

AN ABSTRACT OF THE THESIS OF

Michelle Elizabeth Hardy Fournet for the degree of Master of Science in Marine Resource Management presented on January 10, 2014.

Title: SOCIAL CALLING BEHAVIOR OF SOUTHEAST ALASKAN HUMPBACK WHALES (*MEGAPTERA NOVAEANGLIAE*): CLASSIFICATION AND CONTEXT.

Abstract approved:

Andrew R. Szabo

Humpback whales (*Megaptera novaeangliae*) are vocal baleen whales that exhibit complex social interactions that vary spatially and seasonally. Across their range, humpback whales produce a wide array of vocalizations including ‘song’, foraging vocalizations, and a range of vocalizations known as social calls -- unclassified non-song vocalizations. This study investigates the vocal repertoire and social calling behavior of Southeast Alaskan humpback whales from a sample of 299 vocalizations paired with 365 visual surveys collected over a three-month period on a foraging ground in Frederick Sound in Southeast Alaska. The results of this study describe a more varied and diverse repertoire of social vocalizations than has been previously documented, and identifies variability in vocal behavior as a function of social-spatial context.

We used a three-part classification system that included aural-visual analysis, statistical cluster analyses, and discriminant function analysis to describe and classify social vocalizations. Vocalizations were classified into sixteen individual call types nested in seven vocal subclasses, within four vocal classes. The vocal repertoire of Southeast Alaskan humpbacks shows that call stereotypy ranges from discrete to continuous. This discrimination occurs at the vocal class and vocal subclass levels, and may be associated with call function. Social calls from Southeast Alaska showed anecdotal overlap with

song from the 2012 North Pacific breeding season, and moderate overlap with vocalizations recorded in North Atlantic foraging grounds and along the East Australian migratory corridor. At the vocal class level aural-visual analysis had 83% agreement with cluster analysis and 90% agreement with discriminant function analysis.

Results indicate that call use is not indiscriminant, and that some call types were commonly produced while others were rare. Moreover, calling rates in one vocal class, the pulsed (P) vocal class, were negatively correlated with mean nearest neighbor distance, indicating that P calling rates increased as animals clustered. This suggests the use of P calls may be spatially mediated. Results of a Poisson log linear (PLL) regression indicated that whale abundance in the survey area had no effect on vocal behavior; however, vocal behavior did vary significantly based on the spatial proximity of animals. The highest calling diversity occurred when whales were in clustered dispersion states, while the lowest calling diversity occurred when only a single whale was present. The type of calls produced during each dispersion state (clustered, random, evenly dispersed, single) varied significantly. While calls from all four vocal classes were detected during surveys containing clustered or randomly dispersed whales, calls from only two of the four classes were detected when whales were evenly distributed, and only one vocal class was detected from solitary whales. Our results indicated that vocal behavior is not correlated with abundance, that vocal behavior does vary based on social context, and that vocal behavior trends toward complexity as the potential for social interactions increases. Our evidence supports the hypothesis that social vocalizations serve a communicative purpose and may be used to maintain animal spatial proximity.

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SOCIAL CALLING BEHAVIOR OF SOUTHEAST ALASKAN HUMPBACK
WHALES (*MEGAPTERA NOVAEANGLIAE*): CLASSIFICATION AND CONTEXT

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I understand that my thesis will become part of the permanent collection of Oregon State University libraries. My signature below authorizes release of my thesis to any reader upon request.

Michelle Elizabeth Hardy Fournet, Author

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TABLE OF CONTENTS

	<u>Page</u>
CHAPTER ONE: General Introduction.....	1
Acoustic Communication in Cetaceans	1
Humpback Whale Vocalizations: Historical Background.....	3
Humpback Whale Vocal Behavior	4
Descriptions of Social Calls.....	5
Social Call Context.....	6
Research Needs	8
Research Approach.....	9
Literature Cited	11
CHAPTER TWO: Vocal repertoire of Southeast Alaskan humpback whales (<i>Megaptera novaeangliae</i>).....	17
Introduction.....	17
Methods	19
Data Processing and Analysis.....	20
Results	22
Description of Vocalizations	23
Discussion	28
Classification Methods.....	28
Regional Similarities	30
Vocal Continua	31
Conclusions	34
Literature Cited	35
Tables.....	38
Figures.....	45
CHAPTER THREE: Vocal behavior in Southeast Alaskan humpback whales (<i>Megaptera novaeangliae</i>): Communication and context	53
Introduction.....	53
Methods	58
Visual and Acoustic Data Collection	58
Inclusion Criteria	59
Visual and Acoustic Data Analysis.....	59
Results	63
Discussion	66
Differences Between Vocal Classes.....	66
Abundance, Dispersion, and Calling Behavior	70
Communication	73

TABLE OF CONTENTS (Continued)

Conclusion	74
Literature Cited	75
Tables.....	82
Figures.....	85
CHAPTER FOUR: General Conclusions and Future Directions	93
Primary Findings and Contributions	93
Future Research	95
BIBLIOGRAPHY	97
APPENDIX.....	107
Potential Call Types (Preliminary)	107

LIST OF FIGURES

<u>Figures</u>	<u>Page</u>
Figure 1. Map showing survey area in Frederick Sound, SE Alaska, including the location of the research station at the Five Finger Lighthouse (starred).	45
Figure 2. Results of aural-visual classification of calls into a hierarchical tree. Call types are nested within vocal subclasses, which are further nested within vocal classes. Acoustic summaries for each call type can be found in Tables 4-7. Spectrograms of call types can be found in Figures 4-8.	46
Figure 3. Dendrogram results of quantitative cluster analysis. A different color and number represent each cluster.....	47
Figure 4. Spectrograms of call types from the Low-Frequency Harmonic (LFH) vocal class. Subjectively determined call types and subclasses (left to right from top): Trilled: LFH-F-1, LFH-F-2; Complex: LFH-F-3, LFH-F-4; Simple- LFH-F-6, LFH-F-5.	48
Figure 5. Spectrogram of the LFH-F-2 (Wop) call (left) and LFH-F-1 (Purr) call (right). Note the similarity in call structure.....	49
Figure 6. Spectrograms of call types from the Pulsed (P) vocal class. Subjectively determined call types are grouped by subclass. (Left to right from top) (a) Complex: P-F-1, P-F-2, P-F-4. Simple: P-F-3. Note difference in frequency scale for spectrogram of P-F-4 call (max frequency 8 kHz) versus other spectrograms (max frequency 2.5 kHz).	50
Figure 7. Spectrograms of call types from the Noisy/Complex (NC) vocal class. Subjectively determined call types are grouped by subclass. (Left to right from top) Frequency Modulated: NC-F-1, NC-F-2, NC-F-3. Harmonic: NC-F-4, NC-F-4. Note difference in frequency scale for spectrograms in Frequency Modulated subclass (max frequency 2.5 kHz) versus the Harmonic subclass (max frequency 16 kHz).	51
Figure 8. Spectrogram of the sole call type within the Tonal (T) vocal class: T-F-1.	52
Figure 9. Map showing survey area in Frederick Sound, southeast Alaska. Blind spots and survey area boundaries are shaded in gray. Five Finger Lighthouse observation tower is marked with a star.	85
Figure 10. Percentage of total surveys represented by each dispersion state.	86
Figure 11. Percentage of total calls represented from each class.	87
Figure 12. Mean (\pm SEM) calling rates (calls per whale per minute) for each vocal class.	88

LIST OF FIGURES (Continued)

<u>Figures</u>	<u>Page</u>
Figure 13. Outlier box plot of Pulsed (P) call production (calls per whale per minute) in four different dispersion states: clustered, random, dispersed, and single. Asterisks indicate outliers.	89
Figure 14. Pulsed (P) calling rate of production (P calls per minute per whale) plotted against average nearest neighbor distance (m) and coded by dispersion state. Solid circles represent clustered dispersion states, hollow circles represent random dispersion states, and gray circles represent dispersed states.	90
Figure 15. Percentage of calls represented from each vocal class (LFH, P, NC, and T) at each dispersion state (clustered, random, dispersed, and single). Dispersion state is calculated on a per survey basis; calls from all surveys of a given state are pooled to calculate percentage of calls from each vocal class for each dispersion state. Sample size (number of total vocalizations detected at a given dispersion state) is note above the x-axis.	91
Figure 16. Rate of total call production (total calls per whale per minute) plotted against the change in average nearest neighbor distance (m). Change is measured as the average nearest neighbor distance observed in a given survey minus the average nearest neighbor distance of the survey directly previous. Solid circles represent clustered dispersion states, hollow circles represent randomly distributed dispersion states, and gray circles represent dispersed states.	92
Figure 17. Potential call types, preliminarily identified through AV classification. L-R from top: NC-F-6 (Creaky), NC-F-7 (Shake), NC-F-8 (Creek*), P-F-5 *Bullet), LFH-F-7 (Harmonic Moan). Naming precedents set by Dunlop et al. 2007 are denoted with an asterisk. Note differences in frequency scale.	110

LIST OF TABLES

<u>Table</u>	<u>Page</u>
Table 1. Description of acoustic variables used for three-part classification of humpback whale social calls. Feature from the Noise Resistant Feature Set (NRFS) are denoted with an asterisk (*). Variables that were log transformed for analysis are denoted with a plus sign (+).....	38
Table 2. Confusion matrix showing overlap between aural-visual (AV) analysis classification and hierarchical agglomerative cluster classification. High values are shown in bold. Agreement (%) is calculated as the percentage of calls determined through AV classification to be in the same vocal class to be placed into a single statistical cluster. .	39
Table 3. Summary of select acoustic parameters for each group identified by hierarchical cluster analysis. Mean parameters are in bold; standard deviations are below and listed in italics. Class and Call Types refer to results of aural-visual analyses.	40
Table 4. Summary of select acoustic parameter for samples subjectively classified within the Low Frequency Harmonic (LFH) vocal class. Mean values are in bold and standard deviations in italics. Naming precedents set by Dunlop (2007) are marked with an asterisk (*). See Figure 4 for corresponding spectrograms.....	41
Table 5. Summary of select acoustic parameter and sample size for samples subjectively classified within the Pulsed (P) vocal class. Mean values are in bold and standard deviations in italics. See Figure 6 for corresponding spectrograms.	42
Table 6. Summary of select acoustic parameter for samples subjectively classified within the Noisy/Complex (NC) vocal class. Mean values are in bold and standard deviations in italics. Naming precedents set by Dunlop et al. (2007) are marked with an asterisk (*). See Figure 7 for corresponding spectrograms.	43
Table 7. Summary of select acoustic parameters for subjectively classified calls within the Tonal (T) vocal class. Mean values are in bold and standard deviations in italics. See Figure 8 for associated spectrogram.	44
Table 8. Results of a Poisson Log-Linear regression testing the effects of abundance and dispersion on calling rates.....	82
Table 9. Description of vocal behavior by dispersion state including: total number of surveys of each state containing vocalizations, Shannon-Weiner Index assessing calling diversity of vocalizations detected at each dispersion state (pooled), and number of vocalizations of each vocal class detected in each dispersion state.....	83
Table 10. Summary statistics for calling rates and counts by dispersion states. Sample size (number of surveys at a given dispersion state) is listed in the heading. Mean calling rates and mean call counts for each vocal class are listed in bold; standard deviations are italicized below.	84

LIST OF TABLES (Continued)

<u>Table</u>	<u>Page</u>
Table 11. Selected acoustic parameters for potential call types. Call types were classified based on aural-visual analysis alone. Means are presented in bold, standard error are below in italics.	108
Table 12. Justification for omitting potential call types.	109

For Rapunzel

SOCIAL CALLING BEHAVIOR OF SOUTHEAST ALASKAN HUMPBACK WHALES (*MEGAPTERA NOVAEANGLIAE*): CLASSIFICATION AND CONTEXT

CHAPTER ONE: General Introduction

Communication is critical to all social species. Communication helps to coordinate group behaviors, allows for individual or group recognition, facilitates mating interactions, aid foraging events, assists territorial spacing, and enables the passage of cultural knowledge (Dudzinski et al., 2002; Bradbury and Vehrencamp, 2011). Effective organization of coordinated activities among individuals is achieved through the exchange of information about conspecifics, other species, and the environment (Dudzinski et al., 2002; Bradbury and Vehrencamp, 2011). In the marine environment, communication can be particularly challenging; the vastness of the ocean reduces the likelihood that individuals will encounter one another by chance, and light-attenuation properties impose severe limitations on the transmission of signals dependent on sight. Under the clearest conditions, sunlight penetrates ocean water in the range of tens to hundreds of meters, and this is considerably reduced in biologically productive waters utilized by some baleen whale species as foraging grounds. By contrast, acoustic energy propagates efficiently and over great distances in the marine environment (Urick, 1983). Because of this, many marine organisms, cetaceans among them, depend on sound as their primary sensory modality (Dudzinski et al., 2002; Bradbury and Vehrencamp, 2011).

ACOUSTIC COMMUNICATION IN CETACEANS

Among marine mammals, cetaceans produce the broadest band of acoustic frequencies (Dudzinski et al., 2002). Blue whales (*Balaenoptera musculus*), the largest known creatures to ever inhabit the earth, produce sounds with frequencies as low as 9 Hz (Mellinger and Clark, 2003). Frequencies this low are capable of travelling thousands of kilometers through the ocean (Richardson et al., 1995; Stafford et al., 1998; Dudzinski et al., 2002). In comparison, white-beaked dolphins (*Lagenorhynchus albirostris*) emit echolocation clicks at frequencies as high as 250 kHz, well beyond the range of hearing in many mammal species (Rasmussen and Miller, 2004). The variation in frequency

corresponds in part to the variability in cetacean size, with larger animals producing lower frequency sounds. Yet the distinction also corresponds to the suborder of cetacean producing the sounds.

Animals in the suborder *Odontoceti*, - the suborder including toothed whales, dolphins, and porpoises - produce shorter-traveling, mid- to high frequency (1-250 kHz) clicks, creaks, whistles, and moans used for communication and echolocation (Au, 2008). Echolocation - the process of making an environmental assessment by emitting sounds and listening to echoes associated with sound wave reflection - is believed among the cetaceans to be unique to odontocetes, and is used in foraging, navigation, predator avoidance, and social interactions (Madsen et al., 2002; Au, 2008). In odontocetes individual- or pod-recognition through vocal signature is used by many species: killer whale (*Orcinus orca*) communicate with pod specific dialects (Ford, 1991; Deeke et al., 2002), bottlenose dolphin (*Tursiops truncatus*) calves recognize the unique vocal signatures of their mothers (Sayigh et al., 1998), narwhal (*Monodon monoceros*) pods may demonstrate group cohesive whistles (Shapiro, 2006), and certain types of clicks produced by sperm whales (*Physeter macrocephalus*) have been identified as ‘clan calls’ (Rendell et al., 2003). Individual recognition calls are believed to play a key role in maintaining social bonds necessary to ensure harmony within tightly knit social groups favored by odontocete species.

