and those N04 calls that possessed more energy in all other sidebands (non-SB2). A comparison of energy in the sidebands to movement behaviors was examined when a mother and offspring were separated and when they were together. A Fisher’s Exact showed that non-SB2 N04 call production during foraging and traveling were not equivalent when a mother was separated from an offspring and when she is with all of her offspring ($n = 30, p = 0.0043, H_0$ was rejected). Non-SB2 N04 production was greater during foraging when mothers were separated from an offspring, while non-SB2 N04 call occurrence was low when mothers were together with offspring. In contrast, there was no difference found in SB2 N04 call production between foraging and traveling when a mother was separated or with her offspring ($n = 82, p = 0.8206, H_0$ was not rejected). Non-SB2 N04 call usage varied between directional movement tracks when a mother was separated from an offspring and when she was with all her offspring ($n = 31, p = 0.0128, H_0$ was rejected). However, N04 usage during SB2 N04 calls was uniform when a mother was with or without her offspring ($n = 89, p = 0.4371, H_0$ was not rejected). In the non-SB2 analysis, mothers
with offspring either did not make or did not produce N04 calls around the time of single
turns (as they did with the SB2 analysis).

5.5 Discussion

The rate of matched calling by killer whales when a mother was separated from an
offspring(s) was greater than mixed pulsed call rates for both encounters and bouts. Despite
the conservative analysis of choosing 50/50 comparison of matched and mixed
calling behavior, matched calling was still significantly higher. Killer whale discrete
pulsed call repertoires have anywhere from 7-17 calls in their discrete pulsed calls (Ford,
1991). The probability of matching a call would potentially be a 1/7 to a 1/17 chance,
while the probability of getting a mixed call sequence would be much greater. Even if the
hierarchical calling behavior seen in Northern Resident vocal production was assumed to
be innate and not resultant of a certain distribution or swimming pattern, the probability
of matched calling would still be much greater than mixed. Killer whales also showed a
wide variability of the rate of pulsed call production during both encounters and bouts
seen by the variability in the 95% confidence intervals. In contrast, there was no difference
in call rate found per number of individuals or number of pods for encounters, however,
matched calling rates were higher for bouts. An increase in calling rates per number of
individuals or per number of pods for bouts would potentially accent a series of calls
so that individuals could maintain contacts even in larger or more diverse groups. The
rate of matched calling also appeared to vary some by pods. Match and mixed calling
was nearly equivalently for the 3 A pods (A1, A4, A5), while the III pod (of the G clan)
matched calls more often than they mixed calls when a mother was separated from one
of her offspring. As in the encounter and vocal bout analyses, there was a great deal of
variability in pulsed call production (matched, mixed) during a given vocal vocal bout
by pods.

Pattern calling, like match call-types, requires an added complexity to vocal ex-
changes (Boughman and Moss, 2003; Miller et al., 2004; Sugiura, 1998; Todt and Naguib,
2000). The increased presence of matched calls in vocal exchanges would provide mother
and offspring (who are often amongst other matrilines or pods) with call pattern dis-
tinctiveness. The driving force for mother offspring to maintain intra-group cohesion
would favor a more conspicuous or complex vocal production when mother/offspring
groups were among other killer whales. Killer whales appear to contain individual infor-
mation in their vocalizations (Nousek et al., 2006), so mothers and offspring would be
able to identify one another by those means. However, individual identity information may not be enough alone to coordinate changes in intra-group movements or re-joinings (Boughman and Moss, 2003). As the density of killer whales increase, the complexity of vocalizations and exchanges would probably assist individuals to not only find each other amongst a large group (Green, 1975; Nottebohm, 1969), but it may also assist them in maintaining contact. The number of mother/offspring groups (4) in the I11 pod I15 matriline is greater than the other matrilines in this study where there are usually one to two mother/offspring groups (Ellis et al., 2007). This greater number of mother/offspring groups within a matriline may drive the need to increase matched calling during separations, so mothers and offspring can maintain cohesion (Table 2.4).

Matched call types may also provide a learning or developmental experience for younger animals to practice their pod’s vocal repertoire (Boughman and Moss, 2003; Todt and Naguib, 2000). Matched calling is produced by all age/sex class of individuals seen in this study, so it is most likely an intrinsic complexity of killer whale vocal exchanges. The slight increase in matched calling rates heard during mother/offspring separations may be indicative of a learning process where offspring develop and refine not only the structure but also the use of those vocalizations (Boughman and Moss, 2003; Falls et al., 1988; Gerhardt et al., 2000; Janik, 2000a; Krebs et al., 1981; Miller et al., 2004; Todt and Naguib, 2000). The point at which offspring refine call structure and practice call usage most likely depends on the age or development of individuals. As animals age they begin spending more time past the visual range of their mothers, and it is during this time that they can begin to apply the use of vocalizations.

Initiated and first response to calls varied between age class groups when mothers were separated from one of their offspring (Fig. 5.4). Immature juveniles (3 to 12 yr) initiated pulsed calls equally as much as they responded. Mothers also initiated calls quite often. However, both solo mothers and calves (to 2 yr) initiated pulsed calls more often than they responded. Only first response calls were examined in this study, and analysis was only on solo individual (calves, immature juveniles and mothers) (left graph). In addition, Fig. 5.4 shows that mothers with offspring (MotherPlus, stripped bars) exhibited the same proportion of initiated and first responses as the mother swimming by herself. Examination of the number of initiated calls of all the solo offspring groups (solid red) compared to the first response calls of the solo mother (solid gray) shows that the mother is only responding approximately 20% of the time to her (solo) offspring’s vocalizations. Examination of the number of vocals in vocal bouts showed a high number of ‘0’ or no responses to initiated calls (42%) (Fig. 5.5). The lack of response by mothers (78%)
constitutes the majority of the 42% no responses. This argument assumes, of course, that mothers are supposed to respond. During 79% of the time mothers were not responding they were foraging. Implications are that mothers may not want to alert prey while they are foraging. In addition, 56% of the total thirty-six no responses ended in the individuals joining within a short time period of the initiated call. Receivers may localize the signaling animal and some other response such as increasing speed, changing direction to join would be the least costly response.

Swimming distances of offspring, approximately, increases linearly with age, with calves swimming closest to their mothers and the oldest offspring swimming the farthest away (Bigg et al., 1990). Middle offspring depending on how recently they were displaced by the arrival of a calf, may still remain relatively close to their mothers compared to the oldest sibling. In 2006 and 2007, the offspring age class with the largest number of individuals are immature juveniles. Therefore, it would be expected that the sum of initiated and first response calls would be higher than for other offspring age categories (Fig. 5.4). However, when animals were separated it was expected that animals would equally initiate as well as respond to initiated calls. Though the calf category only includes animals which are under three years of age, and is therefore smaller, calves initiated calls four times more often than they responded. The result of young animals increasing vocalizations during separations from their mother is not a novel concept. Calves are fully or partially dependent on mothers for food supplementation (Olesiuk et al., 2005). And though it was not examined here, they may be some distance or time separation parameter which elicits vocal responses by young. A similar vocalization pattern was seen in another study where bottlenose dolphin calves, when separated from their mothers, increased whistle production and appeared to be the individuals who maintained contact with the mothers when they were beyond visual range (Smolker et al., 1993). Another example can be seen with rhesus monkeys infants who increase cooing calls when they are isolated from their mothers (Kalin et al., 1992).

Due to the close bonds of killer whale mother and offspring associations within matriline (Bigg et al., 1990), and the results in Fig. 5.4, both calves and immature juveniles appear to be initiating a large number of calls. The higher occurrence of initiated call production by calves may indicate an excitedness due to the separation (Todt and Hultsch, 1998), or it may be part of vocal development of young. For instance, during separations, young offspring (calves or juveniles) can practice localizing abilities in varying environments or ranges (Boughman and Wilkinson, 1998; Miller et al., 2004; Smolker et al., 1993). Offspring may also practice when it is beneficial or not for them
to vocally respond or initiate calls. Swimming distances to mother dictate if response is a vocal response or not (Smolker et al., 1993). The low first response calls for calves may be due to the fact that calves, especially the youngest ones, do not swim far from their mothers. In all instances when the calves did not respond, they shortly joined with their mothers. Quick examination of the data indicated that 2/3 of calves were only two adult body lengths (approximately 20 m) away from their mothers, while the other 1/3 were within 40-50 m away. Calves, especially younger ones, may not need to always vocally respond to their mothers because of their inherent swimming position near to their mothers. Hence, visual cues may ultimately displace the need to vocally respond in order to rejoin. In contrast, older offspring are often one hundred meters or more from their mothers, and vocal exchanges may be the most timely and least costly response. Since killer whales lack predators, there may not be an urgency for young animals to reunite with their mothers. However, factors such prey sharing and coordinating movements in dense aggregations of killer whales may facilitate more urgency for maintaining contact vocally or physically. Investigating excitedness in vocalizations, however, would require carefully thought out data samplings of vocalizations at different separation distances and times and adequate sample sizes on at least a few individuals.

In contrast to the bottlenose dolphin study, mother killer whales appear to initiate a large number of calls when one of their offspring is separated from them (Smolker et al., 1993). In most instances, when the mother initiated a call, most if not all of her separated offspring responded. However, like the bottlenose dolphin study, when a young offspring is initiating the mother does not necessarily respond. This study revealed that the mothers comprised the majority of no responses, and that they were mostly foraging during this time. The implications for this result is that mothers do not want to alert prey while foraging. Successful prey captures would benefit a prey sharing species where younger juveniles may rely on their mothers for supplemental food until they are proficient hunters. Another reason for the large number of no responses are also due to the relative proximity of the animals signaling. In 56% of bouts which terminated in no responses, animals were within 1-1.5 minutes (or approximately two hundred meters or less) of joining. Animals would be able to recognize the close proximity of the signaler and since joinings are a regular movement behavior of killer whales, a vocal response may not be needed, especially by closely related individuals (see Chapter 4). The occasional lone pulsed call may be an overall group dynamic which notifies other members of the signaler’s location so that group cohesion and movement can be maintained. In this latter example, it may be part of the behavioral development of offspring to announce their locations without
their mothers’ vocal feedback. When the mother is on the initiating end, most of the
time her offspring respond. In some instances it may be out of excitement due to the age
of the offspring or the long period of silence between the last vocal exchange. Additional-
ly, the mother (and maybe sometimes older offspring) may be coordinating changes
in movement or speed which dictates that all individuals respond to acknowledge their
awareness of the change. As seen in Chapter 3, an alternative hypothesis is that animals
may use variations in acoustic attributes of calls to relay information to receivers. The
prominent energy of the N04 call occurred more often in non-SB2 during foraging when
mothers and offspring were separated, while this was not the case when mothers and
offspring were swimming together. Variations in signal energy distributions may relay
excited states or periodic urgency to mothers and offspring during separations. Relaying
reliable information (e.g. location, previously transmitted information which resulted in
successful prey capture/sharing or coordination of movements) would assist receivers in
making the most beneficial decision (Seyfarth and Cheney, 2003a; Tyack, 2000), which
would be especially important in coordinating complex movements such as joinings for
prey sharing.

In conclusion, killer whale vocal production appears highly complex and potentially
contains many subtle nuances which are difficult for researchers to decipher. Similar
to some avian and other species, matched call patterns are a distinctive component of
Northern Resident killer whale vocal exchange patterns (exhibited by all five pods in this
study) (Burt et al., 2001; Ford, 1991; Gerhardt et al., 2000; Krebs et al., 1981; Miller
et al., 2004; Sugiura, 1998). The elevated matched calling rates seen in encounters and
bouts when mother and offspring are separated suggests that matched calling is a com-
mon calling dynamic of this population of killer whales. Although matched calling has
previously been described and analyzed (Ford, 1991; Miller et al., 2004), no previous
research has analyzed both matched and mixed calling behavior for the Northern Res-
ident population as a whole, so there is no basis from which to compare matched and
mixed calling patterns for mother and offspring. Thus, the analysis serves as a base the
characterization of call pattern behavior and a basis for future studies. In the initiated
and first response calls analysis, there was no bias for matched first response calling to
initiated calls nor toward animals producing a single call when matching. All individ-
uals in mother/offspring groups initiated and respond to pulsed calls when there was a
separation, however, mothers responded much less than anticipated. Immature juveniles
routinely responded to their mothers initiated calls. In contrast, when mothers initiated
pulsed calls her offspring usually responded within the vocal bouts. Hence, two-way vocal
exchange behavior between mother and offspring, as well as a one-way vocal ‘exchange’ or possible announcement calls from offspring to their mothers were both present. No responses by mothers was high, while in the majority of no responses to initiated calls, mothers were foraging. No responses may also occur because animals are within close proximity of joining. In the predominant energy analysis (also in Chapter 3), non-SB2 N04 production was greater during foraging when a mother was separated from her offspring, but low when a mother was with her offspring; this trend was not seen for the SB2 N04 production. Excitedness naturally encoded into animal vocalizations has the potential to convey reliable information (e.g. announcement of a food catch) that other individuals may detect (Fischer et al., 2001; Manser, 2001; Owren et al., 1997; Scherer, 1989; Seyfarth and Cheney, 2003b). Further research is warranted to determine if arousal states are exhibited in varying energy distributions of killer whale pulsed calls and if killer whales can successfully transmit this information to other conspecifics. Energy studies require a carefully thought out set of trials involving pre-determined time and space parameters for comparison. These control factors would need to be coupled with detailed behavioral and identification information.
Chapter 6

Frequency Energy Split

6.1 Introduction

Killer whale discrete pulsed calls are highly complex in structure and the spectral content of these complex pulsed sounds contain a wealth of information having wide bandwidths comprised of multiple sidebands which are equally spaced (Ford, 1984, 1987, 1989, 1991; Hoelzel and Osborne, 1986; Miller, 2002, 2006, 2007). The sidebands of pulsed calls are modulated in both frequency and amplitude. Some calls contain a broadband click section which transitions into a more traditional tonal-sounding pulsed section, while others only contain the tonal section (Ford, 1989, 1991; Murray et al., 1998). Pulsed calls have much shorter inter-pulse intervals compared to echolocation clicks (Watkins, 1967), and are displayed on a spectrogram by frequency gaps between sidebands (otherwise known as sideband intervals). Killer whales are able to produce two primary frequencies simultaneously, which have been designated as the higher and lower frequency components of the call (Hoelzel and Osborne, 1986; Miller, 2002, 2007). Killer whales (and dolphins) have been seen in captivity to produce clicks and whistles simultaneously (Dahlheim and Awbrey, 1982). These two independent or very loosely coupled components suggests the presence of two sound sources. The presence of two independent or very loosely coupled sound signals (as seen in spectral analysis) is referred to in literature as either biphonation or ‘two-voices’ (Aubin et al., 2000; Cranford et al., 1996; Filatova et al., 2007; Fitch et al., 2002; Foote et al., 2008; Mann et al., 2006; Miller, 2007; Tyson et al., 2007).

Complex sounds are prevalent in many aspects of nature ranging from musical instruments, to bells, to biological organisms (Benade, 1990; Yuen et al., 2007). Simple resonators consist of two reactive elements such as a mass and a spring (elasticity),
and freely vibrate after some initial impulsive driver (Bennet-Clark, 1999; Kinsler et al.,
2000). The vibration of most resonators are dampened due to frictional forces, and the
sound decays exponentially. Biological sounds are usually produced by driven resonators,
where the resonators are continuously re-stimulated to sustain the vibration over an ex-
tended period (Benade, 1990; Bennet-Clark, 1999). The transmitted sound from animals
is dependent not only on these driven resonators, but also on various cavities, fluids and
membranes the sound encounters (Benade, 1990; Bennet-Clark, 1999). In insect species,
for example, the type of resonator varies from a simple mass/spring system to more
complex systems which may involve multiple types of resonators (Bennet-Clark, 1999).

Pulsed calls are vocals which are compound signals comprised of only a few pulses
with short time intervals between them (Bradbury and Vehrencamp, 1998; Watkins,
1967). The rapidness of the pulses creates sidebands around the fundamental side-
band (or carrier frequency) when viewing signals in spectra. Fundamental frequencies
of harmonic sounds are the lowest frequency band which contain the most energy, while
sideband fundamentals are often produced at a higher frequency with sidebands of lower
energy above and below it (Bradbury and Vehrencamp, 1998; Watkins, 1967). Biolog-
ical filtering and amplitude modulation can often obscure which frequency band is the
carrier or the fundamental (Bradbury and Vehrencamp, 1998). The difference between
harmonics of some sounds and sidebands due to pulsed sounds is thought to be due to
the sound generation mechanism. Often the sidebands of pulsed sounds appear to be
‘harmonically’ related, however the frequency difference between sidebands results from
the pulse repetition rate of the sound generation mechanism (Watkins, 1967).

Odontocetes have two unique anatomical features which may assist in successfully
transmitting sound: lipid-based tissues (‘acoustic fats’) of varying sound speeds and
asymmetrical skulls (Cranford et al., 1996; Norris, 1968). The melon, which contains
these fatty tissues, is located in the dolphin forehead and has two separate appendages,
called monkey-lips dorsal bursae (MLDB) complexes, which protrude into the air pas-
sages located beneath the blowhole (Cranford et al., 1996). A single MLDB complex
consists of a pair of fatty dorsal bursae, a pair of ribbed monkey lips encasing each
dorsal bursae, a cartilaginous blade and a stout ligament, so each MLDB complex has
a pair of ‘monkey lip-dorsal bursa’ (or MLDB) (Fig. 6.1) (Cranford et al., 1996). The
length and symmetry of the two MLDBs vary by species (e.g. the bottlenose dolphin
right dorsal bursae are two times longer than their left dorsal bursae) (Cranford et al.,
1996). It is thought that the sound generators are pneumatically driven by pressurized
air from the nares (Cranford et al., 1996). This air passes through the spiracular cav-
Figure 6.1. Skull anatomy of an odontocete whale showing a single monkey-lip/dorsal bursa (MLDB). This schematic shows only a single MLDB (anterior and posterior) which penetrates the air passageways beneath the odontocete blowhole (yellow). Odontocetes have two pairs of MLDBs. The monkey lips (black) sheath both the anterior dorsal bursa (blue) and the posterior dorsal bursa (pink). MLDBs are appendages of the melon (green). Schematic courtesy of oceanlink.island.net.

Air passes through the nasal cavity which is divided into two nasal air passageways separated by a nasal membranous septum and then over the MLDB complexes forcing them to vibrate and the phonic lips (or monkey lips) to slap shut, temporarily restricting air flow (Cranford et al., 1996). The air is then thought to be captured by the vestibular cavity (air sac) so it can be recycled later (Dormer, 1979). These vibrations travel through the main portion of the melon embedded in the forehead. The melon acts as an acoustic impedance matching medium and with the assistance of some cartilaginous structures located behind it and the telescoping of the skull, impulsive sounds are focused out from the forehead and into the seawater (Cranford et al., 1996). A later analysis using video microscopy on a live dolphin showed that the MLDB complexes vibrated at the same rate as the echolocation clicks (Cranford, 2000), strengthening the hypothesis that they are the sound sources. It is also thought that these two MLDB complexes can slap independently of each other (Cranford, 2000), thereby acting as two independent or loosely coupled sources. Though this hypothesis has only been examined on clicks, the same general process is assumed for other impulsive sounds, like pulsed calls (Cranford, 2000).

Biphonation results in two distinctive frequencies which are produced by two independent or very loosely coupled sound sources (Fitch et al., 2002; Tyson et al., 2007).
Ideally, it is thought these two frequencies need not be related by integer multiples to one another (Fitch et al., 2002). In the case of pulsed sounds, each sound source would produce its own fundamental frequency with its sideband or harmonics around it. In the case of killer whales, the lower frequency component (LFC) (due to source 1) may be within the 1-3 kHz vicinity of the spectrum, while the higher frequency component (HFC) (due to source 2) may appear in the 8-12 kHz region. The time-frequency contour of the HFC can either closely resemble that of an upper sideband of the LFC or it can vary some, however, the HFC often begins and terminates around the same time as the LFC. The interval between sidebands (SBI) for the LFC and HFC, may vary some (few hundred Hz), but are often similar. What appear to be frequency splits within the sounds occur for killer whales (e.g. N04 call), however, these frequencies splits are probably due to biphonation (Miller, 2002, 2007) and not bifurcations (Fitch et al., 2002). Bifurcations are frequency splits which occur in a tonal sound produced by one sound source (or coupled oscillators) (Fitch et al., 2002). Bifurcations are nonlinear dynamics of the call which occur with biological systems when an animals is excited. Since biological systems are not perfect, excitation can cause the vocal folds to vibrate at different frequencies (initially or in transitions between call components) (Fitch et al., 2002). Usually the system adjusts to the transition and the split is united. As will be seen in this chapter, the merging of two split frequencies is observed in in at least one killer whale call, but since their the LFC and HFC are thought to be produced by two different sound sources and in many calls appear quite independent for the duration of the call, can vary in source levels, frequency splits in the HFC region are thought to be due to biphonation.

The relevance and usage of biphonation within a single call varies among animal species. Many bird species, unlike most mammal species, are capable of producing two sounds simultaneously. For instance, emperor penguins have ‘two-voices’ which are close in frequency, that when the two frequencies (and their harmonics) are potentially driven closer, it creates a beating sound (Aubin et al., 2000). Beating allows animals to process sounds in the time domain which may be more distinctive and advantageous in densely populated conditions where many animals are vocalizing. In contrast, songbird sound sources may be activated simultaneously to produce what appears to be single sound or two sounds produced in succession (Suthers, 1990). The ‘two-voice’ system in the non-nesting emperor penguin is thought to provide identity cues, which contrasts that of many other nesting penguin species (Aubin et al., 2000). When biphonation occurs in Northern Resident killer whale vocalizations, it sometimes consist of two frequencies (and their sidebands) which are widely spaced over a few kilohertz in frequency.
some pulsed calls the higher frequency component (HFC) sound is distinctly different from the sidebands of the lower frequency component (LFC), while in other pulsed calls there may be only subtle or no notable differences other than increased energy. As in the emperor penguin and other species, killer whale biphonation also may play a role in animal identity (Crance, 2008; Nousek et al., 2006). Furthermore, the HFC has also been suggested as a means to provide receivers with the direction of travel of the signaling animal (Miller, 2002, 2007).

This analysis focused on a frequency split in the N04 call which occurs in the region of the higher frequency component and is thought to be one of the two vocals in killer whale biphonation. Spectral content of calls will be examined prior to and after the merge of the two frequency bands. In addition, call usage with this characteristic will also be discussed. The goal of this study was to determine if spectral content and usage of these frequency splits in N04 calls were uniform. This analysis will examine if a) spectral content is modified by the location of the higher frequency component; b) young and adults differ in their call spectral content and usage; c) frequency splits are correlated to call initiation within bouts; and d) N04 calls with frequency splits differ in the spectral content and usage during behaviors. The spectral content examined in the frequency split region was frequency and amplitude parameters. Examination of the energy in the N04 call began with the assumption that killer whales have some signal amplitude flexibility to redistribute energy in their frequency bands for communicative purposes. There are a few reasons for this assumption. First, individuals (adults and young) were observed having predominant energy in different sidebands in the analysis in Chapter 3. Second, killer whale HFCs appear to differ among calls, so there appears to be some differentiation not only in frequency but also intensity (noting that there may be some directionality factor influencing the intensity difference). Third, killer whales are known to have both frequency and amplitude modulated pulsed calls; if they can modulate the frequency content for communicative purposes (e.g. pod identity) than they should be able to modulate energy distribution in their frequency bands to accentuate certain frequencies (based on learning, physiological structure and emotive states). It would be expected that a distinctive feature within a call, such as this frequency split, would indicate a signaler’s behavioral context or identity from which receiving animals could extract information. Having the capability of producing two sounds simultaneously has the potential to increase an animal’s ability to transmit more complex information, especially for species which produce group-specific vocalizations. The presence of a second sound source may allow animals to enhance call content (animal identity, size, behavior)
while still maintaining the predetermined acoustic envelope of a pod-specific call. Adult and young animals would be expected to differ in some acoustic parameters within their calls based on size and age differences. First, the physical size difference alone may influence call spectral features (e.g. energy distribution) based on size and sex of individuals (Miller, 2007). Second, very young animals may not be as adept at accurately pulsating sounds with both sources simultaneously or at equal amplitudes, for it may require practice. If a second sound source plays a role of providing additional or a more complex packet of information to receivers it may also provide indirect cues to identifying younger animals. Since young animals were also seen varying energy distributions within sidebands, it is conceivable that they too are capable of frequency and amplitude flexibility. For example, noticeable differences in amplitude between sources, or the lack of a second primary frequency may alert receivers that the vocalizing animal is young.