Comparatively, baleen whales (Suborder: *Mysticeti*), generally specialize in sounds in the frequencies ranging from 10-2000 Hz (Weilgart, 2007), which are more appropriate for long distance communication. Long distance communication is critical for baleen whale species that may migrate up to 10,000 miles annually, and who, in some cases, are widely dispersed throughout a population’s range (Stern, 2000). Blue whales, fin whales (*B. physalus*), right whales (*Eubalaena japonica* and *E. glacialis*), and humpback whales (*Megaptera novaeangliae*) all utilize long-range vocal signals to facilitate interactions between conspecifics. It is well documented that male mysticetes of several species produce highly stereotyped songs, often for many hours per day during breeding seasons, that are detectable at great distances (Clapham and Mattila, 1990; Charif et al., 2001; Croll et al., 2002; Clark and Clapham, 2004; Au et al., 2006; Delarue et al., 2009). Baleen

whales use vocalizations in foraging contexts, and may gain environmental information by producing low frequency calls. Bowhead whales (*Balaena mysticetus*) appear to use sound to perceive and avoid ice floes in advance of being able to detect them visually (Ellison et al., 1987, Clark 1989). North Pacific humpback whales use prey manipulation calls in combination with the emission of bubbles to corral herring (*Clupea pallasii*) aggregations during cooperative foraging events (Jurasz and Jurasz, 1979; D'Vincent et al., 1985), and low frequency clicks have been documented during night foraging bouts in North Atlantic humpback whales (Stimpert et al., 2007). Other proposed social functions proposed for baleen whale vocalizations include mating and parental behavior (Payne and McVay, 1971; Parks and Tyack, 2005; Zoidis et al., 2008), long-range contact (Cummings and Thompson, 1971; Clapham and Mattila, 1990; McDonald et al., 2001; Croll et al., 2002), assembly (Clark and Clark, 1980; Dunlop et al., 2008), sexual advertisement (Tyack, 1981; Winn et al., 1981; Parks et al., 2005; Smith et al., 2008), greeting (Tyack, 2000), spacing (Tyack, 1981; 1983; Frankel et al., 1995), threat (Silber, 1986), and individual identification (Tyack, 1999; 2000).

HUMPBACK WHALE VOCALIZATIONS: HISTORICAL BACKGROUND

Despite historic whaling reports (Aldrich, 1889) to the contrary, as recently as the 1940's many scientists maintained the belief that baleen whales were mute. Increasing numbers of reports of unidentified marine sounds by naval hydrophone operators throughout the 1940's, coupled with evidence of odontocete sound production, however, sparked an interest in baleen whale vocal potential (Fraser, 1946; Schevill and Lawrence, 1948). Unidentified humpback whale vocalizations, generally classified as 'marine life', were first recorded off of the island of Oahu in 1952 (Schreiber). Throughout the 1950's and 1960's unidentified humpback whale vocalizations were recorded in the sub-tropical Pacific Ocean and both the sub-tropical and northern latitude Atlantic Ocean (Schevill and Watkins, 1962; Schevill, 1964; Kibblewhite et al., 1967). Humpback whale song was positively attributed to the species by Roger Payne in 1970, and formally described shortly thereafter (Payne & McVay, 1971). As a result of the 1970 LP *Songs of the Humpback Whale*, which contained a portion of Payne's original recordings, humans listened to humpbacks more than any other whale species on the planet.

HUMPBACK WHALE VOCAL BEHAVIOR

Humpback whales are among the most vocal of baleen whales, producing a wide range of sounds including stereotyped ‘songs’, (Payne and McVay, 1971) non-song vocalizations (i.e. ‘social sounds’) (Silber, 1986; Thompson et al., 1986; Dunlop et al., 2007), prey manipulation calls (Jurasz and Jurasz, 1979; Cerchio and Dalheim, 2001; Sharpe, 2001) and surface generated percussive sounds (Silber, 1986; Dunlop et al., 2008; Dunlop et al., 2010). These sounds are produced in situation-dependent circumstances and are highly variable between the spatially and temporally isolated foraging and breeding grounds.

While on low latitude breeding grounds humpback whales produce highly stereotyped songs that are (directly or indirectly) related to mating behaviors (Payne and McVay, 1971; Au et al., 2006). Songs are hierarchically organized into themes, phrases, and units, which are predictably repeated by male humpbacks during singing sessions (Payne and McVay, 1971; Winn et al., 1981; Au et al., 2006). Singing is prolific on breeding grounds, and during the peak of the breeding season can be heard in every hour of the day (Winn et al., 1975; Winn et al., 1981). Although at one time singing was thought to be exclusive to breeding grounds, singing has been recorded along migratory corridors (Norris et al., 1999; Charif et al., 2001; Clark and Clapham, 2004), and has been documented to a lesser extent in high latitude foraging grounds (Gabriele and Frankel, 2002; Clark and Clapham, 2004; Vu et al., 2012).

Less studied are non-song signals, or social sounds, which are here defined as any phonation lacking the rhythmic and continuous patterning of song, including surface-generated sounds. This includes single song units produced independently of the song structure, novel vocalizations not present in song units, and percussive sounds (Dunlop et al., 2007). While the term “social sound” encompasses the collection of non-song humpback produced sounds (i.e., either vocalizations or the sound of a pectoral flipper slapping the water), in this study the terms “social calls” or “social vocalizations” refer exclusively to *vocalizations* produced in a non-song context.

DESCRIPTIONS OF SOCIAL CALLS

Though references to social calls are common, quantitative descriptions or catalogs of social calls are few. Acoustic descriptions of social sounds are restricted to Alaska's Inside Passage in the North Pacific Ocean (Thompson et al., 1986), the coastal waters off Peregian Beach in the South Pacific Ocean (Dunlop et al., 2007; Rekdahl et al., 2013), and the Stellwagen Bank of the North Atlantic Ocean (Stimpert et al., 2011).

A 1986 study broadly described social sounds on the northern foraging grounds of Stephen's Passage, Southeast Alaska (Thompson et al., 1986). Vocalizations were recorded via a single dipping hydrophone, a sound-pressure calibration system, and a portable tape recorder, and were classified aurally. Social calls were broadly described as "moans", "grunts", or "pulse trains". Prolonged vocalizations of at least 400ms were classified as moans; shorter prolonged sounds were termed grunts. Both grunts and moans had a reported frequency range of 20-1900 Hz. Pulse trains were described as any series of short (<400 ms) repeated vocalizations with a frequency range of 40-1250 Hz. This was the first, albeit cursory, catalog of social sounds produced for North Pacific humpback whales, and the first widely distributed quantitative description of social calling acoustic parameters. Both the data collection and classification, however, would be considered rudimentary by modern standards, and digital sound files containing samples from the study are not readily available.

Using five bottom-mounted hydrophones, Dunlop et al. (2007) recorded social vocalizations of migrating humpback whales as they departed their northern Australian breeding ground. This study used a combination of aural and visual (spectrographic) analysis as well as statistical analyses of numerous acoustic parameters to describe 34 distinct call types. Of these 34, 21 calls were identified as song units from the current year. Most calls were described as harmonic and were arbitrarily separated into three general frequency bands, with low-frequency harmonic sounds exhibiting fundamental frequencies below 100 Hz, mid-frequency sounds between 160–550 Hz, and high-frequency sounds above 700 Hz. Non-harmonic sounds were described as amplitude modulated calls, 'noisy and complex' calls, and repetitive calls. Of the 34 unique call

types, Dunlop et al. reported ‘wops’, ‘thwops’, and ‘grumbles’ as the dominant call types. Using a combination of qualitative analyses and a quantitative classification and regression tree (CART) approach, a follow up study further reported a total of 46 call types from the region (Rekdahl et al., 2013). Of these 46 call types 19 were found as song units, 15 call types were reported to be “inconsistent” (recorded in 2 years or less), and 12 call types were described as “stable” or appearing with high occurrence across all of the four years surveyed.

Lastly, in 2011 investigators utilized DTAG technology to collect social sounds from humpback whales on Stellwagen Bank in the North Atlantic in conjunction with foraging activities (Stimpert et al., 2011). Social calls within this study were described as having peak frequencies of generally less than 1 kHz and lasting less than 1 s in duration. A statistical cluster analysis objectively classified calls into one of eight categories based on a series of acoustic parameters similar to those used by Dunlop in 2007. The two most stereotyped and distinctive call types (“wops” and “grunts”) were identified through aural and visual analysis. These two call were described as generally comparable to those collected by Dunlop in the Australian migratory corridor, as well as Thompson et al. (1986) in Southeast Alaska. Additionally, the report cites yet unpublished data confirming the presence of these two call types on the Hawaiian breeding grounds.

SOCIAL CALL CONTEXT

To date, scientists have yet to attribute function to humpback whale social sounds. Several studies, however, have begun to contextualize the behavioral conditions under which humpback whale utilize social calls. A study by Silber described the presence of social sounds on the Hawaiian breeding grounds (Silber, 1986). Results of this study found that social sounds in Hawaiian waters are highly correlated with group size and surface activity. Silber reported a “dramatic increase in vocalization rate” when a new whale joined an agonistic group, as well as brief intercall periods with significant periods of vocal overlap. Silber proposed that social sounds demonstrate aggression or agitation as adult males competed for access to females. While the study reports little to no vocal

behavior in single whales or cow-calf pairs it should be noted that survey efforts were disproportionately skewed toward observations of surface-active groups.

A 2008 study suggested that individual social calls were context specific and served variable functions (Dunlop et al., 2008). The previously cited catalog was used in eastern Australia to correlate social calls with social/behavioral contexts including joining events, leaving events, group size, and group composition. “Grunts”, “groans”, and “barks” were observed almost exclusively in joining situations and it was suggested that those calls play a role in social integration. Other calls were positively associated with competitive group behavior, and still others were identified as playing a role in either inter or intra-group communication. Fundamentally, the results of this study demonstrate that “social sounds in humpbacks may have specific social and behavioral functions relating to social group composition, and the mediation of interactions between these social groups” (Dunlop et al., 2008). Additional vocalizations between cow-calf pairs have also been documented along migratory corridors (Dunlop et al., 2008), and calves of both gender are purported to vocalize during their first year (Zoidis et al., 2008).

While the above studies provide some behavioral context for social vocalizations, social calling behavior on breeding grounds and at lower-latitude portions of migratory corridors is not presumed to be representative of social calling behavior on foraging grounds. Humpback whales fast during breeding seasons and rarely feed during migration, relying instead on blubber stores that are seasonally replenished on high-latitude foraging grounds (Chittleborough, 1965; Dawbin, 1966). The vocal behavior described in these studies could not include a foraging component, which would presumably alter vocal behavior. The behaviors between the regions are disparate, and while some overlap in call context may be identified, it is expected that social calling context on foraging grounds will vary from the social calling contexts described in the above mentioned studies.

Two social vocalizations have been associated with humpback whale foraging behaviors that have not been recorded elsewhere. The best understood is the “Feeding Call” or

“Feeding Cry” (Jurasz and Jurasz, 1979; Tyack, 1981; D’Vincent et al., 1985; Cerchio and Dalheim, 2001; Sharpe, 2001). This specific call has only been documented in Southeast Alaska, and occurs predominantly in groups of cooperatively foraging humpback whales. The feeding call, which ranges from 360-980 Hz, has been proposed to coordinate the movements of humpback whales feeding on schools of herring, or drive herring toward the water’s surface for capture (D’Vincent et al., 1985; Cerchio and Dalheim, 2001; Sharpe, 2001). Less definitively, nighttime foraging vocalizations, dubbed “Megapclicks”, have been documented in North Atlantic humpback whales, though the role of this vocalization in nocturnal foraging is not yet determined (Stimpert et al., 2007).

RESEARCH NEEDS

The study of humpback whale social calling behavior is relatively scant; quantitative descriptions of social calls using the best available methods are not currently available for most regions, including Southeast Alaska. Understanding a species repertoire is critical for assessing call function, contextual use, geographic variation, and cultural transmission. Furthermore, the presence of a well-documented catalog of calls paired with detailed descriptions of behavioral context is a fundamental baseline against which to compare future behaviors for evidence of disturbance, adaptation, or resilience. This is particularly important for highly vocal humpback whales that utilize acoustic communication for many critical functions (i.e. mating, foraging) and whose low-frequency vocalizations share a frequency band with pervasively increasing anthropogenic noise.

Between 1965 and 2003 the number of commercial vessels transiting the world’s oceans has doubled; concomitant with this shift is a dramatic increase in ocean-borne anthropogenic noise (McDonald et al., 2006a). Rising ocean noise levels increase the risk of vocal masking (Richardson et al., 1995; Clark et al., 2009). Low-frequency specialists, including humpback whales, are particularly susceptible to the loss of communicative function as signals fail to reach their intended receivers due to increased vessel noise that occupies the same frequency bands. If social sounds facilitate significant interactions

between humpback whales, then masking may have deleterious effects on social behavior, foraging, mating efficacy, and the transmission of information within populations. Heightened ocean noise levels have been associated with significant behavioral shifts in baleen whale species, including changes in calling behavior in humpback and blue whales (Dunlop et al., 2010; Melcón et al., 2012). Anthropogenic noise has also been associated with potentially deleterious physiological shifts in baleen whales, including increased stress hormones levels in right whales (Rolland et al., 2012). It is likely that increased anthropogenic noise may have further harmful impacts on acoustically oriented marine species that have not yet been documented.

Methods have been recently developed to assist in quantifying the potential effect of masking for a given species; however, these methods are contingent on an understanding of the acoustic parameters associated with a species' repertoire. Furthermore, attributing shifts in behavior to anthropogenic interactions is greatly facilitated by documentation of undisturbed behavioral states. While this thesis does not directly quantify the effects of vessel noise on humpback whale vocal behavior, it does propose to lay the acoustic and behavioral groundwork necessary to pursue this goal in the future.

RESEARCH APPROACH

I used passive acoustic monitoring concurrent with visual observations to quantify and contextualize the social vocal behavior of humpback whales in Southeast Alaska. My objectives in Chapter 2 were to (1) describe the structure of humpback whale vocal behavior in Southeast Alaska; and (2) develop a catalog of humpback whale social vocalizations from the region. There is a lack of documentation of the social calling repertoire in humpback whales, and specifically Southeast Alaska; Chapter 2 seeks to fill this data gap. My objective in Chapter 3 was to (3) assess whether humpback calling serves a communicative function; this objective was pursued by investigating the relationship between humpback whale abundance and vocal behavior, and patterns of dispersion and vocal behavior. With the exception of the well documented feeding call there are no studies to date that place Southeast Alaskan vocalizations into a social

context. The results of this study will fill a known data gap on humpback whale vocal behavior in Southeast Alaska and will broaden the body of knowledge on humpback whale communication. It is my hope that the results of this study will lay the foundation for future studies that assess calling function, social interactions, and species resilience to environmental and anthropogenic change.