6.2 Frequency Split Variation

Frequency and power spectral density (PSD) data were obtained where the frequency split occurred and after the two frequencies have merged. Dolphins discriminate best between the frequencies of 2 to 55 kHz and can detect changes in frequency as little as 0.2 – 0.4% (Au, 2003; Jacobs, 1972; Thompson and Herman, 1975; Tyack and Clark, 2000). Hence, these killer whales should be able to differentiate between small differences in frequency, as well as their subsequent merging. Likewise, killer whales should be able to successfully discriminate 1 dB differences (Ketten, 2000) in regions where their hearing is more sensitive (Szymanski et al., 1999). If notable contrasts in energy content (and frequency) between the two sidebands (SB7 and HFC) exists, the implications are that killer whales are capable of perceiving fine-resolution spectral variations. If killer whales are capable of adjusting acoustic parameters within their calls, they can transmit information on body size (Miller, 2007), identity (Nousek et al., 2006), behavioral content or other contextual circumstances.

A total of 199 N04 calls examined in Chapter 3 were examined to see if there was a frequency split at the front portion of the calls (Fig. 6.2). The recording sampling frequency was 48.0 kHz with a 16 bit analog-to-digital converter. Signal analysis frequency resolution was 46.9 Hz. In this analysis, a frequency split is defined as two different frequencies at the same time location which eventually merge with time. In Fig. 6.2, the N04 call starts off with 2 primary frequencies around 9 – 10 kHz which eventually come together into one primary frequency band. The region where this frequency split occurs
is the same region of the higher frequency component (HFC) as described in (Miller, 2002). Hence, one of the split frequency bands is a sideband of the lower frequency component (LFC), while the other frequency band in the split is the HFC.

**Figure 6.2.** Spectrogram of N04 call highlighting 2 frequencies merging into a single frequency. A spectrogram of an N04 call is shown. The first portion of the N04 call shows two frequencies in the 9–10 kHz region where which eventually merge into a single frequency around time 0.504 seconds.

The N04 pulsed call is defined in terms of its sideband numbers and sideband intervals (Fig. 6.3) (Ford, 1989, 1991). In this figure, the sideband 1 (SB1) is the lowest sideband in frequency, sideband 2 (SB2) the next lowest, etc. Fig. 6.3 only shows sidebands up to SB7; however sidebands have energies well beyond this region as seen in Fig. 6.2. On the righthand side are listed the different sideband intervals. For instance in this study, SBI1-2 is the frequency difference between sideband 1 and sideband 2 in Hz, while SBI6-HFC is the difference between sideband 6 and HFC (or the non-SB7 frequency band in the split) (Fig. 6.3).

Power spectral densities (PSDs) and frequency data were taken at five points in the
Figure 6.3. Spectrogram of N04 call defining sideband and sideband intervals. The spectrogram of the N04 call defines the sideband numbers from 1-7 (SB1-SB7), the higher frequency component (HFC) (green), and sideband intervals. For sideband intervals, SBI1-2 is the frequency difference between SB1 and SB2 in Hz, etc. This spectrogram is the same as seen in Fig. 6.2. In this N04 call example the HFC is below SB7. Also, though SBs go well above SB7 as seen in this spectrogram, this illustration only defines up to SB7 and the HFC location.

N04 call (Fig. 6.4). PSDs and frequency have previously been shown to differ among adult males and adult females (who differ in body size) (Miller, 2007), so PSDs may also differ among adults and young killer whales. Data measurements were taken in the two regions where killer whales are thought to produce their 'two-voices' or biphonation. Three of the points were in the band region where the frequency split occurred (Pt1, Pt2 and Pt3, in the HFC region), while two of the points (Pt4 and Pt5) were taken along the lower sideband which had the most energy (in the lower frequency component region (Miller, 2002)). Pt1, Pt2 and Pt4 were all taken at the same time, while Pt3 and P5 were taken at the same time along the spectra. The designators of Pt2 and Pt1 only indicate the top and bottom frequencies in the split, respectively, and do not indicate if these bands are the HFC or an upper sideband of the LFC. Since the frequency split and
the merge of the two frequencies varied between calls, ratios of linear PSD \((Pa^2/Hz)\) were calculated within a call for Pt2/Pt1, Pt1/Pt3, Pt2/Pt3, Pt1/Pt4, Pt2/Pt4 and Pt3/Pt5. These particular ratios were chosen to examine spectral content of the two frequency/energy bands (SB7 and HFC) involved in the frequency split both prior to and after the merge (SB7-HFC) and how both relate to the frequency and energy in the LFC sideband. These ratios may provide insight into spectral differences in this region which animals may use as identification or behavioral indicators. Since the ratio on a linear scale (e.g. Pt2/P1) is equivalent to the difference on a logarithmic scale \((10\log_{10}(Pt2/Pt1) = 10\log_{10}(Pt2) - 10\log_{10}(Pt1))\), ratio data for PSDs between N04 calls were converted into \(10\log_{10}(ratio)\) for analysis (units = dB re 1 \(Pa^2/Hz\)). Fig. 6.5 provides an example of the PSDs of the two frequencies prior to and after (this is from the same call as seen in Fig. 6.3). At time 0.311 into the spectrum (left graph), the bottom frequency is at 9280 Hz with a PSD of 106 dB, while the top frequency is at 9700 Hz with a PSD of 104 dB. Once the two frequencies merge the frequency is 9100 Hz with a PSD of 103 dB (at 0.504 seconds into the spectrum).

N04 calls were also examined to determine which frequency band (the top or bottom) was the actual HFC and which was a resultant sideband of the LFC. The sideband involved in the split which was associated with the LFC was also recorded. Once the frequency band of the HFC was determined, the energy ratios of the Pt2/Pt1 was examined using a independent sample t-test (see Appendix C for description and symbols). Data was checked to meet normality assumptions and variances were examined for equality.

### 6.2.1 Results

A total of 48 (24.1\%) of the 199 N04 calls examined in this thesis exhibited the energy split of two different frequencies at the front half of the call which later merged. Some calls had shown only a single frequency or sideband in the HFC region at the beginning of the call (25.7\%). In 47.7\% of N04 calls, energy was too low within the SB7 region to actually determine if a split was present. In 2.5\% of the calls, the start of the call differed from the cases above or the two frequencies never merged (i.e. acted independently throughout the call).

Similar to the lower frequency component (LFC), the higher frequency component (HFC) also appeared to have its own sidebands. The sideband with the greatest energy of the HFC always occurred in the vicinity of SB7 associated with the lower frequency component (LFC). There was only one HFC instance where the energy was also high in the SB6 region, along with the SB7 region, of the LFC. The HFC also shifted with the
Figure 6.4. Spectrogram illustrating PSD data points along SB7/HFC and LFC locations. Spectrogram shows where 5 data points of PSD differences were taken in the N04 call. Pts 1, 2, and 4 were all taken at the same time, though different frequency bands. Pts 3 and 5 were also taken at the same time along the N04 spectrum. Pts 4 and 5 were taken along the sideband with the most energy, while Pts 1, 2, and 3 were taken along the region where the frequency split occurred.

The location of SB7 varied between N04 calls from approximately 9 kHz to 12 kHz. In each instance the HFC was associated with SB7 regardless of what frequency was produced. The relationship of the highest energy HFC and SB7 varied between N04 calls. The number of times the HFC was above SB7 was exactly equal to the number of times it was below SB7. Fig. 6.6 illustrates the relationship between the HFC and SB7 (of the LFC). Overall this figure illustrates the distinct difference between the HFC and the sidebands of the LFC of the N04 call up to the merge in frequencies (Fig. 6.2). The top two graphs of two different N04 calls shows the sideband interval (SBI) relationship of the front portion of the call (once the HFC begins) to just where the two primary frequencies merge (indicated by the arrow). Sideband 2 (SB2) has been highlighted in blue since it was often the sideband with the most energy as
Figure 6.5. Power spectral densities of 2 frequencies in HFC vicinity merging into a single frequency. Two PSDs are shown from a single representative N04 call (the same as in Fig. 6.2). The PSD on the left shows the levels of the two independent frequencies prior to the merge (at approximately 0.311 sec), while the PSD in the right graph reveal the level after the merge (0.504 sec). Frequencies and source levels are indicated for the peaks in the HFC location on each graph.

noted in Chapter 3, while the HFC is indicated in green. The top left graph has HFC below SB7, while the top right graph of call 2 has HFC above SB7. The bottom two graphs of Fig. 6.6 show the same two calls as above, but displays the SBI frequencies between each sideband of the LFC (Fig. 6.3). In both lower figures, the SBIs are nearly equivalent in frequency (approximately 1300-1500 Hz). In contrast, calculations of the frequency difference between SB6 and HFC (SBI6-HFC, shown in green) differed from that of SBI6-SBI7; the expected difference if the two sounds were equivalent. SBI6-7 is highlighted in magenta to illustrate the difference in frequency from a representative sideband interval associated with the LFC to that of a sideband comparison to the HFC. In both bottom graphs, the SBI6-HFC differs from expected with call 1 SBI6-HFC being lower by approximately 400 Hz (left) and call 2 having a SBI6-HFC being greater in
frequency by 800 Hz (right).

The energy of the HFC when it was above SB7 and when it was below SB7 was calculated. The null hypothesis ($H_0$) was that energy difference was uniform between Pt2 and Pt1 regardless of the location of the HFC (i.e. whether the HFC was above or below SB7 before the merge) (Fig. 6.4). An independent-samples t-test revealed that PSDs were greater when the HFC was above SB7 and lower when it was below SB7 ($\delta \mu = -13.8377, \delta \sigma = 3.0536, \alpha = 0.05, df = 46, t = -4.53167, p < 0.0001$) $H_0$ was rejected) (Fig. 6.7). Bars in the figure represent the 95% confidence interval about the mean. Killer whales should be able to resolve differences in levels of 10 – 20 dB in the 9 – 11 kHz region (where their hearing threshold is more sensitive) (Szymanski et al., 1999), since odontocetes can successfully discriminate 1 dB differences (Ketten, 2000). Notable differences in PSDs could be used to transmit information such as body size (Miller, 2007), identity and other behavioral contexts.
Figure 6.6. Higher frequency component relationships with sidebands and sideband intervals. Higher frequency component (HFC) in relationship with sidebands (SB) and sideband intervals (SBI) is shown for two calls. The top two graphs show the SB frequencies (for SB1 through SB7) for two N04 calls, sidebands greater than SB7, which are normally seen in spectrograms, are not shown here. In call 1 the HFC is below SB7 (left top), while for call 2 the HFC is above SB7 (right top). HFCs are highlighted in green while SB2 is highlighted in blue (top graphs). The lower two graphs represent the SBI frequencies which are relatively consistent between sidebands for both call (bottom two graphs), however the difference between SBI6 and HFC (SBI6-HFC) (green), greatly contrasts all the other SBIs. SBI6 – SBI7 and should be equivalent to SBI6 – SBI7 (magenta) if they were the same sound. At the last point in both of the calls, SB7/SBI7 and HFCs merge, indicated by the arrows.
Figure 6.7. Power spectral density difference when HFC is above and below SB7. The PSD difference is shown in relation to the HFC location near SB7. PSD here is defined as $10\log_{10}(\text{Top/bottom sideband})$ (Fig. 6.4). HFC has a greater PSD when it is above SB7 compared to when it is below it. Bars represent the 95% confidence intervals around the mean.
6.3 N04 Frequency Split Usage

6.3.1 Young versus Adults

Killer whales were divided into two categories, young and adult. In this analysis, young killer whales were immature juveniles and younger (i.e. twelve years old or below). Logarithmic PSD differences (along with frequency differences) were calculated within a call for Pt2/Pt1, Pt1/Pt3, Pt2/Pt3, Pt1/Pt4, Pt2/Pt4 and Pt3/Pt5 (Fig. 6.4). Scatterplots were examined and the energy ratios and frequency differences between these points were examined using an independent sample t-test. Data was checked to meet normality assumptions and variances were examined for equality.