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CHAPTER TWO: Vocal repertoire of Southeast Alaskan humpback whales (*Megaptera novaeangliae*)

INTRODUCTION

In recent years, efforts to use acoustical research methods to study marine mammals have intensified. Species' vocalizations have been used to investigate population structure in several cetaceans, including blue whales (*Balaenoptera musculus*; McDonald et al., 2006b), fin whales (*B. physalus*; Castellote et al., 2010), common minke whales (*B. acutorostrata*; Mellinger et al., 2000; Gedamke et al., 2001), and killer whales (*Orcinus orca*; Ford, 1991). Estimating marine mammal abundance and density using acoustics has been proposed as a cost-effective supplement to traditional ship-based visual surveys (Mellinger and Barlow, 2003). Additionally, the use of acoustic data is essential for studying vocal communication in marine mammals, and acoustic data collected in an undisturbed state may be an importance reference against which to assess species' resilience to changes in the marine soundscape. Interpretation of acoustic data, however, is often contingent on understanding a species' vocal repertoire.

The vocal repertoire of humpback whales (*Megaptera novaeangliae*) is broad and complex. While on low-latitude breeding grounds, humpback whales produce highly stereotyped songs that are directly or indirectly related to mating behaviors (Payne and McVay, 1971; Au et al., 2006). Initially, singing was thought to be exclusive to breeding grounds; however, singing has been recorded along migratory corridors (Norris et al., 1999; Charif et al., 2001; Clark and Clapham, 2004) and to a lesser extent on high-latitude foraging grounds (Gabriele and Frankel, 2002; Clark and Clapham, 2004; Vu et al., 2012).

Although the bulk of research addressing humpback vocal behavior has focused on song, humpbacks also produce many non-song vocalizations – calls – across their geographic range. Silber (1986) coined the term 'social sounds' to describe non-song vocalizations that occurred in groups of competing male humpbacks on the Hawaiian breeding ground. He defined social sounds as “any phonation that does not possess the rhythmic and

continuous patterning of song”. This definition has been expanded to include single song units produced independently of the song structure, novel vocalizations not present in song units, and surface-generated sounds (Dunlop et al., 2007). While Silber (1986) described the behavioral context associated with social sounds in Hawaii, only basic acoustic parameters (duration, frequency range, and fundamental frequency) were included in the study, and a catalog of social sounds was not produced.

The first quantitative acoustic description of social sounds that attempted to discriminate between vocalizations was recorded in Southeast Alaska (Thompson et al., 1986). Calls were classified as “moans”, “grunts”, or “pulse trains”. Acoustic parameters of these vocalizations were described, but no effort was made to systematically distinguish one call type from another, or to generate a catalog of unique call types. Notably, a call associated with cooperatively foraging humpbacks in Southeast Alaska was absent from Thompson’s report, but has been well described by D’Vincent et al. (1985), Sharpe (2001), and Cerchio and Dalheim (2001). The call, dubbed a “feeding call” by D’Vincent et al., has not been documented in any other population or in any other behavioral context.

The first comprehensive catalog of non-song vocalizations described the vocal repertoire of migrating humpbacks in eastern Australia (2007). By using thirteen acoustic parameters, aural-visual analysis, and various multivariate analysis techniques - including principal component analysis and discriminant function analysis - 34 discrete call types were identified. Using a combination of qualitative analyses and a classification and regression tree (CART) approach, a follow-up study by Rekdahl et al. (2013) identified a total of 46 call types from the same region.

In a study of non-song vocalizations produced by North Atlantic humpbacks, Stimpert et al. (2011) used a cluster analysis to separate humpback vocalizations into eight groups with similar acoustic properties. Two highly stereotyped calls (“wops” and “grunts”) were identified through aural-visual analysis and were proposed as ideal candidates for passive acoustic monitoring. While quantitative descriptions of the resultant groupings

were reported, wops and grunts were the only call types uniquely described. The authors did not report acoustic parameters or provide spectrograms for other qualitatively identified call types. The study benefited from increased objectivity; however, the broad results limit comparison of vocalizations from different regions.

While efforts to describe non-song vocalizations have intensified, few humpback populations have been adequately surveyed. That humpback whales produce a diverse array of vocalizations suggests that communication between conspecifics is an important aspect of humpback behavior. An essential step toward understanding the function of these vocalizations is to develop catalogs of humpback whale vocalizations from different populations and in different social contexts. To address this data gap, the goals of this study are (1) to quantitatively describe social calls from a Southeast Alaska foraging ground, and (2) to classify social calls recorded on Southeast Alaskan foraging grounds. This study will expand the known vocal repertoire for Southeast Alaskan humpback whales and for the species as a whole. For the purpose of this study, the term ‘social call’ refers to any vocalization produced in a non-song context, excluding surface-generated percussive sounds. We present a three-part classification system to classify humpback whale vocalizations that includes (1) an aural-visual (AV) analysis, corroborated by (2) a statistical cluster analysis, and validated (3) with a discriminant function analysis (DFA). This classification system is used to develop a catalog of social sounds from Southeast Alaskan humpback whales that can be compared to catalogs developed for other regions and/or migratory contexts.

METHODS

Acoustic data were collected from June-September 2012 in the waters of Frederick Sound, Southeast Alaska, within a one nautical mile radius of the Five Finger Lighthouse (57° 16' 13" N, 133° 37' 53" W; Figure 1). Acoustic recordings were made via two omnidirectional hydrophones (Cetacean Research Technology, C-55), each with a built in +20 dB preamplifier, an effective sensitivity of -165 dB, and a flat frequency response (± 3 dB) from 10 Hz -10 kHz. The hydrophones were connected to a digital audio recorder (S4N Zoom Handy) with operated with a 44.1 kHz sampling rate and 16-bit

sample resolution. Hydrophones were separated by 4.5 m (or 3.3 m when ocean surface conditions necessitated) and deployed to a depth of 20 - 25 m from the port and starboard side of a 3 m inflatable vessel. Five-pound weights were attached to each hydrophone to facilitate sinking. All recordings were obtained when the vessel was adrift with the engine off. No other baleen whale species were seen in the study area, and all vocalizations that fell within reasonable parameters for baleen whale vocalizations were assumed to be produced by humpbacks.

Data Processing and Analysis

Spectrograms of recordings were generated using RavenPro 1.4 with 4096-point Fast Fourier Transform (FFT), Hann window (providing 42.7 Hz resolution) and 75% overlap, and the Matlab-based program Osprey (Mellinger, 2007) with the same parameters except a Hamming window. Recordings were manually reviewed in their entirety and samples were extracted using RavenPro 1.4 (Cornell Laboratory of Ornithology). The signal-to-noise ratio (SNR) of each extracted sample was calculated using the method described by Mellinger and Bradbury (2007). To be included in the analysis, humpback whale vocalizations had to have a SNR of 10 dB or higher (Dunlop et al., 2007; Dunlop et al., 2008; Stimpert et al., 2011; Rekdahl et al., 2013) and have visually and aurally distinguishable start and end points to ensure accurate parameter measurements. Consistent with Dunlop (2007), Stimpert et al. (2011) and Rekdahl et al. (2013), call parameters relating to both frequency and time were measured and extracted from spectrogram samples for statistical analyses (Table 1).

In addition to traditional acoustic measurements, we selected parameters from a pre-programmed Noise-Resistant Feature Set (NRFS; Mellinger and Bradbury 2007) within the Matlab based program Osprey (Mellinger 2007). NRFS was designed for detection and classification of marine animal sounds in noisy environments. Based on Fristrup's (1993) "Acoustat" approach, NRFS includes robust methods for assessing a number of acoustic features, including frequency, duration, amplitude modulation, upsweep, entropy, and central tendencies of intensity and frequency. In lieu of taking measurements from an observer-drawn annotation box, when using the NRFS a smaller

time-frequency region, known as the feature box, is de-noised and calculated based on an algorithm that ranks summed energy within the sound relative to background noise. In this manner the louder parts of the spectrogram, which remain evident in high-noise situations, have the strongest influence on the calculated feature values (Mellinger and Bradbury, 2007). These features correspond to more traditional acoustical measurements but have the additional benefit of being robust to variable noise conditions and sound attenuation. This was particularly important for this study given that hydrophones were cabled to a drifting vessel, subject to flow and vessel noise, and affected by variable environmental conditions.

Vocal Classification and Statistical Analysis

Three separate analyses were conducted to classify vocalizations: Aural-Visual (AV) classification by humans, hierarchical agglomerative cluster analysis, and discriminant function analysis (DFA). Sample files were stripped of identifying information and randomly ordered for the AV analysis. Samples were visually inspected in Raven Pro 1.4 by a single observer (MF), while simultaneously listening to the sample. Initially, samples were broadly grouped based on visual and acoustic similarities. Samples within the resulting groups were then re-randomized and subsequently sorted into smaller sub-groups. This process was repeated until the variation between samples was not discernible enough to be considered unique. Neither the classification structure nor the number of groups or sub-groups was pre-determined. To account for possible outliers and individual variation, only unique vocalizations that were present on a minimum of two non-consecutive sampling days were included in the final results.

Select acoustic parameters used in the analysis (Table 1) were log-transformed, to minimize skew and to better approximate the mammalian perception of pitch (Richardson et al., 1995; Parks and Tyack, 2005; Dunlop et al., 2008; Stimpert et al., 2011). These parameters were used in a hierarchical agglomerative cluster analysis (JMP Pro 9) to generate unsupervised call groupings (clusters). A dendrogram was generated using a Ward's distance linkage method and a conservative cutoff point on the resulting tree was determined based on distance values and information retained (Stimpert et al., 2011). The resultant clusters were compared to the results of the AV analysis to determine the level

of agreement between the two methods. If all of the calls placed together in a single group through AV classification were also placed in a single cluster, then agreement was said to be 100% for that call group.

DFA with cross validation was used as a supervised method to determine the likelihood of vocalizations being correctly classified to each of the possible groups through the AV analysis. DFA has been used in studies classifying dolphin vocalizations (Boisseau, 2005), southern right whales (*Eubalaena australis*) (Clark, 1982), and humpback whale social sounds (Dunlop et al., 2008). Supervised methods, including DFA, differ from the unsupervised clustering technique in that they use existing data as a training set and make predictions based upon the dataset as a whole. The same call parameters used in the cluster analysis were used to conduct DFA. Pooled DFA, where a DFA is run on the total data set, was conducted to assess the total agreement between methods; within group DFA, or a DFA run on the calls of a given vocal group, was used to assess classification agreement at finer scales. Acoustic parameters identified through AV analysis to characterize each grouping were tested using Wilcoxon Rank-Sum statistical analyses. Multiple comparisons were made using the non-parametric Steel-Dwass method (non-parametric form of Tukey's Honest Significant Difference Test; (Hollander and Wolfe, 1999).

RESULTS

A total of 32 sampling days between June and September 2012 resulted in 92.6 h of recordings. From these, 299 samples of humpback whale vocalizations met the criteria for analysis. Acoustic parameters varied widely among vocalizations. Starting fundamental frequency ranged from 31 Hz – 3.24 kHz with an average of 277 Hz (\pm 398 Hz), and a mean peak frequency of 341 Hz (\pm 601 Hz). Call duration ranged from 0.2 – 100.7 s, averaging 3.5 s (\pm 10.3 s), with a median of 1.1 s. Most calls (n=293) were under 15 s. Bandwidth for all calls ranged from 49 Hz to 15.2 kHz with a mean of 919 Hz (\pm 1572 Hz). The smallest identifiable unique units of sound, identified by AV classification, which were produced in isolation and separated from other sounds by

silence, were defined as ‘call types’. Sixteen call types were identified, nested within seven vocal subclasses, within four general vocal classes (Figure 2).

The hierarchical agglomerative cluster analysis identified four principal statistical clusters, which were chosen based on the amount of information retained by each sample (~73%) and proportional distance between splits (Figure 3). Each cluster corresponded with a high degree of overlap to one of the vocal classes identified by AV analysis, although no single vocal class was encompassed within a cluster (Table 3). There was 83% agreement ($n=247$) between clusters and vocal classes (Table 2). When samples were pooled, a DFA correctly assigned 90% ($n=269$) of samples into the same vocal class as determined through AV classification, 78% ($n=233$) of samples into the same vocal subclass as determined through AV classification, and 72% ($n=215$) of samples into the same call type as determined by AV classification.

Description of Vocalizations

The following results describe call classes, subclasses and types based on AV classification. Vocal classes and subclasses were named according to salient acoustic properties, which are described below. Call types were named using the vocal class acronym (e.g., LFH refers to Low-Frequency Harmonic), followed by a letter indicating where the recording was made (F= foraging ground; B= breeding ground; M= migratory corridor), and were numbered in order of largest to smallest sample size. This system was developed in an attempt to encourage a consistent naming system for social calls across the entirety of the humpback whale migratory range. However, qualitative naming precedents set by Dunlop et al. (2007) and Stimpert et al. (2011) are included when appropriate and are marked with an asterisk. Qualitative names for previously undocumented vocalizations are included in parentheses in an effort to abide by the currently preferred naming system, as well as to provide an approachable – though subjective – method for remembering call names.

Low-Frequency Harmonic Calls

The low-frequency harmonic (LFH) vocal class was the vocal class represented most in the study ($n=147$). Samples placed in this class were characterized by low fundamental frequencies (mean $108.7 \text{ Hz} \pm 98.7 \text{ Hz}$), with most of the energy concentrated below 500 Hz (mean peak frequency $135 \text{ Hz} \pm 77 \text{ Hz}$; Table 4). Wilcoxon Rank-Sum tests indicated that the mean lower starting frequency ($\chi^2=176.5$; $p<0.001$) and mean peak frequency ($\chi^2=173.03$; $p<0.001$) varied significantly across vocal classes. Steel-Dwass post-hoc tests indicated that samples in the LFH class had significantly lower starting frequency ($p<0.001$) and peak frequency ($p<0.001$) than samples in the remaining three vocal classes.

LFH calls were further characterized by tightly spaced harmonics, identified visually in the corresponding spectrograms (Figure 4). The number of repeated units of sound contained in a single call was significantly lower in LFH calls than any other call class ($p<0.001$), with vocalizations typically occurring as a single non-repeated unit of sound (mean Bout length $1.17 \text{ units} \pm 0.95 \text{ units}$). Vocalizations were generally short in duration, averaging $1.4 \text{ s} (\pm 0.8 \text{ s})$ (Table 4). Mean duration was significantly shorter than calls in the Tonal vocal class ($Z = 9.34$; $p < 0.001$). There was 80% ($n=117$) overlap between samples placed in the LFH class by AV analysis and those grouped into Cluster 1 (Table 2). Within-class DFA predicted the same vocal subclass and call types as AV classification for 90% ($n=133$) and 73% ($n=108$) of samples, respectively.

The LFH class was divided into three subclasses: Trilled, Complex, and Simple (Table 4; Figure 4). The most salient acoustic features of each subclass, as determined through AV examination, are described here: Trilled calls had noticeable rapid temporal structure, which exhibited more amplitude modulation than the other two subclasses and appeared ‘smeared’ from reverberation when recorded at a distance. Average bandwidth of Trilled calls was narrower than other subclasses (mean Band= $253 \text{ Hz} \pm 233 \text{ Hz}$; $p < 0.001$). Complex calls had organized harmonic structure with more widely spaced formants. Simple calls had fewer harmonics and less noticeable frequency or amplitude modulation.

Calls in the Complex subclass and Simple subclass were also poorly represented in the data set ($n=8$ and 6 , respectively).

Six call types were classified as part of the LFH vocal class (Table 4; Figure 4). Call types in the LFH vocal class included LFH-F-1 (Purrs; $n=100$), LFH-F-2 (Wops*; $n=33$), LFH-F-3 (Modulated Moans*: $n=4$), LFH-F-4 (Descending Moans*; $n=4$), LHF-F-5 (Groans; $n=3$), and LHF-F-6 (Variable Moans; $n=3$). LFH-F-1 and LFH-F-2 composed the Trilled subclass. LFH-F-3 and LFH-F-4 composed the Complex subclass, and LFH-F-5 and LFH-F-6 composed the Simple subclass (Table 4; Figure 4). LFH-F-1 was the most frequently detected call type in the data set, making up nearly a third of all detected vocalizations ($n=100$; Figure 4).

Pulsed Calls (P)

This was the second-most represented call class ($n=83$). Call types in the P vocal class typically included repeated units of sound within each vocalization (Table 5, Figure 6). The mean number of repetitions in the P call class was significantly higher than in other vocal classes ($p<0.001$; mean Bout= 5.4 units \pm 5.3 units). Samples in the P vocal class were characteristically short in duration, averaging 0.76 s (\pm 0.46 s) per call (Table 5). The mean duration was significantly shorter than calls in the Tonal call class ($Z=9.35$; $p<0.0001$). Samples in the P vocal class had low fundamental frequencies (mean Start= 260 Hz \pm 333 Hz), and the mean starting fundamental frequency was significantly higher in the P vocal class than in the LFH vocal class ($Z=8.3$; $p<0.0001$), and significantly lower in this class than the two remaining vocal classes ($p<0.001$). There was 83% ($n=69$) overlap between samples placed in this vocal class and samples quantitatively grouped into Cluster 2 (Table 2). Within class DFA predictions agreed with AV classification for 83% of samples ($n=68$) at the vocal subclass level and 81% of samples ($n=67$) at the call type level.

Samples in the P vocal class fell into one of two subclasses: Simple or Complex (Table 5; Figure 6). Complex calls in the P vocal class were characterized by more amplitude modulation and greater mean bandwidth (mean Band 979 ± 1309 Hz) than samples in the

Simple subclass. Simple calls in the P vocal class were highly stereotyped, were more narrowband on average than samples in the Complex subclass (mean Band= 667 Hz \pm 744), and lacked harmonics (Figure 6).

Four call types were classified in the P vocal class based on AV examination (Table 5; Figure 6). Call types in this class, following the aforementioned coding system, included P-F-1 (Swops; $n=58$), P-F-2 (Teepees; $n=12$), P-F-3 (Droplets; $n=9$), and P-F-4 (Horses; $n=4$). P-F-1, P-F-2, and P-F-4, were all classified as Complex P calls; P-F-3 were the exclusive call in the Simple subclass. P-F-1 calls were the second-most represented call type ($n=58$; Figure 6).

Noisy/Complex Calls (NC)

This was the least represented call class ($n=27$). Samples in the NC vocal class were characterized by wide bandwidths (mean=3032 \pm 3902 Hz), high peak frequencies (mean 986 Hz \pm 956 Hz), and high aggregate entropy (mean 5.8 \pm 1.8; Table 6). Results of a Wilcoxon Rank-Sum test indicate that the means of these three acoustic parameters – bandwidth, peak frequency, and aggregate entropy – varied significantly between vocal classes ($p<0.0001$). Post-hoc Steel-Dwass tests indicated the means bandwidth of NC calls is higher than calls in T and LFH vocal classes ($p<0.001$), but not significantly different from calls in the P vocal class ($Z = -2.9$; $p<0.07$). The mean peak frequency of NC calls is significantly higher than calls in LFH and P vocal classes ($p<0.0001$), but not significantly different from calls in the T vocal class ($Z = 5.22$; $p=0.45$). Mean entropy of calls is significantly higher in the NC vocal class than in LFH or T vocal classes ($p<0.0001$), but not significantly different than in the P vocal class ($Z=-2.1$; $p=0.15$).

Samples in the NC vocal class fell into two subclasses: Harmonic and Variable (Table 6; Figure 7). The two subclasses within the NC vocal class were particularly stratified. Samples within the Harmonic subclass exhibited widely spaced harmonics and were not characteristically pulsed. Mean entropy levels for samples in this vocal subclass were significantly higher than in the Variable subclass (mean Start=1380 Hz \pm 1279 Hz; $Z=2.66$; $p=0.008$), as were mean bandwidths (mean Band=1018 Hz \pm 916 Hz; $Z= 2.76$;

$p=0.006$). Calls within the Variable subclass were characterized by multiple inflections (slope reversal of the fundamental frequency), and temporal patterns that varied widely from one call to the next (Figure 6).

There was 70% ($n=19$) overlap between samples subjectively placed in this vocal class and samples quantitatively grouped into Cluster 3. Within-class DFA correctly predicted the subclass for 93% of samples ($n=25$), and call types for 100% of samples within the NC vocal class ($n=27$).

Five call types were identified within the NC vocal class (Table 6, Figure 7). Calls types included NC-F-1 (Squeegees; $n=8$), NC-F-2 (Aerial Trumpets; $n=5$), NC-F-3 (Ahoogas; $n=5$), NC-F-4 (Ascending Shrieks*; $n=5$), and NC-F-5 (Descending Shrieks*; $n=4$). Based on concurrent visual observations, NC-F-2 calls (Aerial Trumpets) are believed to occur during surface exhalations. Visual observers corroborated the NC-F-2 call occurring simultaneously with an exhalation in four of the five events. NC-F-3 (Ascending Shrieks*) and NC-F-5 (Descending Shrieks*) were broadband and harmonic in nature and were included in the Harmonic subclass (Figure 7). NC-F-1 calls (Squeegees), NC-F-4 calls (Ahoogas), and NC-F-2 calls (Aerial Trumpets) were considerably less “musical” than other call types in the NC vocal class, contained inconsistent temporal structure, and were included in the Variable subclass (Figure 7).

Tonal Calls (T)

This was the third most represented vocal class ($n=43$). Samples in the T vocal class were characterized by narrow bandwidths (mean Band = $129 \text{ Hz} \pm 24 \text{ Hz}$), low fundamental frequencies (mean Peak = $461 \text{ Hz} \pm 122 \text{ Hz}$), and low aggregate entropy (mean Entropy = 3 ± 0.77 ; Table 7). There is evidence that the mean bandwidth of samples within this class is significantly narrower than in other call classes ($p<0.0001$). There is also evidence that aggregate entropy was significantly lower in samples from the T vocal class than in other vocal classes ($p<0.0001$).

There was 98% ($n=42$) overlap between samples subjectively placed in this vocal class and samples quantitatively grouped into Cluster 4 (Table 2). However, based on AV examination, only one call type, T-F-1 (“Feeding Call”; Cerchio and Dalheim, 2001), was classified within the T vocal class; no subclasses were determined to be present within this vocal class. With only a single identified call type, it did not make sense to calculate within-class DFA.

T-F-1 calls lacked harmonics or amplitude modulation and may occur in short bouts (Table 7, Figure 8)

DISCUSSION

Humpback whales are well known for the complexity of their vocal behavior on the breeding grounds; this study demonstrates humpback whales also produce a diverse array of social sounds on an Alaskan foraging grounds. The 16 call types identified by this study add a level of specificity to the broad call descriptions proposed for Southeast Alaska by Thompson (1986) and form the foundation for a comprehensive catalog of social calls from the region. Further, this study identifies an inherent acoustic structure in humpback whale social calling from this region.

The combined results of AV classification and hierarchical agglomerative cluster analysis suggest that, based on acoustic parameters, social calls documented in this study fall into one of four vocal classes. The hierarchical structure identified by the two methods is strengthened by high agreement with DFA and statistical hypothesis testing, which further revealed significant differences between some vocal classes, sub-classes, and call types. The strength of the resulting catalog lies in the corroborating results based on multiple classification methodologies.

Classification Methods

There are inherent problems with each of the three methods when used independently that are minimized when used concomitantly. When used in isolation, AV classification

is highly subjective, particularly if there is individual or inter-group variation. Observers may not examine vocalizations with the same degree of scrutiny, leading some observers to broadly classify similar vocalizations as one call type, while other observers may delineate call uniqueness at a level explained by individual variation. To address these issues, statistical methods may allow for more objective assessments of group membership. Cluster analyses reduce the likelihood of observer bias by quantitatively identifying groupings in the data set that may be overlooked, but are not entirely objective; the investigator chooses both acoustic parameters and the level at which to limit grouping inferences. Alternatively, DFA is a good tool for ground truthing predetermined group membership, yet cannot identify structure inherent in the data set and is contingent on predefined groupings and observer defined parameters.

Additionally, there is a degree of subtlety that may be assessed by a human observer that is not maintained by either cluster analyses or DFA. In this study, despite the cluster analysis' ability to group calls into vocal classes and the ability of DFA to corroborate their membership, a human observer was necessary to describe salient differences between vocal classes in order to use traditional statistical hypothesis testing. Acoustic parameters that were identified through AV analysis to be good indicators of call types within vocal classes (e.g., low fundamental frequencies for LFH call types; increased number of repeated sound units per call in P call types) were found to vary significantly between vocal classes and vocal subclasses. These acoustic parameters could not be identified by the cluster analyses or DFA, and notably, despite differences in acoustic parameters, neither the cluster analysis nor DFA were able to consistently identify differences between some groupings within the data set.

As an example, two of the most commonly detected call types were LFH-F-1 calls (Purrs) and LFH-F-2 calls (Wops). The two calls are members of the same subclass and thus share many acoustic properties. The two calls are visually and acoustically comparable with the exception of a characteristic terminal upsweep in the LFH-F-2 (Wop) call, and were clearly distinguished through AV examination by the investigator, as well as by multiple field assistants. Despite this, and the two calls were commonly

confused by DFA, and no statistically significant difference between the two call types was identified. It is possible that measurements of call parameters may not have been sensitive enough to detect the differences, especially in light of variable environmental conditions and attenuated call states. It is evident, however, that although the call types are uniquely different, one call (LFH-F-2) encompasses the other call in its entirety. This would suggest that the LFH-F-2 call may be a unique variation of the LFH-F-1 call, or a combination of the LFH-F-1 call and another call type. These nuances would have been missed had only a single classification method been employed in this study, and similarly the credibility of the AV classification would be subject to doubt in the absence of corroboration by more quantitative classification techniques.

Regional Similarities

In general, social calls in this catalog are slightly higher in frequency than social calls described for eastern Australia (Dunlop et al., 2007), but appear to be similar in frequency to calls described for the North Atlantic foraging grounds (Stimpert et al., 2011). Fewer unique call types are described in this catalog than have been described for the east Australian migratory region (Rekdahl et al., 2013); comparison to the number of unique call types in the North Atlantic is not directly comparable, but more call types are described here than for the North Atlantic population (Stimpert et al., 2011).

Some similarities in call types from the three regions are evident. The LFH-F-2 call appears to have a cosmopolitan distribution; it was visually and aurally confirmed as occurring in both east Australia (Dunlop et al., 2007) and the North Atlantic (Stimpert et al., 2011). The call was highly represented in both studies, and was identified by Stimpert et al. (2011) as a candidate for use in passive acoustic monitoring (PAM) due to its frequency of occurrence. Further, Stimpert et al. (2011) cites unpublished data confirming the presence of this call type on the Hawaiian breeding grounds, and aural examination of unpublished data confirms the presence of the call type in Cormorant Channel in British Columbia, Canada as well. Additionally, this call type was present and highly represented throughout the four year study in east Australia (Rekdahl et al., 2013).

The occurrence and persistence of this call type in independent populations suggests that its use is not culturally dependent. Dunlop (2008) proposed that the call type may function for either intra- or inter-group communication. This hypothesis is anecdotally supported through observations in Southeast Alaska where this call type was acoustically identified in calling bouts occurring between multiple animals.

Similarly, three call types - NC-F-3 (Ascending Shrieks), NC-F-4 (Descending Shrieks), and LFH-F-3 (Modulated Moans) – were visually similar to spectrograms reported by Dunlop et al. (2007) to be song units. In this study, the three call types were poorly represented, making up only a small portion of the data set, but did appear to be stereotyped (corroborated by high levels of classification agreement) and occurred in short calling bouts similar in structure to song. Song was not recorded in this study; however, comparisons to song recorded in November 2012 in Glacier Bay National park (Gabriele, pers. communication) confirmed that the same three call types were used as song units in Southeast Alaska in the same year. Samples from other regions were not subjected to the aforementioned classification system, so it is not possible to extend inference directly; however, it is likely that continued recording in Frederick Sound into the fall may have resulted in the detection of singing humpback whales.

Vocal Continua

As noted, LFH-F-1 and LFH-F-2 calls were acoustically very similar - resulting in lower overall classification agreement at the call type level; while not consistent across all vocal classes, a similar phenomenon was observed for calls in the P Complex subclass. The P-F-1 (Swop) call type was difficult to classify with AV analysis, and difficult to verify with DFA. Although samples were grouped in the same vocal class with a high degree of agreement across classification methods, at finer scales distinguishing differences between samples met with moderate, though reduced, success. The P-F-1 call was visually and aurally different from other call types; however, it was structurally more variable than other call types. AV examination revealed that this call appeared to be intermediate between other call types, namely the P-F-2 (Teepee) call and the P-F-4 (Horsey) call. If one increases the frequency of the P-F-2 calls, similarities to the P-F-1

call become evident. If one changes the temporal pattern of the P-F-1 call, similarities to the P-F-4 call become evident. These type of variations were present in some samples within the data set. Anecdotally, in one 30-second recording, a single animal was recorded transitioning from a call that was clearly a LFH-F-2 call into a series of clearly delineated P-F-1 calls and further into a series of P-F-2 calls, indicating that some call types may be fluid.

Comparatively, calls in the T and NC vocal classes and P simple subclass are comparably discrete, and were thus classified with a high degree of agreement between the three methods. T-F-1 (Feeding Cry) calls and P-F-3 (Droplet) calls were described in AV analysis as highly stereotyped; and at the pooled sample level, calls classified as T-F-1 calls or P-F-3 calls had highest agreement value of any call types. Further, within-class DFA for all call types in the T vocal class, NC vocal class, and P simple subclass agreed completely with AV classification for all of the samples classified as either call type. This indicates that while some call types (e.g., Purrs & Wops) may be acoustically related, some calls (e.g., Feeding Cries and Droplets) are highly stereotyped. Notably, the T-F-1 call was the sole member of its vocal class and the P-F-3 call was the sole member of its subclass, indicating that stereotypy might extend to the class or subclass level.