In terms of call usage, N04 calls with frequency splits were examined to see if there was a disproportionate production of frequency splits between young and adult killer whales. A binomial test was used to examine whether young or adult killer whales produced these frequency splits more often. Post hoc power of these binomial tests were calculated by a binomial or normal approximation based on the sample size and if the probability of the successes was near zero or one (Jones, 2002). In addition, young and adult killer whales N04 calls were examined for differences in the location of the HFC with respect to SB7, using 2-tailed Fisher’s Exact test.

6.3.1.1 Results

N04 calls with frequency splits were examined to see if there was variation in spectral content (PSDs, frequency) by adults compared to young killer whales. The null hypothesis ($H_0$) was that spectral content of frequency splits were uniform between young and adults. An independent samples t-test revealed that there was a difference in PSDs of the SB7/HFC after the merge and the LFC (i.e. Pt3/Pt5) between adults and young killer whales ($\delta \mu = 7.259, \delta \sigma = 2.975, \alpha = 0.0080, df = 46, t = 2.439, p = 0.021$) $H_0$ was rejected) (Fig. 6.8). Negative psd difference levels indicate that for both young and adult killer whales, the LFC had more energy than the HFC. However, the difference in PSDs between the SB7/HFC and LFC regions was smaller or more equivalent for adult animals, while young killer whales tended to have more energy in the LFC than the SB7/HFC region. No other statistical tests were run in this analysis, due to extreme overlap seen in scatterplots of PSD levels or frequency differences (Table 6.1). Since only one statistical test was run on this analysis the Bonferroni correction (which is used to adjust the alpha value when more than one statistical analyses is used on the same dataset) was not applied.
Figure 6.8. Power spectral density difference between post merge SB7/HFC and LFC for adults and young. The PSD difference of the the energy in the post merge SB7/HFC region and the LFC. PSD here is in defined as $10\log_{10}(P_{t3}/P_{t5})$ (Fig. 6.4). Negative PSD difference levels indicate that for both young and adult killer whales, the LFC had more energy than the HFC. However, the difference in PSD between the SB7/HFC and LFC regions was smaller or more equivalent for adult animals, while young killer whales tended to have more energy in the LFC than the SB7/HFC region ($p = 0.021$). Bars represent the 95% confidence intervals around the mean.

Table 6.1. Analyzed N04 power spectral densities for adults and young. PSDs were compared to see if data distributions in scatterplots overlapped by half or less. Only one test was run for post merge SB7/HFC and LFC (i.e. $P_{t3}/P_{t5}$) as seen in Fig. 6.8. As indicated in this table as ‘no sig’, all other PSDs did not meet the scatterplot overlap criteria, so no statistical tests were conducted.

<table>
<thead>
<tr>
<th>Ratio</th>
<th>PSD (dB)</th>
<th>Frequency (Hz)</th>
</tr>
</thead>
<tbody>
<tr>
<td>$P_{t2}/P_{t1}$</td>
<td>no sig</td>
<td>no sig</td>
</tr>
<tr>
<td>$P_{t1}/P_{t3}$</td>
<td>no sig</td>
<td>no sig</td>
</tr>
<tr>
<td>$P_{t2}/P_{t3}$</td>
<td>no sig</td>
<td>no sig</td>
</tr>
<tr>
<td>$P_{t1}/P_{t4}$</td>
<td>no sig</td>
<td>no sig</td>
</tr>
<tr>
<td>$P_{t2}/P_{t4}$</td>
<td>no sig</td>
<td>no sig</td>
</tr>
<tr>
<td>$P_{t3}/P_{t5}$</td>
<td>0.021</td>
<td>no sig</td>
</tr>
</tbody>
</table>

Frequency splits in terms of usage were also examined between adults and young. The null hypothesis ($H_0$) was that the presence of frequency splits were uniform between young and adults. A binomial test indicated that N04 calls produced by adults occurred slightly more often ($n=21$) than by young killer whales ($n=9$) ($\alpha = 0.05, n = 30, p = 0.043, power = .60, H_0$ was rejected). Of all the N04 calls with the frequency split ($n=48$), it was seen with adult animals 45.3% of the time, 18.9% with young killer
whales and 35.8% with mixed groups (only the adults versus young were tested). All types of individuals (adult male, adult female, juveniles and calves) were seen to produce frequency splits in the HFC region, however, only one calf (2 years or younger) was seen doing this. N04 calls were also examined to see if young and adult killer whales differed by the location of the HFC in relation to SB7. A difference in production of the HFC in relation to a sideband of the LFC may indicate developmental differences in sound production. If one band is always above the other, and animals are capable of differentiating these frequencies and amplitude differences, than this pattern may be used for a means of detecting adult or young killer whales. The null hypothesis ($H_0$) was that the location of the HFC was uniform between young and adults. A 2-tailed Fisher’s Exact test indicated that the location of the HFC in relation to SB7 was not equivalent between young and adults ($\alpha = 0.05, n = 30, p = 0.0417, H_0$ was rejected). There was no difference in the location of the HFC compared to the SB7 for adults, but the young almost always produced the HFC below SB7.

6.3.2 Call Initiators

N04 calls with frequency splits were examined to see if they were the first N04 call in a bout of pulsed calls between multiple animals or if they were the first N04 produced by that specific animal(s). In this analysis, a call bout is a series of vocals within seconds of one another usually produced by multiple animals. If a N04 call was considered the first pulsed call in a bout then no other vocals were produced a minute prior to that N04 call. The second analysis examined the first N04 call produced by individuals within a bout, so it could, for example, be the bout’s first pulsed call or the bout’s seventh pulsed call. Binomial tests were used to test both circumstances. If significant differences were found, a post hoc power of these binomial tests were calculated by a binomial or normal approximation based on the sample size and if the probability of the successes was near zero or one (Jones, 2002).

6.3.2.1 Results

The first null hypothesis ($H_0$) was that the occurrence of N04 frequency splits were uniform regardless of whether the N04 call was the first N04 in a vocal bout or whether it was not. A binomial test indicated that there was no difference in the presence of N04 frequency splits with where it occurred in a vocal bout ($\alpha = 0.05, n = 48, p = 0.193, H_0$ not rejected). N04 calls with the frequency split were also tested to determine if they occurred more often when it was the signaler’s first N04 call in a bout. The null
hypothesis ($H_0$) was that N04 frequency splits were uniform regardless of whether or not it was the animal’s first N04 call. A binomial test indicated that the N04 frequency split occurred approximately the same amount when it was an animal’s first N04 call in a bout compared to when it was not their first N04 call ($\alpha = 0.05$, $n = 48$, $p = 0.193$, $H_0$ not rejected).

### 6.3.3 Behaviors

Correlations to foraging and traveling behaviors were examined in terms of spectral content, as well as, call usage. Logarithmic PSD differences (along with frequency differences) were calculated within a call for Pt2/Pt1, Pt1/Pt3, Pt2/Pt3, Pt1/Pt4, Pt2/Pt4 and Pt3/Pt5 (Fig. 6.4). Scatterplots were examined and the energy ratios and frequency differences between these points were examined using an independent sample t-test. Data was checked to meet normality assumptions and variances were examined for equality. In addition, correlations of foraging and traveling behaviors with regards to the location of the HFC (in relation to SB7) were also explored and distributions examined using a fisher’s exact test.

#### 6.3.3.1 Results

In this study, the presence of an N04 frequency split was equivalent during foraging and traveling behaviors. Behaviors were then examined to determine if behaviors varied with respect to the location of the HFC to SB7. The null hypothesis ($H_0$) was that the location of the HFC in relation to SB7 of N04 calls was uniform across behaviors. A Fisher’s Exact test revealed that the production of the HFC below and above SB7 during foraging and traveling were not uniform ($\alpha = 0.05$, $n = 46$, $p = 0.038$, $H_0$ was rejected) (Fig. 6.9). Distributions indicated a slight bias for the HFC to be produced below SB7 when the signaler was foraging compared to being produced above SB7 when the vocalizing animals were traveling.

Based on scatterplots of the data, no convincing correlations were found comparing PSD level or frequency differences prior to and after N04 frequency merges for foraging and traveling behaviors (Fig. 6.2).

### 6.4 Discussion

Odontocetes appear to be capable of producing two sounds simultaneously as witnessed in analysis of spectra and anatomical sound generation mechanisms in earlier
Figure 6.9. HFC location to SB7 during foraging and traveling. This figure shows the distribution of the signaler’s behaviors around the time the N04 was produced and whether the HFC was below or above SB7. In this study, signaler’s producing the N04 call had a slight tendency, to produce the HFC below SB7 when foraging and above SB7 when traveling (Fisher’s Exact test, p=0.038).

Table 6.2. Analyzed N04 power spectral densities during foraging and traveling. PSDs were compared to see if data distributions in scatterplots overlapped by half or less. As indicated in this table as ‘no sig’, neither PSDs no frequencies during behaviors meet the scatterplot overlap criteria, so no statistical tests were conducted.

<table>
<thead>
<tr>
<th>Ratio</th>
<th>Forg PSD (dB)</th>
<th>Forg Frequency (Hz)</th>
<th>Trav PSD (dB)</th>
<th>Trav Frequency (Hz)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Pt2/P1</td>
<td>no sig</td>
<td>no sig</td>
<td>no sig</td>
<td>no sig</td>
</tr>
<tr>
<td>Pt1/P3</td>
<td>no sig</td>
<td>no sig</td>
<td>no sig</td>
<td>no sig</td>
</tr>
<tr>
<td>Pt2/P3</td>
<td>no sig</td>
<td>no sig</td>
<td>no sig</td>
<td>no sig</td>
</tr>
<tr>
<td>Pt1/P4</td>
<td>no sig</td>
<td>no sig</td>
<td>no sig</td>
<td>no sig</td>
</tr>
<tr>
<td>Pt2/P4</td>
<td>no sig</td>
<td>no sig</td>
<td>no sig</td>
<td>no sig</td>
</tr>
<tr>
<td>Pt3/P5</td>
<td>no sig</td>
<td>no sig</td>
<td>no sig</td>
<td>no sig</td>
</tr>
</tbody>
</table>

studies (Cranford, 2000; Cranford et al., 1996; Dahlheim and Awbrey, 1982; Ford, 1989; Miller et al., 2004). This study investigated the frequency split and subsequent merging of two frequencies in the SB7/HFC region of the N04 calls; both spectral content and call usage distributions were examined. In all instances, prominent energy of this frequency split of the N04 call (between an upper LFC sideband and HFC) occurred in the vicinity of SB7 of the LFC. The association of HFC with the SB7 appeared to be stable and HFC shifted with SB7 when sideband intervals of the LFC varied between N04 calls. This intriguing observation suggests at least a loose coupling between the sounds, or limitations to where the HFC is produced. The location of the HFC in these frequency splits and merges raises questions about possible usage to transfer signaler information, as well as, anatomical (and physiological) relationships of the two sound sources or MLDB complexes. In the dolphin head the two dorsal bursae which are thought to produce the
two sound sources are both appendages of the melon (Cranford, 2000; Cranford et al., 1996).

The HFC component varied in its relative frequency location to SB7 and tended to have more energy when it was above SB7 compared to when it was below it. Killer whales should be able to resolve differences in levels of 10–20 dB in the 9–11 kHz region, since odontocetes can successfully discriminate 1 dB differences (Ketten, 2000). Being able to activate a second sound source would also help accent it (in terms of energy and/or contour) in relation to the upper LFC sideband. Killer whales appear to be capable of resolving differences between HFC and SB7, so if they are intentionally beginning calls with frequency splits then they may be able to use it as some behavioral, contextual or individual cue to conspecifics. In this study, the N04 calls often exhibited less distinctive HFC as might be seen in analysis of some other Northern Resident pulsed call spectrograms previously described (e.g. N09 call) (Miller, 2002). The two independent or loosely coupled signals found in killer whale spectra are discretely spaced in frequency by at least 7 kHz in the N04 calls seen here. Thus, unlike the emperor penguin, these killer whales producing N04 calls do not reduce the frequency difference between the sources to create beating (Aubin et al., 2000). Beating would not seem useful to killer whales since they already have a predominant call type which could be resolved temporally within close proximity. Whether killer whales can phase lock the frequency of one source (HFC) to the upper sideband of another source (SB7) and merge the frequencies as witnessed in this study is something that needs to be further investigated (Keolian and Rudnick, 1986). Understanding why some killer whale calls have more distinctive spectral differences between their HFC and LFC (contour, energy), while others do not (e.g. N04) may be important in assessing their sound generation and airflow capabilities, as well as, possible call intent. In the case of the N04 call, the two sources conforming to one another may strengthen the overall signal making it even more viable and successful in longer distance vocal communication compared to other proposed long-range vocals (Miller, 2006).