High agreement between AV and DFA classification methods at the call type level was found within the NC vocal class, indicating call stereotypy for types in this group. Classification agreement at the vocal class level, however, was only moderately successful. This may be a function of limited samples size; calls in the NC vocal class were the least represented in the data set. AV comparisons to vocalizations detected in song recorded in Glacier Bay in the same year, however, anecdotally confirm the discreteness of calls in the NC Harmonic subclass. Song in humpbacks is highly stereotyped; it is unsurprising that social units identified as independent song units would also be stereotyped.

Based on these descriptions, I suggest that some humpback social calls in Southeast Alaska form a vocal continuum, and other calls are used discretely. This hypothesis is

supported by the varying degrees of classification agreement between the vocal types, with the LFH vocal class and P Complex vocal subclass appearing to contain continuous call types, and the T vocal class, P Simple subclass, and NC vocal class containing discrete call types. Vocal continua pertaining to humpback whale social sounds were suggested in this population (Silber, 1986) and in two other populations of humpbacks, North Atlantic and eastern Australian ones (Dunlop et al., 2008; Stimpert et al., 2011). Similarly, Clark (1982) reported a combination of continuous calls and discrete calls in southern right whales, reporting that some call types in the continuum were more common than others; this was similarly found in this study, with LFH-F-1 calls disproportionately detected.

It is possible that highly stereotyped calls serve specific behavioral functions that, while present on the foraging grounds, are only relevant during particular forms of social communication. On breeding grounds, humpback whale song is highly stereotyped and has been associated with a specific behavioral context (Tyack, 1981; Winn et al., 1981). Similarly the T-F-1 (Feeding) call, which was the most stereotyped call in this study based on AV analysis and classification agreement, has been associated with cooperative foraging events in Southeast Alaska (D'Vincent et al., 1985; Cerchio and Dalheim, 2001; Sharpe, 2001). Conversely, in migrating humpbacks the LFH-F-2 (Wop) calls has been proposed to serve multiple functions, including acting as a contact call, an inter- or intra-group social call, and a mother-calf affiliation call (Dunlop et al., 2008). It is possible that during specific activities (i.e. courtship displays, cooperative foraging) that discrete calls may be favored, while when less specific social interactions occur (e.g., contact calling), calls from the call continuum may be favored. This has been observed in northern right whales, where males produce the highly stereotyped gunshot call in association with mate attraction, while females favor a repertoire of variable calls when interacting in surface active groups (Parks and Tyack, 2005; Parks et al., 2011). Further research into the behavioral context of call types, and the biological relevance of vocal classes in Southeast Alaska, is warranted to address these questions. This research will be pertinent for comparison of social communication between foraging and breeding grounds and populations.

Conclusions

The social sounds analyzed in this study were recorded exclusively in the summer of 2012, and therefore are not believed to be indicative of the entire non-song repertoire of Southeast Alaskan humpbacks. This study would benefit from a long-term data set that would allow for more adequate measurements of underrepresented calls. Additional research is needed on individual call variation; calling behavior as a function of age, gender, and reproductive status; calling behavior from other populations; and vocal behavior along the entirety of the humpback whale migration. It is possible, and indeed probable, that with a greater sample size, calls grouped together within the current qualitative classification system may be split into multiple call types, or merged with other calls to form a single call type with a higher level of variability. A greater sample size would allow for more robust statistical inferences, which could be useful in making objective classification decisions at the call type level.

Despite this, this study presents the first quantitatively described catalog of social calls for Southeast Alaskan humpback whales, and expands the known vocal repertoire for humpback whales in the population. This study also proposes a hierarchical classification structure that may be applied to social calls from this region and elsewhere. Additionally, similar to other regions and species, humpback whale vocalizations seem to consist of a combination of discrete calls and continuous ones, which may be produced under specific contexts. It has been suggested that publications that are digitally available be accompanied by spectrograms, sound files, and associated recording information. This would greatly enhance the ability to compare call types between contexts. In the absence of available media, comparisons between regions, while useful, remain exploratory. Copies of sample call types referenced in this paper are made available upon request.

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TABLES

Table 1. Description of acoustic variables used for three-part classification of humpback whale social calls. Feature from the Noise Resistant Feature Set (NRFS) are denoted with an asterisk (*). Variables that were log transformed for analysis are denoted with a plus sign (+).

Measurement	Notation	Description
Duration (s)*	Dur	Length of feature box
Vocalizations per Bout	Bout	Number of repetitions of the same unit of sound within a single calling event (“Bout”)
Lower Frequency (Hz)*+	Low	Lowest frequency limits of feature box
Upper Frequency (Hz)*+	Max	Highest frequency limit of feature box
Start Frequency (Hz)+	Start F_0	The fundamental frequency at the start of the call
End Frequency (Hz)+	End F_0	The fundamental frequency at the end of the call
Peak Frequency (Hz)+	Peak	Frequency of the spectral peak
Bandwidth (Hz)*+	Band	Height of feature box
Median Frequency (Hz)*+	MedF	Frequency where cumulative sum of cell values reach 50% of the total energy
Frequency Quartile (Hz)*+	FreqQ	Frequency where cumulative sum of energies is 25% of total energy in Feature Box
Amplitude Modulation Rate*	AM Rate	Dominant rate of Amplitude Modulation
Frequency Modulation Rate*	FM Rate	Dominant rate of frequency modulation
Upsweep Fraction*	UpFrac	Fraction of time in which median frequency in one block is greater than that in preceding block, weighted by total energy in each block
Frequency Trend+	FreqTrend	Start F_0 / End F_0
Aggregate Entropy	Entropy	A measure of total disorder in the call

Table 2. Confusion matrix showing overlap between aural-visual (AV) analysis classification and hierarchical agglomerative cluster classification. High values are shown in bold. Agreement (%) is calculated as the percentage of calls determined through AV classification to be in the same vocal class to be placed into a single statistical cluster.

	Cluster 1	Cluster 2	Cluster 3	Cluster 4	Total
T	0% (n=0)	98% (n=42)	2% (n=1)	0% (n=0)	43
P	4% (n=3)	0% (n=0)	83% (n=69)	12% (n=10)	82
LFH	80% (n=117)	1% (n=1)	18% (n=27)	1% (n=2)	147
NC	7% (n=2)	4% (n=2)	15% (n=4)	70% (n=19)	27
Total	122	45	101	31	299

Table 3. Summary of select acoustic parameters for each group identified by hierarchical cluster analysis. Mean parameters are in bold; standard deviations are below and listed in italics. Class and Call Types refer to results of aural-visual analyses.

Cluster	Class	Call Types	n	Dur (s)	Bout (n)	Start (Hz)	End (Hz)	Peak (Hz)	Cent. (Hz)	Lower (Hz)	Upper (Hz)	Band (Hz)	MedF (Hz)	AM	FM	Up
1	Amp. Mod.	Des. Moan, Des. Shriek, Mod. Moan, Purr, Purrdrop, Swop, Teepee	122	1.0 <i>1.4</i>	1.0 <i>0.4</i>	89 <i>38</i>	93 <i>34</i>	114 <i>45</i>	159 <i>45</i>	71 <i>24</i>	276 <i>97</i>	205 <i>91</i>	129 <i>47</i>	1.9 <i>1.9</i>	1.9 <i>1.4</i>	-1.3 <i>2.5</i>
2	Tonal	Feed, Ahooga	45	16.7 <i>23.9</i>	3.5 <i>4.9</i>	463 <i>102</i>	461 <i>103</i>	479 <i>86</i>	480 <i>81</i>	422 <i>91</i>	525 <i>86</i>	103 <i>51</i>	474 <i>84</i>	0.8 <i>1.7</i>	0.3 <i>0.4</i>	0.0 <i>0.3</i>
3	Pulsed	Desc. Moan, Drop, Groan, Horse, Mod. Moan, Purr, Purrdrop, Squeegie, Swop, Teepee, Var. Moan, Ahooga	101	0.8 <i>0.8</i>	5.2 <i>6.0</i>	207 <i>200</i>	316 <i>381</i>	252 <i>117</i>	360 <i>166</i>	135 <i>56</i>	880 <i>672</i>	745 <i>654</i>	280 <i>124</i>	2.2 <i>1.8</i>	2.6 <i>2.2</i>	3.1 <i>12.8</i>
4	Noisy	Asc. Shriek, Desc. Shriek, Horse, Squeegie, Swop, Trumpet, Var. Moan	31	1.6 <i>1.0</i>	1.3 <i>1.0</i>	999 <i>732</i>	1192 <i>1037</i>	1307 <i>1335</i>	1486 <i>1163</i>	696 <i>550</i>	3459 <i>3689</i>	2762 <i>3219</i>	1269 <i>978</i>	2.1 <i>2.9</i>	1.5 <i>1.2</i>	0.1 <i>32.7</i>

Table 4. Summary of select acoustic parameter for samples subjectively classified within the Low Frequency Harmonic (LFH) vocal class. Mean values are in bold and standard deviations in italics. Naming precedents set by Dunlop (2007) are marked with an asterisk (*). See Figure 4 for corresponding spectrograms.

Low Frequency Harmonic Calls (n=147)

Subclass Call Type	Trilled				Complex				Simple			
	LFH-F-1 n=100		LFH-F-2 n=33		LFH-F-3 n=4		LFH-F-4 n=4		LFH-F-5 n=3		FH-F-6 n=3	
Description	Purr		Wop*		Mod. Moan*		Desc. Moan		Groan		Var. Moan	
Bout (n)	1	<i>2</i>	1	<i>1</i>	2	<i>2</i>	1	<i>0</i>	1		1	
Peak (Hz)	128	<i>75</i>	132	<i>81</i>	223	<i>102</i>	147	<i>28</i>	209	<i>0</i>	180	<i>0</i>
Lower (Hz)	79	<i>50</i>	76	<i>38</i>	153	<i>81</i>	122	<i>18</i>	142	<i>70</i>	135	<i>71</i>
Upper (Hz)	336	<i>286</i>	325	<i>108</i>	923	<i>207</i>	675	<i>528</i>	576	<i>59</i>	612	<i>65</i>
Duration(s)	1.0	<i>0.7</i>	0.7	<i>0.2</i>	1.3	<i>0.6</i>	1.4	<i>0.6</i>	3.3	<i>113.9</i>	2.5	<i>240.8</i>
Band(Hz)	257	<i>266</i>	249	<i>82</i>	770	<i>173</i>	553	<i>520</i>	434	<i>2</i>	477	<i>1</i>
Median (Hz)	143	<i>73</i>	144	<i>71</i>	299	<i>50</i>	145	<i>31</i>	227	<i>59</i>	266	<i>269</i>
Freq. Q. (Hz)	76	<i>46</i>	88	<i>43</i>	163	<i>67</i>	88	<i>77</i>	84	<i>61</i>	205	<i>51</i>
AM	2	<i>1</i>	2	<i>3</i>	1	<i>0</i>	1	<i>1</i>	0	<i>34</i>	1	<i>77</i>
FM	2	<i>1</i>	3	<i>2</i>	2	<i>1</i>	1	<i>1</i>	0	<i>0</i>	0	<i>0</i>
Upsweep	44	<i>12</i>	45	<i>10</i>	51	<i>4</i>	38	<i>14</i>	50	<i>0</i>	38	<i>0</i>
Start (Hz)	90	<i>39</i>	112	<i>158</i>	170	<i>33</i>	225	<i>91</i>	207	<i>5</i>	341	<i>12</i>
End (Hz)	92	<i>38</i>	129	<i>146</i>	219	<i>121</i>	168	<i>80</i>	229	<i>38</i>	167	<i>120</i>

Table 5. Summary of select acoustic parameter and sample size for samples subjectively classified within the Pulsed (P) vocal class. Mean values are in bold and standard deviations in italics. See Figure 6 for corresponding spectrograms.

Pulsed Calls (n=82)

Subclass Call Type	P-F-1 n=57		Complex P-F-2 n=12		P-F-4 n=4		Simple P-F-3 n=9	
	Description	Swops		Teepee		Horse		Droplets
Bout (n)	6	<i>7</i>	4		7	<i>5</i>	5	<i>3</i>
Peak (Hz)	328	<i>287</i>	191		1732	<i>3046</i>	309	<i>140</i>
Lower (Hz)	169	<i>150</i>	100	<i>2</i>	557	<i>743</i>	156	<i>46</i>
Upper (Hz)	1063	<i>755</i>	428	<i>85</i>	3604	<i>4074</i>	919	<i>810</i>
Duration(s)	0.6	<i>0.3</i>	0.6	<i>40.5</i>	2.1	<i>0.6</i>	0.5	<i>0.1</i>
Band (Hz)	894	<i>717</i>	327	<i>253</i>	3047	<i>3337</i>	763	<i>795</i>
Median (Hz)	361	<i>271</i>	181	<i>0</i>	1212	<i>1773</i>	343	<i>152</i>
Freq. Q. (Hz)	266	<i>251</i>	121	<i>230</i>	1062	<i>1293</i>	233	<i>236</i>
AM	2	<i>1</i>	2	<i>80</i>	5	<i>6</i>	3	<i>3</i>
FM	3	<i>2</i>	3	<i>85</i>	2	<i>3</i>	2	<i>1</i>
Upsweep	56	<i>16</i>	52	<i>1</i>	43	<i>6</i>	72	<i>16</i>
Start (Hz)	244	<i>242</i>	142	<i>1</i>	882	<i>1115</i>	238	<i>146</i>
End (Hz)	292	<i>262</i>	142	<i>15</i>	986	<i>1441</i>	1109	<i>696</i>

Table 6. Summary of select acoustic parameter for samples subjectively classified within the Noisy/Complex (NC) vocal class. Mean values are in bold and standard deviations in italics. Naming precedents set by Dunlop et al. (2007) are marked with an asterisk (*). See Figure 7 for corresponding spectrograms.

Noisy/Complex Calls (n=27)

Subclass Call Type	Variable									
	NC-F-1 n=8		NC-F-2 n=5		NC-F-3 n=5		Harmonic NC-F-4 n=5		NC-F-5 n=4	
Description	Squeegie		Trumpet		Ahooga		Asc. Shreik*		Desc. Shriek*	
Bout (n)	5	<i>10</i>	1	<i>0</i>	1	<i>0</i>	1	<i>0</i>	1	<i>0</i>
Peak (Hz)	766	<i>698</i>	859	<i>491</i>	380	<i>134</i>	1701	<i>1279</i>	1506	<i>1452</i>
Lower (Hz)	466	<i>326</i>	539	<i>290</i>	240	<i>44</i>	1175	<i>795</i>	778	<i>708</i>
Upper (Hz)	1643	<i>1317</i>	1666	<i>321</i>	720	<i>611</i>	7955	<i>5990</i>	3518	<i>3061</i>
Duration(s)	2.2	<i>1.0</i>	0.9	<i>0.4</i>	1.1	<i>0.5</i>	1.6	<i>0.7</i>	0.9	<i>0.2</i>
Band(Hz)	1177	<i>1177</i>	1126	<i>604</i>	480	<i>647</i>	6781	<i>5204</i>	2740	<i>2419</i>
Median (Hz)	828	<i>686</i>	929	<i>375</i>	369	<i>128</i>	1864	<i>1161</i>	1430	<i>1294</i>
Freq. Q. (Hz)	521	<i>620</i>	390	<i>376</i>	45	<i>38</i>	843	<i>539</i>	658	<i>564</i>
AM	2	<i>1</i>	4	<i>5</i>	3	<i>2</i>	1	<i>0</i>	4	<i>5</i>
FM	1	<i>1</i>	1	<i>1</i>	1	<i>1</i>	1	<i>0</i>	2	<i>1</i>
Upsweep	51	<i>7</i>	55	<i>20</i>	38	<i>18</i>	61	<i>15</i>	47	<i>8</i>
Start (Hz)	1006	<i>950</i>	724	<i>200</i>	269	<i>68</i>	1459	<i>974</i>	1302	<i>1197</i>
End (Hz)	1200	<i>1034</i>	681	<i>477</i>	283	<i>19</i>	2028	<i>1382</i>	1574	<i>1238</i>

Table 7. Summary of select acoustic parameters for subjectively classified calls within the Tonal (T) vocal class. Mean values are in bold and standard deviations in italics. See Figure 8 for associated spectrogram.

Tonal Calls (n=43)

Call Type	T-F-1 n=43	
Description	Feeding Call	
Bout (n)	1	<i>0</i>
Peak (Hz)	460	<i>119</i>
Lower (Hz)	404	<i>117</i>
Upper (Hz)	505	<i>120</i>
Duration(s)	16.6	<i>23.1</i>
Band(Hz)	101	<i>53</i>
Median (Hz)	456	<i>116</i>
Freq. Q. (Hz)	36	<i>26</i>
AM	1	<i>1</i>
FM	0	<i>0</i>
Upsweep	50	<i>6</i>
Start (Hz)	459	<i>106</i>
End (Hz)	451	<i>113</i>

FIGURES

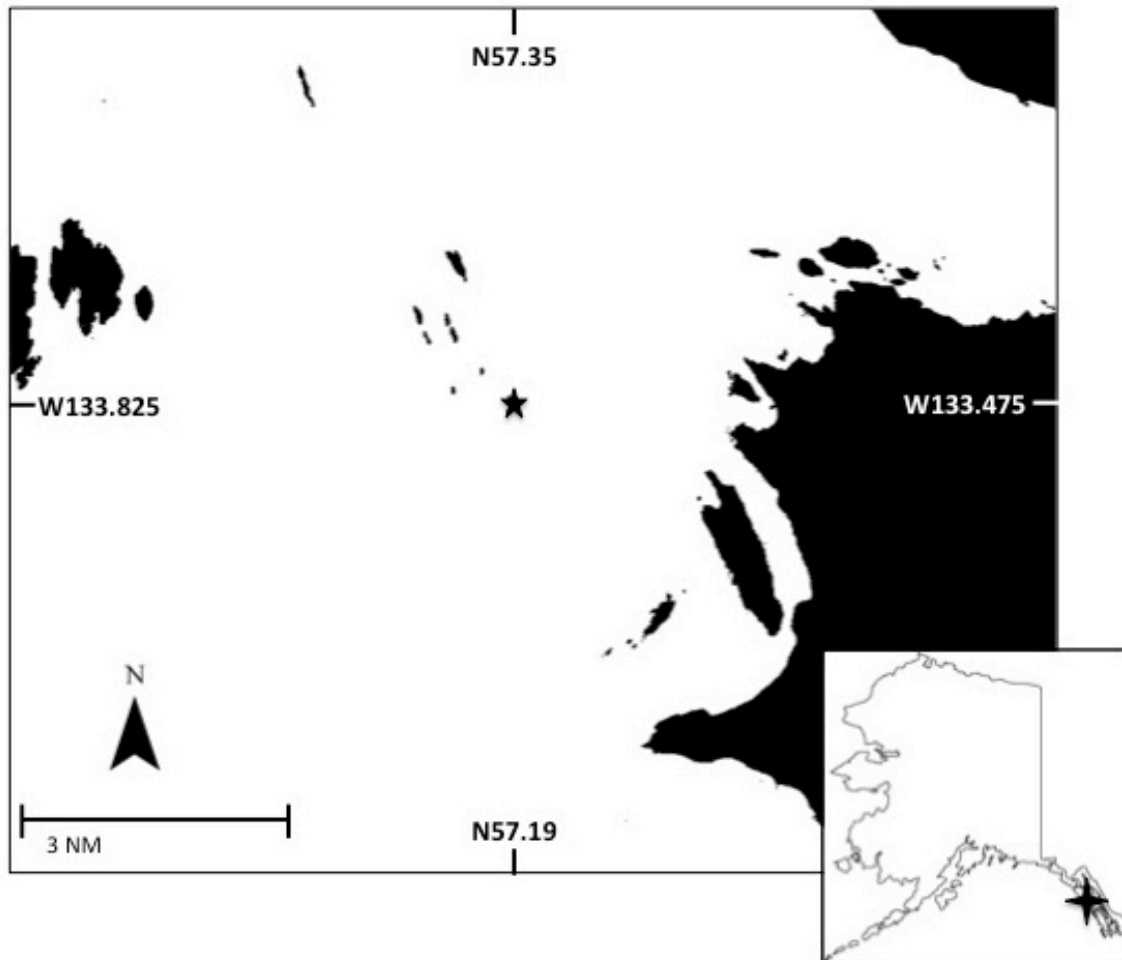


Figure 1. Map showing survey area in Frederick Sound, SE Alaska, including the location of the research station at the Five Finger Lighthouse (starred).

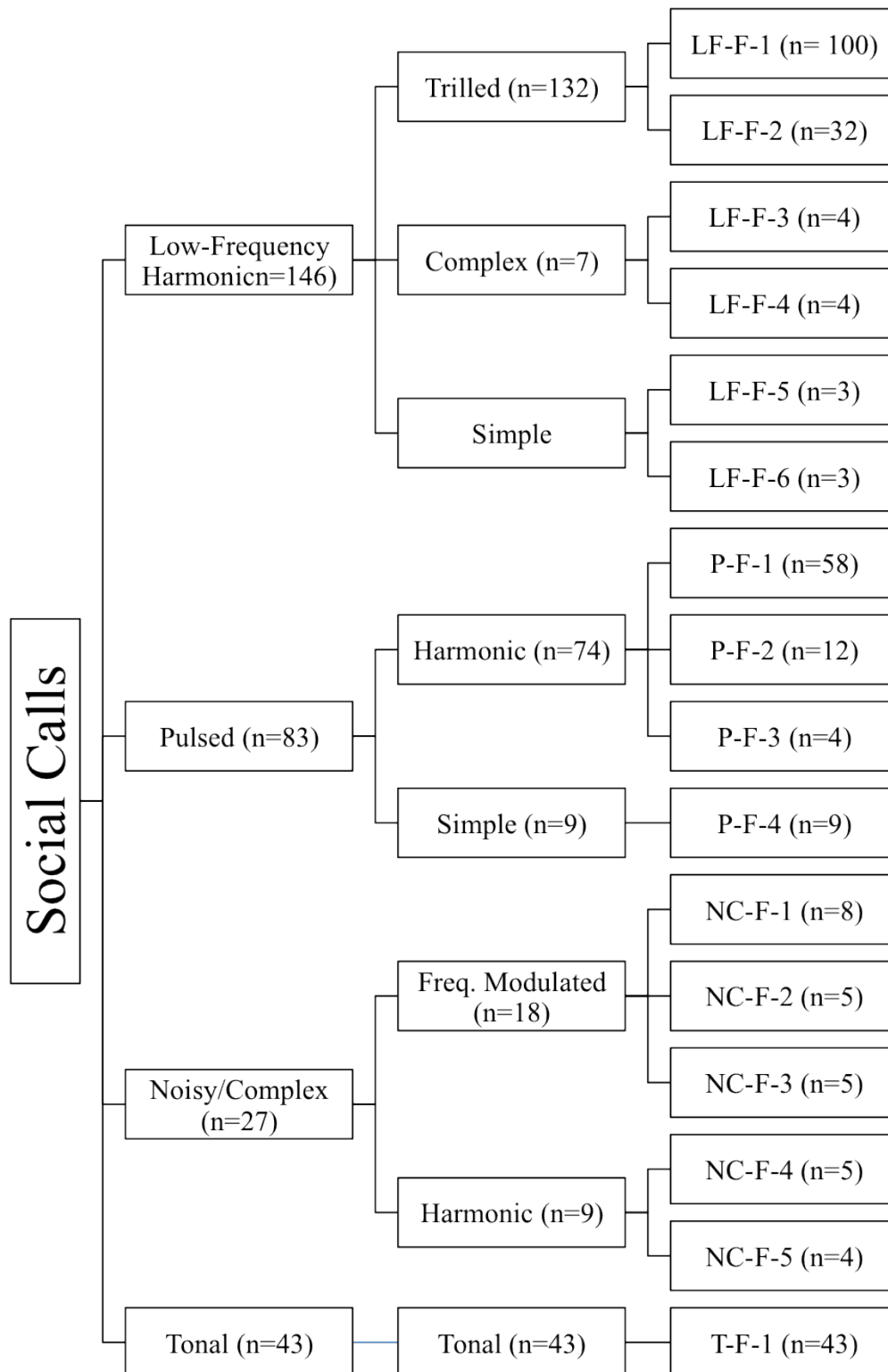


Figure 2. Results of aural-visual classification of calls into a hierarchical tree. Call types are nested within vocal subclasses, which are further nested within vocal classes. Acoustic summaries for each call type can be found in Tables 4-7. Spectrograms of call types can be found in Figures 4-8.

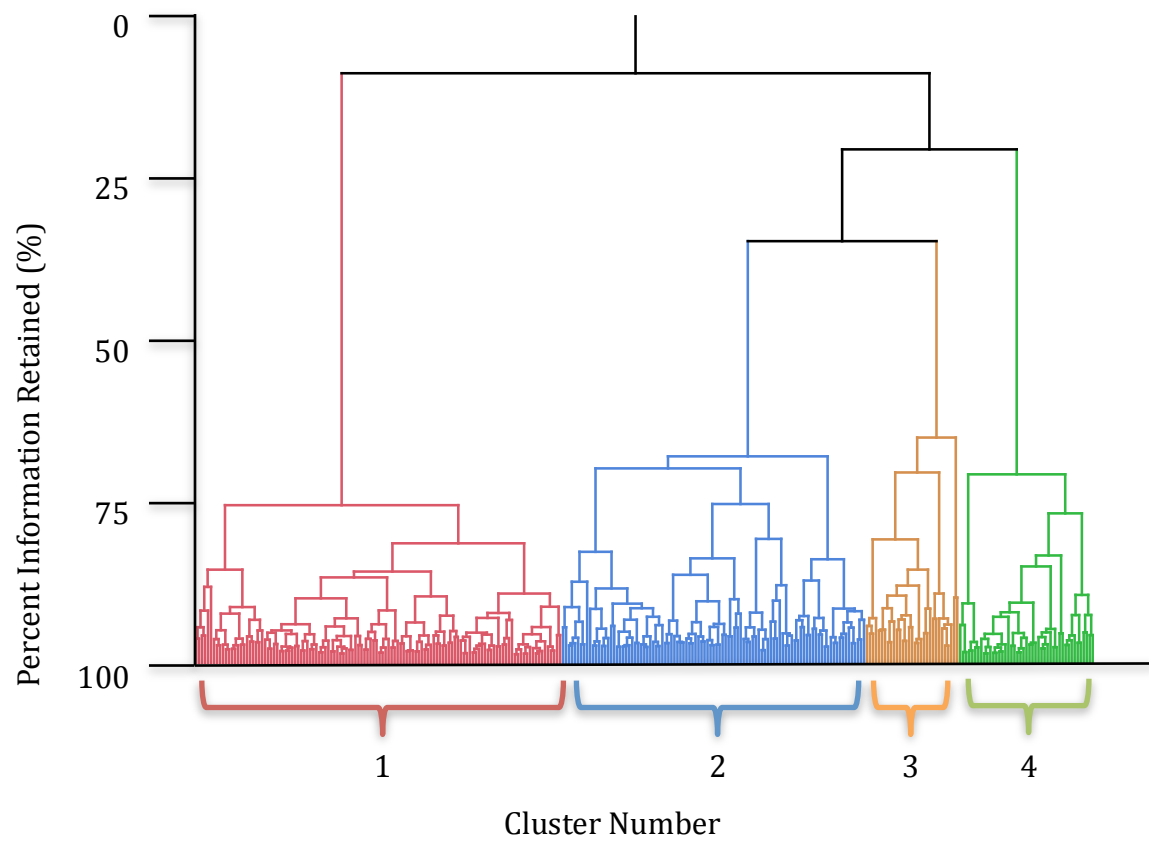


Figure 3. Dendrogram results of quantitative cluster analysis. A different color and number represent each cluster.

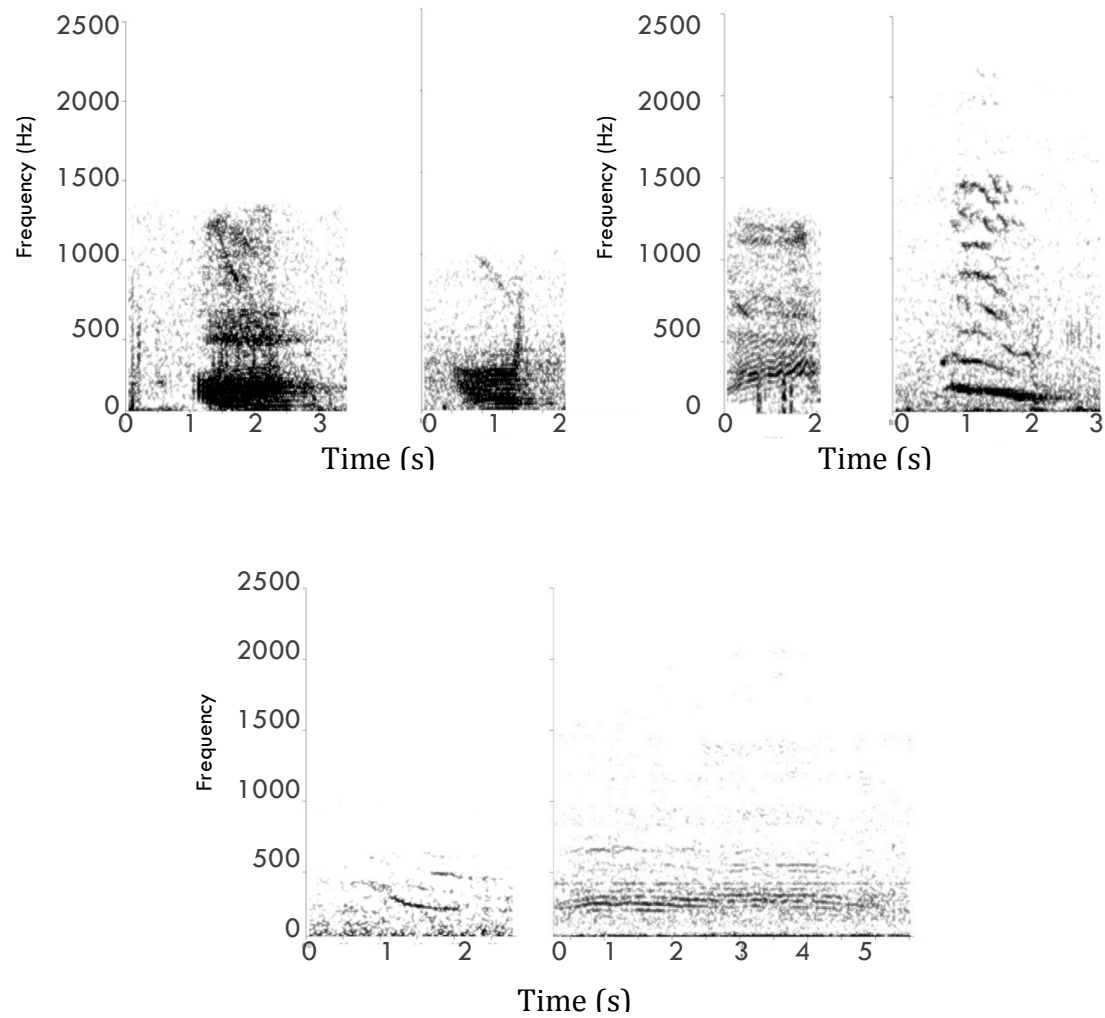


Figure 4. Spectrograms of call types from the Low-Frequency Harmonic (LFH) vocal class. Subjectively determined call types and subclasses (left to right from top): Trilled: LFH-F-1, LFH-F-2; Complex: LFH-F-3, LFH-F-4; Simple- LFH-F-6, LFH-F-5.