Differences in spectral content due to body size or age are prevalent in many species. In this study, adults and young differed in PSD levels after the merge in the SB7/HFC region when comparing this sideband with that of the LFC. In both age groups the LFC had less energy than the HFC, however adults exhibited a smaller mean difference (7.0 dB) between HFC and LFC energy compared to younger killer whales (-17 dB difference). All types of killer whales appeared to be able to produced the frequency split at the beginning of the N04 call, though in this study more adults were seen doing so. Adults
also equally produced the HFC above and below the SB7 frequency while young killer
whales predominantly produced the HFC below SB7. Whether young killer whales expe-
rience limitations or less precision in the production of the HFC is not currently known.
Younger animals might have to practice fine-tuning frequencies for their pod-specific
calls, as well as, successfully recycling air and vibrating two sources simultaneously.

In this analysis no correlations were found for the N04 frequency split for call initia-
tion, however some trends in usage were found for behaviors. The frequency split in the
SB7/HFC region does not appear to be associated with any N04 call initiation either for
the first pulsed call in a vocal bout or for the first N04 call produced by an individual
in a bout. For behaviors, there was a slight bias for killer whales to produce the HFC
below SB7 during foraging compared to above SB7 during traveling. Previously, internal
variations were found within the stereo-typed acoustic structure of the N04 (Chapter 3).
Whether killer whales can use this split as an indicator of some contextual circumstance
needs to be examined more closely.

In summary, the findings in this study indicate that the predominant sideband of
the HFC is strongly associated with SB7 of the LFC for the Northern Resident killer
whale N04 call. Since the biphonation in other killer whale discrete pulsed calls varies
in uniqueness between the proposed ‘two-voices’ within a call (Miller, 2002), it appears
killer whales are capable of manipulating the source outputs to some degree (based on
spectra). These frequency splits were seen in 24% of the N04 calls analyzed in Chapter
3. An important question is whether frequency splits are intentional or whether they are
an indirect bi-product of the sound generation mechanism (i.e. honest signalling)? It is
conceivable that this frequency split could be due to differences in the sound generation
startup, however, these splits occur well past the initial phase of the signal and they do
not merge until well after the call’s onset (approximately 1/5 into the call). In some
instances they did not merge until half way through the call, so the time variation in
merging can be high. Killer whales appear to be conjoining the HFC with SB7 of the
LFC, perhaps to emphasize the higher frequency band. Other pulsed calls produced by
the same pods (e.g. N09) exhibit more distinct simultaneous sounds in spectra which do
not merge (Miller, 2002), indicating that killer whales have some control in separately
varying the HFC from the LFC contours. As seen in this study, killer whales seem
capable of having the frequencies of two separate outputs overlap as nesting birds do
(Suthers, 1990; Suthers et al., 2003). Whether killer whales can regulate between single
and separate airflows to stimulate their two sources remains to be see, but since they are
capable of producing clicks and whistles simultaneously it appears probable (Dahlheim
This preliminary analysis was meant to highlight the presence of the N04 frequency splits and explore a few acoustic parameters associated with the split and its usage (with the assumption that this split is intentional). Killer whales are capable of varying frequency and spectral information of their calls and they may be able to increase the types of information they transmit. Killer whales appear to have body size frequency and amplitude information with in their calls (Miller, 2007). Preliminary findings in this analysis suggests that there are some acoustic features and potential usages of N04 calls with this split which vary between age groups. In addition there appears to be acoustic features in the N04 frequency split which killer whales would be able to discriminate between in terms of relative location of the HFC. Since, killer whales should be capable of perceiving fine frequency and time resolution like other dolphins (Au, 2003; Jacobs, 1972; Ketten, 2000; Thompson and Herman, 1975; Tyack and Clark, 2000), they may be able to transmit information within this region. Overall this analysis did not lead to further insight of the potential use of frequency and energy in the frequency split region as a communicative tool by killer whales. Though this analysis may have raised more questions than it answered, it is still a convincing argument that killer whales are capable of some signal energy distribution flexibility which has potential impact in communication and should be further investigated. Only a few circumstances were examined for the few acoustic parameters obtained in this analysis, so a more in depth analysis within the SB7-HFC region is warranted. Future research on both the sound production level and spectral analysis level during varying contextual circumstances would eventually help determine if there is a relevance to this frequency split and if animals are capable of phase-locking (Keolian and Rudnick, 1986) the frequency of one source to the sideband of another to successfully merge two frequencies within a call or if they vary air flow patterns over their sources. In any outcome, the ability to produce two sounds would enhance overall signal complexity and make signals more robust to masking (Andrew, 1962; Miller, 2006; Richardson, 1995).
Chapter 7

Conclusions

7.1 Summary

The scientific goal of this dissertation was to carefully study the signal structure of killer whale communications and consequent vocal complexity and link them to behavioral circumstances. The focus was on communication related to physical and social circumstances of killer whales when they are apart and how they use vocalizations in these instances. In this analysis, aspects of call content and vocal usage were examined. Northern residents have a long cultural tradition with long-term family associations and dialects (Ford, 1989, 1991; Ford and Fisher, 1983). Documentation of this population through photo-identification catalogs has been updated since the early seventies with individuals and their familial associations (Bigg, 1982; Bigg et al., 1983, 1990). The vast database on Northern Resident killer whale life histories and vocal repertoires make them an ideal candidate to begin examination of individual (and small group) vocal behavior during well documented varying behavioral and precisely measured movement circumstances. In addition, the natural swimming distribution patterns and clustering of individuals on short and long-term time scales make this population of killer whales ideal for trying to localize animal sounds and examine intra-group behavioral patterns. Localization of the Northern Resident sounds was previously carried out using a newly developed towed hydrophone array system (Miller, 2000).

Chapter 3 was focused on the spectral content of a single discrete pulsed call (N04) produced by the three pods (A1, A4, and A5) and its usage during varying behavioral circumstances. The N04 call has been previously studied and found to be shifting over time (for the A12 and A34 matrilines), which contrasted the N09 which was stable over the 12-13 year period. The analysis in this thesis focused initially on slopes along
the contour of the call and other acoustic parameters which may vary with behavioral movements. The N04 call could be divided into 4 subtypes which though they exhibit some discreteness at different slopes, may be often a continuum within the spectral envelope of the discrete N04 call. Individual killer whales were found to produce more than one N04 subtype indicating that divergence may be due to a gradual evolution of the call. Slopes and other acoustic parameters (duration, frequency, source levels, peak frequency, max source level at peak frequency, etc.) varied greatly. This analysis showed no significant ties to those acoustic parameters within the call that could be correlated to foraging, traveling or movement behaviors. Energy within Northern Resident killer whale calls was often predominant in the second sideband, while variations in predominant sideband energy appeared to vary with subtype. In this study, the distribution of data when energy was in the second sideband for all N04 calls combined was biased toward traveling behavior and straight movement patterns. Like the baboons, which exhibited a more strident, unstable internal call structure when separated from group members, killer whales may also exhibit excitation or urgency when they are beyond visual range of family members. Killer whales may also be able to vary the energy distributions in their calls to better meet optimal conditions for changing environments.

Chapter 4 studied killer whale calling behavior for pre- and post-joining events. The findings in this study indicate that discrete pulsed calls play an important role in the vocal exchanges between killer whales prior to joining events (there were only three events of forty-three where pulsed calls were absent). Two-way vocal exchanges prior to joinings between individuals and small groups of killer whales were more commonly seen than one-way vocal production. Solitary animals initiated pulsed calls more often than small groups. No specific vocal was correlated to pre-joining events, but the the proportion of some calls were elevated during this time period. N04 production revealed that pre-joining N04 usage during foraging was greater than expected by chance. In addition, N04 usage was greater around the time animals were turning and lower during straight path swimming.

The goal of Chapter 5 was to determine if the rate of call patterns were uniform across encounters, vocal bouts and pods and if vocal exchange behavior was uniform amongst mother/offspring groups during separations. The elevated matched calling rates seen in encounters and bouts suggest that they are a regular feature in killer whale vocal production as seen in previous studies with a few isolated individuals. However, there was no bias for matched first response calling to initiated calls nor toward animals producing a single call when matching. All individuals in mother/offspring groups initiated and
respond to pulsed calls when there was a separation. However, mothers responded much less than anticipated and offspring especially immature juveniles responded as much as they initiated calls. The majority of no responses were due to mothers who were foraging, which has implications of prey alerting. During examination of energy distributions in the N04 call, the non-SB2 N04 production was greater during foraging when a mother was separated from her offspring, but low when a mother was with her offspring; this trend was not seen for the SB2 N04 production.

Chapter 6 examined spectral content and usage of the frequency splits in N04 calls. The findings in this study indicate that the predominant sideband of the HFC is strongly associated with SB7 of the LFC for the Northern Resident killer whale N04 call. Energy in the frequency regime after the SB7/HFC had merged was equivalent to the LFC energy for adults, however young had more energy in the LFC. Also dissimilar to adults, the young almost always produced the HFC below the SB7. Finally, distributions indicated a slight bias for the HFC to be produced below SB7 when the signaler was foraging compared to being produced above SB7 when the vocalizing animals were traveling.

### 7.2 Conclusions

Northern Resident killer whales live in a very intricate social system and have complex vocal traditions and behaviors. This study has expanded upon the vast work conducted by other researchers who established and now maintain the identification catalogs, determined the vocal repertoires/traditions of these animals as well as their behaviors, localized the first individual killer whale sounds and examined call features. One of the strengths of this analysis is the vocalizations of individual whales and mapping movement tracks plus the ability to see and examine vocal trends of many animals from many pods and matrilines including more than one clan.

Killer whale vocal traditions, in terms of call content and usage, appear to be as intricate as their social traditions and interactions. In terms of call usage, as seen in previous studies on this population and Norwegian killer whales, no single call was produced for any of the behavioral circumstances in this study (foraging/traveling, general movement patterns, mother/offspring separations nor joining events). Less frequent calls may serve specific functions, however due to the low rate of production of these calls, they are difficult to analyze. Pattern vocal exchanges such as matched call-types can increase vocal complexity for a pod or matriline without having to add more vocalizations to their repertoires. All five pods (A1, A4, A5, I11, I31) from two clans (A
and G clans) examined in this study produced match call-types. All individuals were found to produce the predominant pulsed calls in their repertoires along with producing matched and mixed call types. An earlier study examined matched calling exchanges between two adult males and their mother, indicating that males also matched call types. Pods from both A and G clans showed an increase usage of pulsed call production prior to joining events compared to post joining events. Also, vocalizations leading up to joining events were more often two-way exchanges of calls between individuals joining, though sometimes only one individual vocalized. In both mother/offspring separations and joining events two-way vocal exchanges were seen along with occasional one-way ‘announcement’ vocals. Mothers did not always respond to their offspring, but immature juveniles responded quite regularly. Further investigation of distance parameters and how they relate to vocal exchanges would help researchers understand the intricacies of mother/offspring and vocal exchanges between other individuals.

Examination of the spectral content of one of the most common pulsed calls, the N04 call produced by the three A pods, showed a high degree of variation and complexity within its discrete spectral envelope. It is not known whether: 1) the inability to find correlations to behavior is due to the high variability between individuals in the call (due to the variable nature of the call, individuality, etc.); 2) the spectral parameters and their locations were not biologically meaningful for behavior and movement information; 3) killer whales do not need to relay such contextual information; or 4) the key parameters in the call were not identified, to allow correlation with behavior. Odontocete abilities to differentiate frequencies and time information is highly acute. The N04 call had some distinctive features between subtypes that animals could extract different slope or frequency trends if behavioral information is indeed encoded in there calls. Also in this same analysis, individual usage of the N04 subtypes was examined. Individuals were found to produce multiple subtypes of the N04 call, indicating that divergence of the N04 call is not the result of individual differences but may indicate the gradual evolution of a new call type.