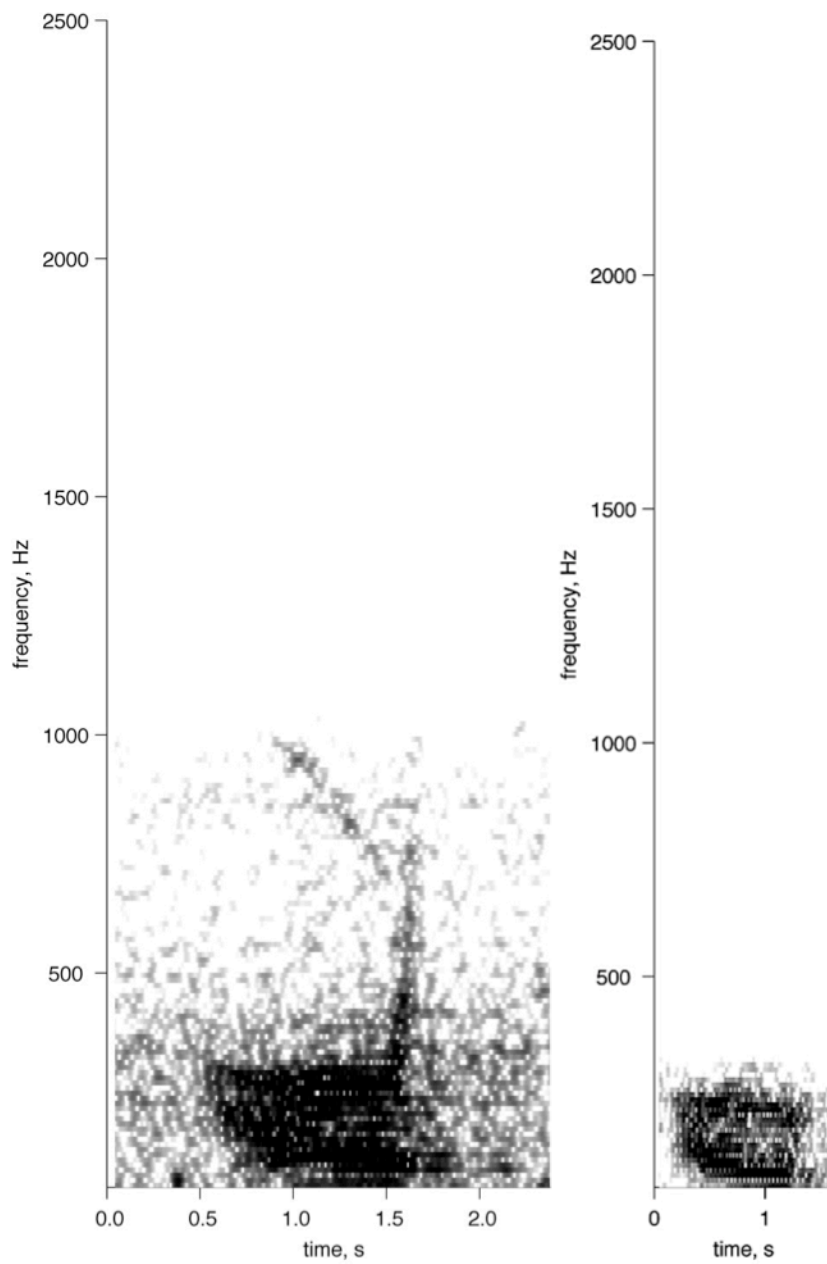


Figure 5. Spectrogram of the LFH-F-2 (Wop) call (left) and LFH-F-1 (Purr) call (right). Note the similarity in call structure.

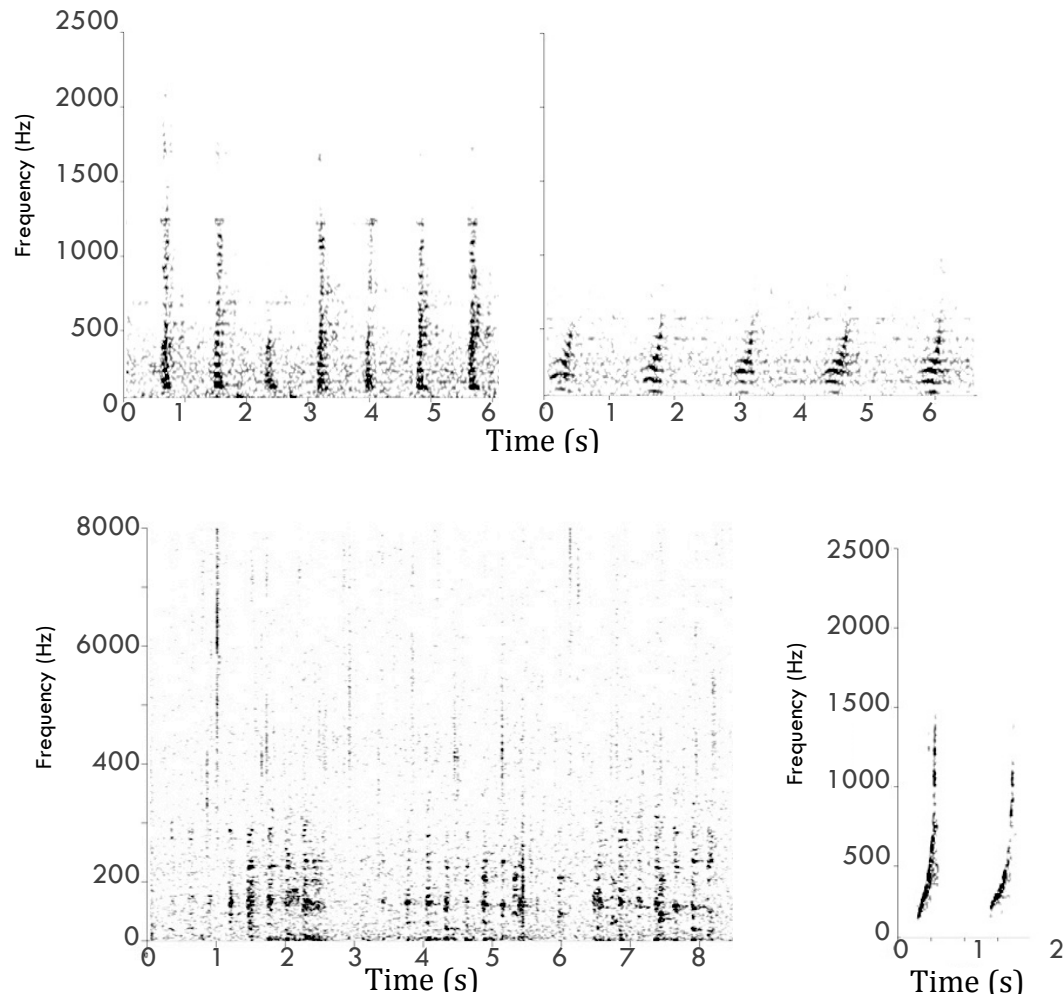


Figure 6. Spectrograms of call types from the Pulsed (P) vocal class. Subjectively determined call types are grouped by subclass. (Left to right from top) (a) Complex: P-F-1, P-F-2, P-F-4. Simple: P-F-3. Note difference in frequency scale for spectrogram of P-F-4 call (max frequency 8 kHz) versus other spectrograms (max frequency 2.5 kHz).

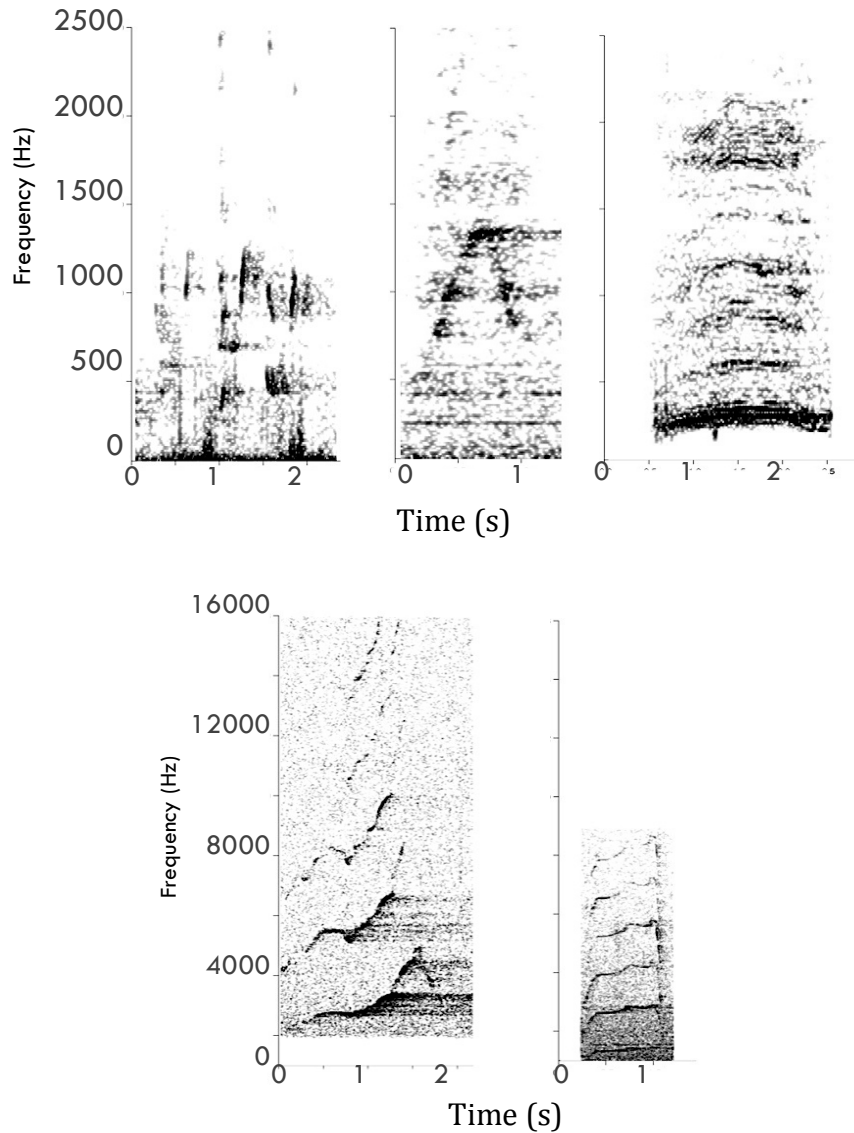


Figure 7. Spectrograms of call types from the Noisy/Complex (NC) vocal class. Subjectively determined call types are grouped by subclass. (Left to right from top) Frequency Modulated: NC-F-1, NC-F-2, NC-F-3. Harmonic: NC-F-4, NC-F-4. Note difference in frequency scale for spectrograms in Frequency Modulated subclass (max frequency 2.5 kHz) versus the Harmonic subclass (max frequency 16 kHz).

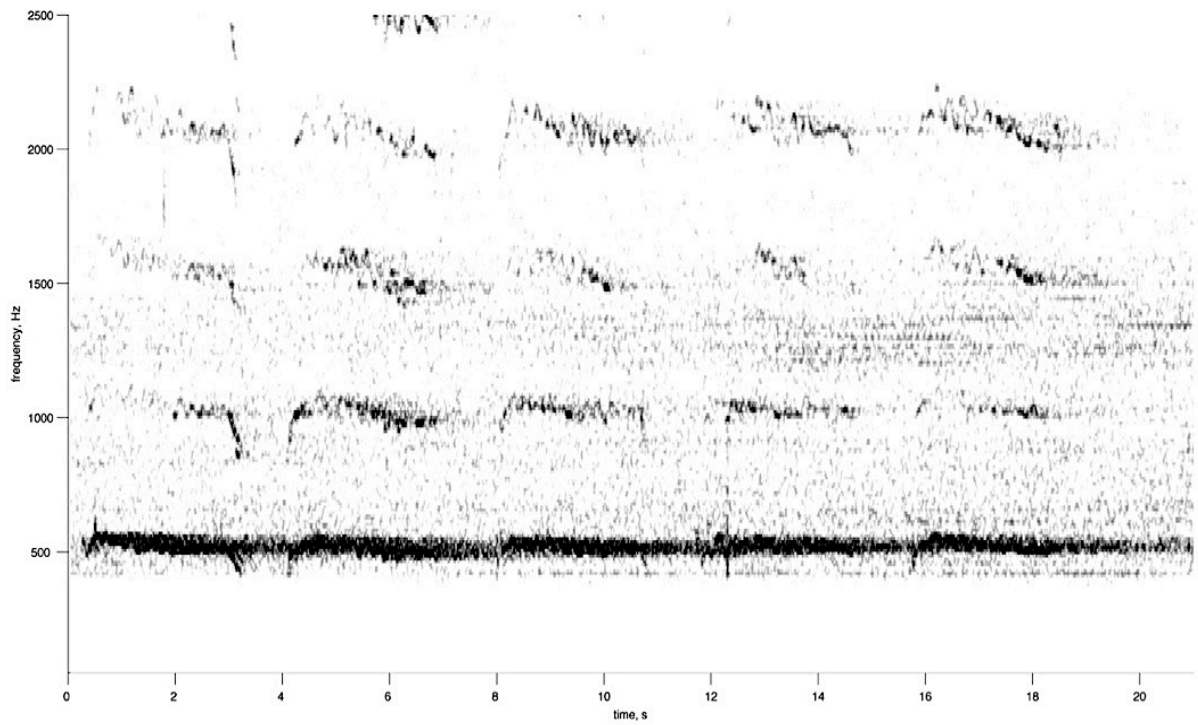


Figure 8. Spectrogram of the sole call type within the Tonal (T) vocal class: T-F-1.