Killer whale vocal content and/or usage reliably transmits enough information to facilitate movements and interactions since matriline and pod members repeatedly locate one another on short time scales. Identifying spectral parameters which would accurately reflect the signaler’s intended output to receivers is vital in understanding communication between these animals. For instance, are there characteristics within these signals (e.g. N04 call) that signalers’ could successfully transmit group, individual, directional, behavior or movement information? And are these parameters limited by
range? Killer whales produce stereotyped calls which are pod-specific. These broadband sounds contain frequency and amplitude modulation, often two primary frequencies, directionality cues, and most likely some identity information. Pod-specific calls would solve the problem of group identity at most ranges. Producing call segments that are more stable (Seg5 of N04 call) would enhance the efficiency of communication. Adjusting energy distributions to more optimal frequencies for the environment would further increase detectability. An animal’s location is determined by directional receivers and transmitters, both of which would be limited by body size and physiological structure of the source and hearing mechanisms. Individual information within calls is most likely identifiable to closely related receivers when they are within close proximity to the signaling animal. Hence, animals may use some features in the call to locate conspecifics over longer ranges, then as they swim within closer proximity they are able to extract more intricate information encoded in the calls.

Another indicator in killer whale vocalizations which may convey information is arousal or excitation which has been seen in other species. Many N04 calls had predominant energy in the second sideband, while others had energy in another band. Accurately assessing a known animal’s identity coupled with variations in arousal state could potential supply reliable information such as a food source. However, it is necessary to link acoustic differences to physiology and anatomy during high stress states. Variations in emotive states may be more difficult for eavesdroppers to interpret while family members may accurately assess the signaler’s intent. Such an indicator would be very important to individuals for intra-family purposes which would include sharing prey.

7.3 Future work

Accurately localizing killer whale sounds allows researchers to examine an individual’s vocal and behavioral interactions within a group. Behavioral observations coupled with the localization sounds produced by individuals could potentially shed light on killer whale dialect usage. Applying multiple data collection techniques (e.g. precise visual recordings, acoustic recording and localization techniques) within the same study could also provide a greater understanding of signal characteristics near the source as well as at greater ranges from the source. Scientists may then isolate signal characteristics from vocalizing animals that are biologically meaningful at varying ranges to receivers. Also, captive research could strengthen the understanding of killer whale sound production and
hearing/perception which would be useful to in free-ranging killer whale communication studies.

One area that could be examined closer is the spatial separation at which calling behavior occurred in the mother/offspring circumstances. Bottlenose dolphin calves were found to start vocalizing at the time they began orienting themselves toward their mothers (Smolker et al., 1993). There may be some distance parameter which may stimulate vocal activity by young once they have swam outside the given range of their mother. This circumstance may also be true for individuals who are joining. At some critical distance, a vocal pattern may emerge which is integral in facilitating movement such as re-joinings. Closer examination of the same individuals during repeated vocal exchanges for the same circumstance, could highlight any acoustic patterns (spectral, call types, pattern sequences) which may exist. However, this requires a carefully collected database. This study was able to provide an understanding of patterns (physical movement, vocals) which may be universal for a larger portion of the population, however, extracting more subtle cues requires focused databases on individuals involved in specific contextual circumstances.

Another area of analysis is to explore the spectral content of other pulsed calls recorded in this study to see if there are trends between calls during different behavioral or contextual circumstances. In addition, it would be useful to compare other discrete pulsed calls to the results in the N04 call. As seen in an earlier study some calls (e.g., N09) may be inherently more stable or consistent than others (e.g., N04) (Deecke et al., 2000) so extracting specific acoustic characteristics will vary between calls. Signals are subject to propagation anomalies and any study of signal content which would be robust at distance may provide a linkage to biologically meaningful acoustic properties. Examination of signals produced across the strait compared to near the hydrophone array indicated that the middle portion of the call withstood propagation compared to the front hump portion or the tail region of the signal. The middle portion of the call may be produced at a frequency that is optimal for propagation conditions in Johnstone Strait. Within closer proximity, finer features in the hump and tail region may contain more valuable close range information such as identity and other behavioral information which may be essential in animals joining or maintaining cohesion. Ultimately it would be advantageous for the study of odontocetes to progress to recording signals at higher sampling frequencies so that inter-pulse intervals can be examined more closely and added to spectral analysis.

Energy usage within pulsed calls should be examined between two sites with known
propagation conditions. Collecting propagation conditions in Johnstone Strait and collecting killer whale sounds and propagation conditions in a different environment such as near Queen Charlotte Islands which is a more open ocean environment, would provide insight into if and how killer whales distribute energy with in their calls. Since shallow water conditions have an optimal frequency for propagation (Jensen and Kuperman, 1983), killer whales may be able to adapt to their ‘propagation environment’.

Energy distribution patterns in initiated and response calls could also be examined if localized vocalizations have been obtained. For example, do initiators increase the amplitude of their calls, and adjust their calls once they are aware of the receivers location? If receiving animals can determine the signalers location can they adjust their call amplitudes depending on their range to the signaler? Is there a change in the distribution of energy within sidebands of their pulsed calls in these exchanges? Potential variation of normal call patterns such as arousal or excitation that would alter the call may provide general information to other family members. However, to do this, more has to be learned on the spectral content of the calls of individual animals and how they may differ from each other. In addition, energy studies would require a careful thought out set of trials or data captures (e.g. a time or space study) within a defined range.

A potentially intriguing study would be to focus on localized sounds around the time of joining events that involve food sharing. Pulsed calls in the vicinity of individuals emitting echolocation clicks should also be examined. When individuals or small groups join to break up and share food, what acoustic indicators are relaying a successful prey capture? In this study, pulsed call production increased before joining events. For joinings which involve prey sharing what call types, patterns and vocal exchanges are occurring? Since joinings of a few animals that have been seen breaking up and sharing food (Ford and Ellis, 2006), there must be some indicator upon which the joining animals rely. Acoustic recordings could be obtained in the vicinity of animals which surface with food captures to investigate if animals capturing the prey initiate vocalizations or if joining animals vocalize or use eavesdropping to join that animal. Animals probably produced echolocation prior to captures but then produce pulsed calls to alert conspecifics to orchestrate food sharing. The series of clicks followed by pulsed calls could be an acoustic indicator of prey capture. It would not be advantageous for other individuals to divert from active foraging unless they were convinced of a food source (e.g. food sharing). Research may also want to investigate which animals are sharing prey, which may provide further insight into the dynamics of killer whale cultural traditions.

Attaching D-tags to record information on individuals coupled with hydrophone array
recordings and behavioral observations may also help to gather fine-scale movement and acoustic data on one individual and examine how that individual interacts with the group. The hydrophone array would capture the vocalizations and keep track of the other individuals (along with the tagged animal). The D-tag would provide near range recordings of the vocalizing tagged animal. The propagation effects on a sound can be examined by comparing signal content close to the animal (D-tag recordings) and farther away (hydrophone array). Understanding of what does not degrade the signal would provide animals with reassurance of what ‘gets through’ to receivers and may assist researchers in determining which acoustic characteristics of a signal are more biologically meaningful to animals at varying ranges. For instance, which part of the signal may be more stable over longer range propagation? Or which part of the signal may be more detectable at closer range? At which point might animals be capable of extracting reliable individual information? It will be difficult to accurately localize killer whale sounds from long ranges, however these questions can be examined in close to moderate range circumstances with the use of multiple tools (D-tag, hydrophone arrays, a location measurement device coupled with behavior and group composition observations).

A great deal of work has been done on bottlenose dolphins in terms of their hearing and time/frequency resolution capabilities, along with their sound generation mechanism and sound sources. It would be advantageous to the killer whale community if there were more extended analysis on sound perception and sound generation conducted specifically on captive killer whales so there would be an estimated baseline of their signaling and receiving capabilities. In this study, predominant energy in the second sideband (approximately 2-3 kHz) and the higher frequency component around the 8-12 kHz region are regions of greater hearing sensitivity for killer whales. Additionally what are their limitations of their biphonation and is what is the loosely coupled relationship of the HFC to the LFC? Further research in sound generation coupled with sound propagation from the head may provide indicators of whether individuals can fine tune their sounds, especially for biphonation. Researchers can then hone in on more biologically meaningful spectral attributes within signals which may be used in communication.

Killer whales appear to have an extraordinary vocalizing capability and an intriguing study would be to examine the vocal adaptability of killer whales to their environment. For instance, are they capable of immediately changing their vocalizations during changes in environmental conditions (e.g. anthropogenic noise)? Do they respond to dynamic events ‘naturally’ by shifting signals? Since killer whales have pod-specific vocals, signal adaptations may be focus on shifts in energy distributions at certain frequencies. This
study could be tested in relatively non-intrusive circumstances by comparing the data set for linearly swimming animals and compare it to the data set of linearly swimming animals nearby a noise source (e.g. ships, projectors, seismic activity, etc.). Such an experiment would isolate if killer whales are readily capable of adjusting or accenting different frequencies during periods of anthropogenic masking. Examining instances where animals alter their signals to increase efficient transmission would help researchers understand mammalian signal characteristics under variable conditions and to establish baselines which can be used in both behavior and conservation studies.
Appendix A

Temperature Probe

The temperature probe is a device which was built that has a thermister at one end to provide resistance readings which can be used to obtain temperature information (Fig. A.1). The temperature probe was built and calibrated in the laboratory (Berchok, 2004). The thermister was soldered to one end of a 150 m coaxial cable and a BNC connector was attached to the opposite end. Soldered connections were protected with shrink wrap. The thermister itself was then dipped multiple times in polyurethane to seal and protect the thermister and connections since they would be exposed to seawater. The thermister or temperature probe was then encased in a t-shaped pvc pipe for protection, while weights were attached to assist in keeping the temperature probe vertical in the water column. The BNC connector was attached to a multimeter to collect the resistance readings when the temperature probe was deployed in the water. The entire temperature probe was coiled onto a wheel for ease of deployment.

Approximately thirty-five resistance readings were obtained at varying depths from a boat. Resistance readings at the different depths were converted to temperatures based on the calibration curve obtained in the laboratory. The temperature-depth profile was then used to calculate the sound speed profiles at the regions of data collection. The mean sound speed profile was used to determine source levels for the killer whale sounds, as well as determining how fast the sound arrived at the hydrophone array. Two profiles were obtained for each field season.

Tape was attached to the coaxial cable at the desired depths to obtain resistance readings. Readings were obtained for every 2 meters until the 50 m mark, then every 10 m from 50 meters up to approximately 110-140 m depth. As the temperature probe was lowered to each of these depths resistance readings was recorded into a field notebook. Once all resistance readings were recorded the temperature probe was removed from the
Figure A.1. Photo of temperature probe. Resistance readings were obtained from the temperature probe at varying depths. Recordings were obtained at each 2 m mark for the first 50 m and then every 10 m up until approximately 120 m.

There were some issues with using this procedure. The first was the issue of inertia while lowering the temperature probe and the time it took for the resistance readings to adjust and equilibrate to the change. In the field, the temperature probe was lowered as rapidly as possible, while trying to keep the boat in the same location. However, this took time and is not an instantaneous measurement of each resistance reading at each depth, so this data set can be considered an average profile. Secondly, even though the temperature probe was weighted amply, any movement of the boat or water would prevent the cabling from hanging perfectly vertical which would affect the location (depth) accuracy of the resistance readings.

A.1 Calibration

The temperature probe was calibrated in the laboratory prior to field data collections so that resistance readings recorded using the multimeter could be later converted to temperatures. In the laboratory, the temperature probe was calibrated in a 15” high bucket, with an inner diameter of approximately 11” (Fig. A.2). Water was filled to approximately the 12” from the bottom. The temperature probe was suspended over the middle of the bucket while a thermocouple was also suspended (Fig. A.2) to record
resistance readings. The thermocouple recorded the temperature of the water at various times in degrees Celcius. Two bags of ice were added to lower the temperature in the water, stirred thoroughly to equilibrate water temperature throughout the bucket. It was important to start off with the water as close to freezing as possible and record the changes in temperature over time until the water had long equilibrated to room temperature. The calibrated temperature range from freezing to the room temperature would include the entire temperature range of the water column of Johnstone Strait. After stirring the bags of ice in the bucket and the temperature was uniform, all ice was removed and data collection began immediately. Calibrations were conducted using a HP34970 Data acquisition unit and the temperature was recorded every 2 minutes until the water was acclimated to room temperature (recordings taken for approximately 12-20 hours). The first calibration was run overnight for a total of twenty hours to ensure the water had reached to room temperature. The time was adjusted the following season since twenty hours was well beyond the time when the bucket water temperature equilibrated to room temperature.

Calibration curves can be seen for both seasons 2006 and 2007 (Fig. A.3,Fig. A.4) (matlab code by Berchok (2004)). The actual data (blue) follows the trend line (red) except at approximately 4° and below. Since the data is nonequivalent to the trend in this region, caution needs to be taken with resistance readings which correspond to temperatures in this region. Since an anomaly of temperature behavior in the bucket was witnessed, the transfer of heat in the bucket around those temperatures was examined more closely. (see next section for examination of upwelling of water in the bucket which occurred from approximately 1 to 4 degrees Celcius).
Figure A.2. Schematic of temperature probe calibration setup. A temperature probe with PVC-pipe attachment and weights was suspended in a bucket for calibration. A thermocouple was also suspended and calibrations were conducted using a HP34970 Data acquisition unit.

Figure A.3. Temperature probe calibration 2006. An example temperature calibration probe with trend line for field season 2006.
A.2 Heat Conduction in the Test Bucket

In the thermister calibrations at and below the 4° mark there is a deviation of the actual data line with the trend for both season calibrations (Fig. A.3, Fig. A.4). This was examined more closely by rerunning trials using four thermisters suspended in the middle of the bucket at the 1”, 4”, 7” and 10” marks (Fig. A.5). The water level in the bucket was again at the 12” marker. For Trial 1 a bag of ice was added to lower the temperature in the water, stirred and removed just prior to data collection. Tests were run for a shorter time period (approximately two hours) to assess the change in heat conduction within the bucket around 4°. Trial 1 results show the warmer and colder water in the bucket changed positions at approximately the sixty minute point in the testing (Fig. A.6). TC107 (pink), TC108 (orange), TC109 (blue), TC110 (green) designated the four different thermocouples. After the churning of colder and warmer water due to changes in densities around 4°, cold, and warm distributions were uniform for the remainder of the measurements.

In Trial 2 an additional bag of ice was added and extra stirring applied to ensure a more uniform water temperature throughout the bucket. As in Trial 1 the ice was removed and calibration began immediately. The graph for Trial 2 shows the heat conduction in the bucket (Fig. A.7). At the onset of the measurements the thermister at the lowest point (TC10) in the bucket (1” mark) was the warmest while TC107 at the
Figure A.5. Temperature probe calibration bucket showing thermister locations. A separate thermocouple was placed at the 1", 4", 7" and 10" marks (the water level is indicated at 12". TC107 (pink), TC108 (orange), TC109 (blue), TC110 (green) designated the four different thermocouples. Measurements were taken for 2 hours or approximately 1200 seconds (or 20 hours) for the first season. Twenty hours was originally chosen to ensure that a complete calibration of the temperature range was obtained in the laboratory.

highest point in the bucket (pink, 10" mark) was the coldest. At approximately 60-70 minutes into the test when the water was approximately 4° the temperatures underwent a shift at all four at the thermocouple locations due to a change in density of the water. Water reaches its maximum density at approximately 4°, while the density gradually decreases both below and above this critical temperature. For instance, TC107 was initially in the coldest water but then switched to the warmest water due to this density shift, while TC108 was in the next coldest water in the bucket and transferred to the second warmest after the conduction.

After resistance measurements were taken with the thermocouple readings, the calibration curves could be used to convert resistance readings of the ocean profile at varying depths. Since measurements in the 4° region did not fit the trendline due to the change in densities characteristic to fresh water, obtaining and converting resistance measurements in this region was done with caution.

In the field, the cabling for the temperature apparatus was marked with tape at varying depths (originally every 2 meters until the 50 m mark, then ten meters after that to approximately 120 m). At each marked depth resistance (kOhms) were recorded from a multimeter. Resistance readings were then compared to the calibration curves to determine the varying temperatures. Temperatures were then input into a sound speed equation using salinity of 31 ppt to determine the sound speed profiles (Candy and Quinn, 1999). The speed of sound (c) of that body of water was calculated from the
Figure A.6. Temperature probe calibration bucket conductivity trial 1. The same methods as described earlier.

temperature profile, depth and salinity (Medwin, 1975):

\[ c = 1449.2 + 4.6T - 0.055T^2 + 0.00029T^3 + (1.34 - 0.010T)(S - 35) + 0.016D \quad (A.1) \]

Where T is the temperature in degrees Celcius (obtained from the calibration charts of resistance measurements at descending depths taken in the field), S is the salinity in ppt (estimated to be 31 ppt) (Candy and Quinn, 1999; Thomson, 1981), and D is depth in meters.
Figure A.7. Temperature probe calibration bucket conductivity trial 2. The setup was the same as in Fig. A.5, however more ice was added.
Appendix B

Acoustic Recording System

B.1 Hydrophones and Audio Recorder

The three elements in the hydrophone array were High Tech, Inc. HTI-96-min hydrophones with built-in pre-amps (Fig. B.1). Sensitivity of 2 of the elements with built-in pre-Amps were -164.1 dB re 1V/uPa, while the sensitivity for the third element was -164.0 dB re 1V/uPa. The frequency response of the hydrophones was flat from 2 Hz to 30 kHz. Beyond the manufacture’s calibrations, the hydrophones were also calibrated in a small pool. The frequency responses are shown in Fig. B.2, Fig. B.3 and Fig. B.4. Due to limitations of the pool size, these additional calibrations could only be conducted down to 2 kHz and not 2 Hz. Calibrations from both the pool site here at the university and High Tech were equivalent.

An Edirol R-4 portable 4-channel audio recorder (Roland Corporation) was used in the field to record the sounds obtained from the three hydrophones as well as the audio spoken during recordings of encounters (Fig. B.5). Channel 1 was the human voice while channels 2, 3 and 4 were designated for hydrophones 1, 2, and 3, respectively. Each hydrophone was connected to an external Sound Professional mono microphone pre-amp (SP-PreAmp-10) which provided 31 dB additional gain to the signal of the first two hydrophones and 32 dB to the third. The sampling frequency was 48.0 kHz with 16 bit analog-to-digital converter. The analog line input was set to 4-channels simultaneous recording to one 4-channel file. This recording option maintained the onset time integrity of the files necessary for post-processing analysis of the sounds. Recording mode was continuous, and recording sessions automatically rolled over to a new file after files reached 2 Gigabytes. The output of each recording was a 4-channel root mean square Volt ($V_{rms}$) .wav file. The recorder was powered daily by a newly recharged 12 V-33/35
Amp scooter battery connected to the DC input. The recorder output was 9 Volts at 2.0 Amp DC (a conservatively rounded-up number), so 18 W were required to run the recorder. The expected current draw on the battery was 2 amps/hour and expected daily battery consumption by the recorder was 16 Amp-hours. The expected hours the recorder could run off the 12 V-35 Amp battery was determined to be approximately 17 hours. The actual observed time that the recorder depleted the battery was 52 hours. The audio recorder drew the least energy compared to the other major field equipment (computer and video camera). Data files were transferred from the recorder and burned onto a compact discs through a laptop.

Figure B.1. Photograph of a HTI-96-min hydrophone with built-in pre-amp. Pre-amp and sensor are indicated in the photograph.
Figure B.2. Calibration curve for hydrophone 1. Calibration of hydrophone 1 (yellow hydrophone) conducted at the university. Calibration only shows form 2 kHz to 30 kHz due to the pool size limitation with lower frequencies. The frequency response is of the HTI-96-min hydrophones with built in pre-amps is actually flat from 2 Hz to 30 kHz.

Figure B.3. Calibration curve for hydrophone 2. Calibration of hydrophone 2 (orange hydrophone) conducted at the university. Calibration only shows form 2 kHz to 30 kHz due to the pool size limitation with lower frequencies. The frequency response is of the HTI-96-min hydrophones with built in pre-amps is actually flat from 2 Hz to 30 kHz.
Figure B.4. Calibration curve for hydrophone 3. Calibration of hydrophone 3 (blue hydrophone) conducted at the university. Calibration only shows form 2 kHz to 30 kHz due to the pool size limitation with lower frequencies. The frequency response is of the HTI-96-min hydrophones with built in pre-amps is actually flat from 2 Hz to 30 kHz.
Figure B.5. Schematic of audio recorder setup. The three hydrophones were connected to the recorder in channels 2-4. Each hydrophone was connected to an external mono SP-PreAmp-10 pre-amp providing 27-31 dB additional gain. Channel 1 was reserved for a voice microphone. Schematic not drawn to scale.

B.1.1 Noise Floor

The noise floor of each channel was isolated by temporarily short-circuiting the other 3 channels on the recorder. Killer whale signals (blue) within the acoustic range of the data collection were well above the noise level of the channels (green, red and black lines) (Fig. B.6).
B.2 Pipe and Plate Instrumentation

A triangular hydrophone array was bottom-mounted (Fig. 2.5, Fig. 2.6) in Johnstone Strait, 50°31′22″N and 126°35′53″W, in July and August 2006-2007, to localize sounds emitted by individual or small groups of killer whales. The spacing between hydrophones in the triangular array was 20 m in the horizontal. Each hydrophone was positioned approximately 1.3 m off the seafloor.

The phase of the array was calibrated in the field using a sound maker made from a metal plate and pipe (Fig. B.7). The bell-shaped pipe was released just under the waters surface and slid down a 10 m rope until it made contact with the plate. An additional weight was added to keep the plate straight, however the plate was naturally heavy. In lab pre-calibration of the sound apparatus generated an impulsive, slightly broadband signal with a peak around 2.1-2.2 kHz. The sound level of the pipe/plate system in the field is shown in (Fig. B.8)
Figure B.7. Pipe and plate photograph. A pipe and plate attached to a 25 m long rope were used to calibrate the triangular hydrophone array.

Figure B.8. Sound level of pipe/plate system. The sound level for when the pipe hits the plate is shown in blue. The highest peak is at approximately 2.2 kHz with an additional peak around 4.5 kHz. Ambient noise is shown in gray.
Statistical Tests

Descriptions of statistical tests used in this dissertation will be presented in this appendix. A list of all statistical symbols can also be found at the end of this Appendix. References providing examples of these tests have been provided. In this dissertation, tests were run in SPSS or calculated in Matlab. These descriptions were obtained from the following sources: Abdi (2007); Devore (2000); Jones (2002); McCrum-Gardner (2008). More in depth definitions can be found at ‘The Statistics Homepage’ http://www.statsoft.com/textbook/stathome.html (McCrum-Gardner, 2008).

Some statistical tests can be separated in these ways: 1) one-sample tests, comparison of 2 groups or comparison of 3 or more groups; and 2) parametric versus non-parametric tests. One-sample tests compare more than 2 categories within a single variable. Comparisons of groups can be between 2 groups as in t-tests or more than 2 groups as seen with multivariate tests. These groupings can further be subdivided depending on if the data is independent or paired (meaning one set is dependent on the other). Many statistical tests can also be separated as parametric or non-parametric testing. Parametric tests usually involve interval-scale data and data must be normally distributed (i.e. bell-shaped, symmetrical about mean, and meet kurtosis and skewness requirements). When possible, data can be transformed (e.g. root-mean-squared, square root, natural log, etc.) to satisfy the normality assumptions. Nonparametric methods are used when data does not meet all of the normality assumptions required for the parametric tests. Nonparametric tests, however, can be less sensitive to outliers which parametric tests are sensitive too.

The type of data can also be divided into different scales of measurement: nominal, ordinal and interval (McCrum-Gardner, 2008). Nominal scale involves categories or names of data with no order. Ordinal scale contained ordered data, while interval scales
are data that are set in intervals (e.g. age, length).

C.1 One-Sample Tests

C.1.1 Chi-Square ($\chi^2$) test

A one-way $\chi^2$ test (also known as one-sample) is a non-parametric test that compares 2 or more categories of a single variable. The equation for the one-sample $\chi^2$ test is

$$\chi^2 = \sum \frac{(O - E)^2}{E}. \quad (C.1)$$

where $O$ is the observed data and $E$ is the expected data which is obtained from a known value for the population or is an expected value of chance. An example of this test can be found in Jones (2002) on pages 179-184.

C.1.2 Binomial test

The Binomial test uses the binomial distribution to decide the outcome of a trial. It is a presence or absence test (i.e. data is given a 1 if it is present, a 0 if it is absent). Test proportions are chosen for each group. The probability of the binomial test is

$$p(x) = \frac{n!}{x! \cdot (n-x)!} \cdot p^x \cdot q^{n-x} \quad (C.2)$$

where $p(x)$ is the probability of recording $x$ observations, $n$ is the sample size, $p^x$ is probability of recording $x$ items and $q^{n-x}$ is the probability of recording a sample with $n-x$ observations (Jones, 2002). Examples of this test for both small and large sample sizes, as well as calculation of the power can be found in Jones (2002) on pages 184-194.

C.2 Comparison of 2 Groups

C.2.1 Independent

C.2.1.1 Independent-samples t-test

An Independent-samples t-test is a parametric test that compares the means of 2 groups of interval data. Data should be normally distributed. The t statistic is

$$t = \frac{(X_1 - X_2) - (u_1 - u_2)}{s_p \sqrt{\frac{1}{n_1} + \frac{1}{n_2}}} \quad (C.3)$$
were $X_1$ and $X_2$ are the two means of the samples, $u_1$ and $u_2$ are the expected mean differences (usually equating to 0), $n_1$ and $n_2$ are the sample sizes, and the pooled standard deviation is

$$Sp = \sqrt{\frac{(n_1 - 1)s_1^2 + (n_2 - 1)s_2^2}{n_1 + n_2 - 2}} \tag{C.4}$$

where $s_1^2$ and $s_2^2$ are the sample variances. The degrees of freedom for a two sample t-test are $n_1+n_2-2$. An example of this test can be found in Devore (2000) on pages 366-370.

### C.2.1.2 Mann-Whitney U test

A Mann-Whitney U test is a non-parametric test that compares the medians of 2 groups of interval or ordinal data to determine if they are equal. The parametric equivalent test is the Independent-samples t-test. The U statistic for the first treatment group (row of data) can be calculated as

$$U = (N_1N_2) + N_1(N_1 + 1)/2 - R_1. \tag{C.5}$$

where $N_1$ is the number of values in group 1, $N_2$ is the number of values in group 2, and $R_1$ is the sum of the ranks (a weighting method) for group 1. The second equation for group 2 is

$$U = (N_1N_2) + N_2(N_2 + 1)/2 - R_2. \tag{C.6}$$

where $N_1$ is the number of values in group 1, $N_2$ is the number of values in group 2, and $R_2$ is the sum of the ranks for group 2. Examples of this test and explanations of ranks can be found in Jones (2002) from pages 228-249.

### C.2.1.3 Fisher’s Exact test

The Fisher’s Exact test is a more robust test than the $\chi^2$ test if the data is sorted in a 2x2 table and has a low sample size. It is calculated by using factorials. The probability is calculated as follows

$$p = \frac{(a + c)! \cdot (b + d)! \cdot (a + b)! \cdot (c + d)!}{n! \cdot a! \cdot b! \cdot c! \cdot d!} \tag{C.7}$$

where a, b, c, d are the four values in the 2x2 contingency table and n equals the
sum of the four values. Examples of this test can be found in Jones (2002) from pages 261-271. The Fisher Exact probability test can also be calculated as a 2x3 table known as the Freeman-Halton extension where the probability is calculated as

\[ p = \frac{(a + b + c)! \cdot (d + e + f)! \cdot (a + d)! \cdot (b + e)! \cdot (c + f)!}{n! \cdot a! \cdot b! \cdot c! \cdot d! \cdot e! \cdot f!} \]  (C.8)

where a, b, c, d, e and f are the six values in the 2x3 contingency table and n equals the sum of the six values. Examples of this test can be found in Bedeian and Armenakis (1977).

C.2.2 Paired

C.2.2.1 Paired t-test

A paired t-test is a parametric test that compares sample means from 1-to-1 pairing between samples (e.g. pre- post- trials). The data is interval and assumed normally distributed. The test statistic is calculated as

\[ t = \frac{X - u}{S_D/\sqrt{n}} \]  (C.9)

where \( X \) is the sample mean, \( u \) is the difference between the means in the pairs, \( S_D \) is the standard deviation and \( n \) is the sample size. Examples of the paired t-test and calculations of its power can be found in Devore (2000) on pages 375-381.

C.2.2.2 Wilcoxon Signed Ranks test

The Wilcoxon Signed Ranks test is a non-parametric version of the paired t-test that compares two paired samples. The data is usually interval or ordinal data. The \( z \) statistic is calculated as follows

\[ z = \frac{T - \frac{n(n+1)}{4}}{\sqrt{\frac{n(n+1)(2n+1)}{24}}} \]  (C.10)

where \( T \) is the smaller sum of ranks, \( n \) is the number of untied pairs of data. Explanations of ranks and examples of this test can be found in Jones (2002) on pages 301-314.
C.2.2.3 Sign test

The Sign test measures is a parametric test that uses the binomial test to measure changes before and after of a dataset (see Binomial test above) (Abdi, 2007).

C.3 Comparison of 3 or More Groups

C.3.1 Kruskal-Wallis test

The Kruskal-Wallis test is a non-parametric multiple comparisons test that is equivalent to a one-way ANOVA. Data is interval or ordinal scale. The equation for the Q test statistic for an asymmetric design is

\[ Q = \frac{r_1 - r_2}{n_1 n_2} \cdot \frac{n(n+1)}{12} \cdot \left( \frac{1}{n_1} + \frac{1}{n_2} \right) \]  \hspace{1cm} (C.12)

where \( r_1 \) and \( r_2 \) are the two ranks for treatment 1 and 2 respectively, \( n \) is the total sample size, \( n_1 \) and \( n_2 \) are the sample sizes for each treatment and the standard error is

A more in depth description of ranking, examples of the Kruskal-Wallis test and Dunn’s post-hoc test can be found in Jones (2002) on pages 436-444.

C.4 Additional Statistical Tests

C.4.1 Discriminant Analysis

Discriminant analysis is used to determine the linear combination of variables which best differentiates between groups. Groups are pre-determined and functions are used to separate out variables from on another. Discriminant analysis is deemed effective if it yields a high percentage (e.g. 90%) within the first two functions.
## C.5 Symbols

<table>
<thead>
<tr>
<th>Symbol</th>
<th>Description</th>
</tr>
</thead>
<tbody>
<tr>
<td>$\alpha$</td>
<td>predetermined acceptance value for statistical tests, known also as the probability of a Type I error</td>
</tr>
<tr>
<td>$\beta$</td>
<td>probability of a Type II error (failing to reject a null hypothesis when it is in fact false)</td>
</tr>
<tr>
<td>df</td>
<td>degrees of freedom, most often sample size minus one</td>
</tr>
<tr>
<td>$H_o$</td>
<td>null hypothesis</td>
</tr>
<tr>
<td>$\chi^2$</td>
<td>test statistic for chi-squared tests</td>
</tr>
<tr>
<td>Q</td>
<td>critical value of significance for the Kruskal-Wallis test</td>
</tr>
<tr>
<td>n</td>
<td>sample size of the data</td>
</tr>
<tr>
<td>p</td>
<td>p-value (probability), measure of the confidence observed in the sample</td>
</tr>
<tr>
<td>power</td>
<td>$1 - \beta$, statistical strength of a test, with 1 being strongest and 0 having no strength, calculated post hoc to each analysis</td>
</tr>
<tr>
<td>$\sigma$</td>
<td>standard deviation</td>
</tr>
<tr>
<td>$\delta \sigma$</td>
<td>change in standard deviation, statistic used in independent-samples t-test</td>
</tr>
<tr>
<td>$\mu$</td>
<td>mean of the data</td>
</tr>
<tr>
<td>$\delta \mu$</td>
<td>change in mean, statistic used in independent-samples t-test</td>
</tr>
<tr>
<td>U</td>
<td>test statistic for the Mann-Whitney U test</td>
</tr>
<tr>
<td>z</td>
<td>test statistic for the Wilcoxon Signed Rank test</td>
</tr>
</tbody>
</table>

Table C.1. Symbols in statistical tests. Symbols for results of statistical tests used in this dissertation are shown with their descriptions
N04 Subtypes

N04 subtypes were examined Chapter 3. The N04 call was originally parsed into five subtypes using discriminant analysis (Fig. 3.2). However, due to considerable overlap of subtypes N04-2 and N04-3, the two subtype categories were grouped into subtypes N04-2/3. Additional examples of the four N04 subtypes are shown in Fig. D.1 and Fig. D.2. The name of each subtype is shown above each spectrogram (e.g. N04-1, N04-2/3 etc.). These example subtypes are produced by both small groups and individuals; individuals seen here correspond to those shown in Table 3.3. Fig. D.1 shows an example of 2 subtypes (N04-1 and N04-2/3) that were produced by the same individual in the same encounter. All three pods that produce the N04 call are represented in Fig. D.1 and Fig. D.2. The discriminant analysis separated the subtypes based on differences in the slopes by using functions (Function 1 and Function 2). Function 1 separated the N04-1 subtype from the other three subtypes based on slopes within the front portion of the call (Seg3, Seg1, Seg4) (Fig. 3.3,Fig. 3.6). N04-1 has a sharper positive slope and descends soon after the peak in the hump (convex portion), while the other subtypes descend in frequency more gradually over time (Fig. D.1 and Fig. D.2). Function 2 then differentiated the subtypes based on features in the terminal or tail component (Seg6). Subtypes N04-1 and N04-2 were found to be the same, with each subtype exhibiting a slight upsweep in frequency with time, while N04-3 remains uniform or lacks a tail component and N04-4 almost steps down in its sideband interval. Names of individual killer whales and those within small groups who produced the N04 subtype is noted underneath each figure.
Figure D.1. Spectrograms N04 subtypes part 1. Additional examples of N04 subtypes are shown. Subtypes are denoted as 1, 2/3, 4 and 5 after ‘N04’. Spectrograms relatively scaled to one another in duration. N04 subtypes were originally seen in Chapter 3. Subtypes N04-1 and N04-2/3 were produced by the same individual A12 (A1 pod) during the same encounter. From different encounters, this example of the N04-4 was produced by A55 of the A1 pod, while the N05-5 subtype was produced by a mother and calf of the A5 pod (A42 and A79, respectively).
Figure D.2. Spectrograms N04 subtypes part 2. Additional examples of N04 subtypes are presented here. Subtypes are denoted as 1, 2/3, 4 and 5 after ‘N04’. Spectrograms relatively scaled to one another in duration. The N04-1 subtype was produced by individual, A24, of the A4 pod. N04-2/3 was produced by a small group of three juveniles (A73, A82 and A70) of the A4 pod. N04-4 was made by a mother with her juvenile and calf (A54, A75 and A86, respectively of the A1 pod), while N04-5 was produced by a juvenile (A69) of the A5 pod. Subtypes in this figure were produced during different encounters.


Lane, S. J. (1996). Associations and the Ontogeny of Calling in a Killer Whale Calf, Orcinus Orca, During Her First Six Months, Master of Science, University of San Diego, CA.


Dawn Grebner was born in New Brunswick, NJ, to Ann and Donald Grebner, and raised primarily in central Massachusetts. In 2002, she earned her M.A. in Biology from Boston University. Her research focused on the vocal repertoire of a captive Icelandic killer whale. During one summer month of both 2000 and 2001 she worked as a research assistant for the Center for Advanced Imaging and Visualization at the Woods Hole Oceanographic Institution and Ocean Futures Society in Vestmannaeyjar, Iceland. During these field trips she collected wild Icelandic killer whale vocals, tracked wild orca for DNA testing, participated in aerial surveys of wild killer whales and other cetaceans and collected behaviors of a captive Icelandic killer whale. During the school year, she volunteered at the New England Aquarium with an emphasis in marine life education. Upon graduation, she worked with Marine Research Consultants, who were contracted with the Woods Hole Oceanographic Institution, processing wild Icelandic killer whale calls, extracted Hi-Def photographic stills from submarine dives and edited Hi-Def film footage of cetaceans. In addition, she participated in blimp surveys of cetaceans off Provincetown, MA. In the fall of 2003, she began her PhD work at the Graduate Program in Acoustics at Penn State under the supervision of Dr. David L. Bradley. The focus of her research was on communication related to physical and social circumstances of killer whales when they are apart and how they use vocalizations in these instances. She was awarded a graduate research assistantship from the Educational and Foundational Funding at the Applied Research Laboratory and received a Kenneth T. Simowitz Citation for a poster presentation held at a conference. Dawn is an ongoing member of the Acoustical Society of America, the Society for Marine Mammalogy and Graduate Woman in Science and regularly presents at conferences.