CHAPTER THREE: Vocal behavior in Southeast Alaskan humpback whales (*Megaptera novaeangliae*): Communication and context

INTRODUCTION

Animal communication can be defined as the process by which an animal transfers information that changes the probability of a future behavior of another animal (Dudzinski et al., 2002). It has been suggested that in acoustic communication natural selection favors signalers who vocalize to affect the behavior of listeners, and listeners who gain information from vocalizations (Seyfarth and Cheney, 2003). This has been demonstrated in animals across taxa in both terrestrial and aquatic systems, with anurans and passerine bird species featured prominently. It is well documented that male frogs use vocalizations to attract females and simultaneously repel male conspecifics (Whitney and Krebs, 1975; Wells and Bard, 1987; Hermans et al., 2002; Simmons, 2013). Similarly, birdsong functions to space competing males, establish territories, and attract mates (Catchpole, 1982; Langmore, 1998; Todt and Naguib, 2000; Garamszegi et al., 2007). In the terrestrial environment, however, hearing and sound production are only one sensory modality that may be used for communication; visual and chemical signaling often play an important role in the transfer of information.

In the marine environment, chemical signals are ineffective except at close range and light quickly attenuates, limiting the use of chemical or visual signaling (Dudzinski et al., 2002). Sound propagates quickly in the marine environment, and is capable of traveling great distances with relatively little loss of energy (Urlick, 1983). Sound, therefore, is favored by aquatic species – including marine mammals – as the primary sensory modality used for communication across a range of spatial scales. Vocalizations serve many functions in the ocean environment – including navigation, foraging, and sexual advertisement (Dudzinski et al., 2002; Bradbury and Vehrencamp, 2011) – but are often produced in social-spatial contexts. During the breeding season, male harbor seals (*Phoca vitulina*) establish underwater territories and use acoustic signals, known as “roars,” to defend against intruder males, resulting in relatively even dispersal of males throughout a

breeding region (Hanggi and Schusterman, 1994; Hayes et al., 2004). Call production and exchange in killer whales (*Orcinus orca*) has been proposed to maintain group cohesion and coordination during pod foraging events by helping individuals to maintain contact within a concentrated group (Ford, 1989; 1991).

Due in part to extensive geographic ranges, seasonally variable behavioral states, and long dive times, call function and behavioral context in baleen whales is less understood than in either terrestrial species or odontocetes. Significant progress has been made toward understanding the role of acoustic communication in baleen whales by combining visual and acoustic data collection methods to correlate animal location and surface activity with acoustically detected underwater vocalizations. For example, by using a land-based theodolite in combination with a hydrophone array and mounted playback speaker, it was demonstrated that southern right whales (*Eubalaena australis*) were able to discern between sounds of conspecifics and heterospecifics, and would approach playbacks of conspecific upcalls while increasing their calling rate (Clark and Clark, 1980; Clark, 1982). This evidence suggests that the upcall functions as contact call meant to facilitate social interaction – though the purpose or benefit of this interaction is not yet clear. Similarly, through use of vessel-deployed hydrophones in combination with vessel based visual observations the northern right whale's (*E. glacialis*) “gunshot” call was determined to be produced by single male animals or groups containing males (Parks et al., 2005). This context suggests that, despite its production on what are traditionally considered foraging grounds, the gunshot call may serve as a breeding advertisement call, an agnostic signal directed toward other males, or a combination of the two. While absolute function of baleen whale calls is still largely hypothesized, using spatial distribution of animals to understand the social context associated with call production enables informed inference to be made about the role of communication in baleen whales species.

Humpback whales (*Megaptera novaeangliae*) are acoustically active baleen whales, well known for complex vocal behaviors that vary spatially, seasonally, and geographically. Their proximity to land makes them an accessible study species, and their extensive

repertoire has been the focus of decades of research (Au et al., 2006). Their vocal repertoire includes complex and stereotyped ‘songs’ (Payne and McVay, 1971), coordinated foraging calls (D’Vincent et al., 1985; Cerchio and Dalheim, 2001), and a variety of social calls. Songs are produced by male humpback whales throughout their low-latitude breeding range, and to a lesser extent along migratory corridors and feeding grounds (Payne and McVay, 1971; Gabriele and Frankel, 2002; Clark and Clapham, 2004). Though the function of songs is unconfirmed, it is presumed to serve either a breeding or mate-selection function (Payne and McVay, 1971; Tyack, 1983; Gabriele and Frankel, 2002; Au et al., 2006; Smith et al., 2008), and some studies suggest that song may function to space male humpback whales on breeding grounds, similar to the aforementioned frogs or birds (Tyack, 1981; Frankel et al., 1995).

Two non-song calls have been observed at high latitudes and strictly in a foraging context. Feeding calls, also known as feeding cries, in Southeast Alaskan humpback whales are produced by male and female humpback whales and are purportedly used in conjunction with bubble production during cooperative foraging events (Jurasz and Jurasz, 1979; D’Vincent et al., 1985; Cerchio and Dalheim, 2001; Sharpe, 2001). Similarly, production of low-frequency click sequences known as “megapclicks” have been documented during night-time foraging events in North Atlantic humpbacks (Stimpert et al., 2007).

To date the social calling repertoire of humpback whales has received considerably less attention than either song or foraging calls. Social calls are defined as phonations that do not possess the rhythmic or continuous patterning of song; this includes single song units produced independently of the song structure, and novel vocalizations not present in song units (Silber, 1986; Dunlop et al., 2007). Social calls have been documented across all stages of the humpback life cycle, and are emitted by males, females, and calves throughout the migratory range (Silber, 1986; Dunlop et al., 2007; Zoidis et al., 2008; Stimpert et al., 2011). Detailed call repertoires exist for only three regions – the North Pacific (Thompson et al., 1986; Fournet, 2014), eastern Australia (Dunlop et al., 2007), and to a lesser extent the North Atlantic (Stimpert et al., 2011). On breeding grounds and

in migratory corridors social calls have been documented in groups of aggressively competing males (Silber, 1986) as well as in cow-calf pairs (Dunlop et al., 2008; Zoidis et al., 2008), indicating that social calling is part of the vocal repertoire across gender and life stage. Playback studies of social calls in Hawaii indicated that singers and non-singers responded differently to social calls, implying the calls serve a communicative function between different social groups (Tyack, 1983). A 2008 study investigating the function of social calls in eastern Australia suggested that call type production was context-specific, with differing call types serving variable functions, including inter- or intra-group communication, including possible maintenance of social cohesion via contact calling (Dunlop et al., 2008). The results of these studies suggest that social calling plays a significant role in humpback whale communication, but that social calls are not used indiscriminately across behavioral contexts.

Although social calling has been reported on high latitude foraging grounds (Thompson et al., 1986), the behavioral context of social calls on foraging grounds has not been investigated; based on geographic and seasonal variability known for other humpback whale behaviors it is presumed that social calling behavior on foraging grounds will not mimic social calling behavior reported elsewhere. On sub-tropical breeding grounds male humpbacks produce social sounds concomitant with agonistic behaviors associated with mate competition (Tyack et al., 1983; Baker et al., 1984); aggression between conspecifics on foraging grounds, however, has not been documented. Similarly, though opportunistic foraging has been documented on rare occasion at low-latitudes (Baraff, et al., 1991), it is typical for humpbacks to fast throughout the breeding season and replenish blubber stores at high latitudes (Dawbin, 1966). Given the behavioral stratification, it is unlikely that social calling – which may occur across a wide range of social situations – will be consistent throughout their range.

The study outlined in Chapter 2 of this thesis describes the acoustic structure of social calls from Southeast Alaskan humpback whales as a hierarchical system consisting of call types and vocal subclasses, nested within four primary vocal classes – Low-Frequency

Harmonic (LFH), Pulsed (P), Noisy/Complex (NC), and Tonal (T). In other humpback populations it has been proposed that, similar to southern right whales, social sounds are composed of discrete call types, as well as call types that make up a vocal continuum (Clark, 1982; Dunlop et al., 2007; Stimpert et al., 2011). Results reported in Chapter 2 show that this distinction could be made at the class or subclass level, and it was hypothesized that discrete calls might serve more specific functions than continuous calls. Calls grouped in the LFH vocal class and Pulsed-Complex (PC) subclass were largely continuous, while calls in the T vocal class, NC vocal class, and Pulsed-Simple (PS) subclass were discrete. Using the results of this classification system and the resulting call catalog, the objective of this study was to assess whether social calling in Southeast Alaska serves a communicative function. This was pursued by investigating differences in the use of calls from each of the four vocal classes, the relationships between calling behavior and animal abundance, and investigating the relationship between calling behavior and patterns of animal dispersion.

Dispersion analyses can be a good indicator of spatial organization, and may provide ecologically relevant information pertinent to habitat use (i.e., anurans; Whitney and Krebs, 1975; Wells and Bard, 1987; Hermans et al., 2002), territoriality (i.e., passerine birds; Langmore, 1998; Todt and Naguib, 2000; Osmun and Mennill, 2011), social structure (i.e., non-human primates; Garber, 1989; Isbell, 1991; White and Chapman, 1994), or foraging behavior (i.e., cetaceans; Kenney et al., 2001; Markowitz and McGuire, 2007; Degradi et al., 2008)). Measures of humpback whale dispersion have been used to investigate foraging behavior in Frederick Sound Southeast Alaska in 2008 (Szabo, 2011), and assessments of distance between humpback whales have been used in conjunction with passive acoustic monitoring to infer song function in humpbacks on breeding grounds (Frankel et al., 1995). Given the scale at which humpback whales function, dispersion analyses may reveal behavioral trends otherwise biased by human perception of ‘social space’. The inclusion of abundance in the analysis accounts for potential for interactions between conspecifics – competitive, altruistic or falling along the social continuum –that may vary with the numbers of individuals present.

METHODS

Visual and Acoustic Data Collection

Data were collected from June-September 2012 in the waters of Frederick Sound, Southeast Alaska, surrounding the Five Finger Lighthouse (57° 16' 13" N, 133° 37' 53" W) (Figure 9). Two survey regions, East and West, were designated based on their position relative to the lighthouse tower. Regions were observed independently in surveys that consisted of 30 minutes of simultaneous visual and acoustic data collection. Surveys were conducted in repeated rounds consisting of two to four surveys of the same area. If possible, rounds alternated between East and West. The choice of a starting survey region was quasi-randomized. In appropriate environmental conditions, choosing the starting survey region was randomized. If only one survey region had conditions acceptable for data collection (i.e., fog in East, clear in West), then the clear survey region would be chosen.

Visual observations were made daily between sunrise and sunset, subject to weather constraints, from the 18.3-meter lighthouse tower. A theodolite (Leica T110) was used in conjunction with a notebook computer to record (“fix”) spatial and behavioral data associated with whales in the survey area. For each theodolite fix time, whale behavior (blow, dive, breach, etc.), group composition, group size, direction of travel, and notes of interest were recorded. Whales travelling within three body lengths of each other and exhibiting coordinated surfacing behavior were said to be members of a single group (Baker and Herman, 1989; Clapham, 1993; Dunlop et al., 2008; Ramp et al., 2010). Each whale was counted only once per survey.

Acoustic recordings were made via two omnidirectional hydrophones (Cetacean Research Technology, C-55), each with a built in +20 dB preamplifier, an effective sensitivity of -165 dB and a flat frequency response (± 3 dB) from 10 Hz -10 kHz. The hydrophones were connected to a digital audio recorder (S4N Zoom Handy) and recorded with a 44.1 kHz sampling rate and 16 bit sample resolution. Hydrophones were separated by 4.5 m (or occasionally 3.3 m when ocean surface conditions worsened) and deployed

to a depth of 20 - 25 m from the port and starboard side of a 3 m inflatable vessel. Five-pound weights were attached to each hydrophone to facilitate sinking. All recordings were obtained when the vessel was adrift with the engine off. No other baleen whale species were seen in the study area, and all vocalizations that fell within reasonable parameters for baleen whale vocalizations were assumed to originate from humpbacks.

Inclusion Criteria

To be included in analysis surveys, had to occur under “fair” or better visual conditions as qualitatively determined by the observers, could not have ended prematurely due to weather conditions or equipment failures, and could not include more than four vessels in the immediate survey area. Any acoustic survey that was qualitatively determined to contain too much vessel noise to detect whale vocalizations, regardless of the number of vessels present, was excluded from analysis. Repeated observer tests indicated that the ability to accurately determine an object’s relative position decreased most dramatically beyond 8.3 km of the lighthouse. Based on this assessment surveys were included in analysis only if all sighted whales were within 8.3 km of the lighthouse. Surveys with any whales sighted outside of that range were omitted.

Visual and Acoustic Data Analysis

Visual Data Processing

The locations of every whale within each individual survey were uploaded into ArcGIS 10 (ESRI). The Arc10 Average Nearest Neighbor Tool in the ArcGIS Toolbox was used to evaluate animal dispersion state for each survey. Nearest neighbor analyses are used to report first order clustering, which was appropriate given the geographic scale of the study. The average nearest-neighbor distance in meters for each survey was calculated using the tool, and the Nearest Neighbor Ratio (NNRatio) was calculated by dividing the mean observed distance between each whale and its nearest neighbor by the mean observed nearest neighbor of an expected random distribution within the same area. Based on this ratio, a Z-statistic was generated and statistical test was performed

comparing the distribution of the observed nearest neighbor distances to a random distribution. Statistical significance was set at the 0.05 level.

When animals were distributed in the survey area with a NNRatio greater than one that varied significantly from a random distribution, then the dispersion state for that survey was reported as “Dispersed”. Dispersion states with a NNRatio less than one that varied significantly from a random distribution were reported as “Clustered”. Dispersion states that were not found to be statistically different from random were reported as “Random”. Average nearest-neighbor distances could not be calculated if only one animal location was reported. All surveys were reviewed individually for evidence of unreported whales, (i.e., sighting notes made from vessel observers) or whales that were reported but fell outside of the survey sampling protocol and were therefore not included in analysis. Surveys that showed no evidence of unreported whales and contained only a single individual were considered to have a “Single” dispersion state.

It should be emphasized that placement into a dispersion state is contingent primarily on the mean observed nearest-neighbor distance of whales within the finite survey area, and therefore dispersion states in this study are closely linked to the animals’ relative distance to one another and the number of animals present. Increases in the observed mean nearest neighbor distance indicate a trend toward dispersion (animals moving away from each other), while decreases in observed nearest neighbor distances indicate a trend toward clustering (animals moving toward each other). Depending on the number of animals observed in the study area, however, low nearest neighbor distances do not necessarily indicate clustered states; for example two whales in the survey area separated by 0.2 km would be considered clustered, but 20 whales evenly dispersed across the survey area may also have a nearest neighbor distance of 0.2 km.

The only other predictor variable calculated from visual data was the total number of whales counted per scan (“Abundance”). Whales were counted only if they were sighted in the survey region being surveyed.

Acoustic Data Processing

In the laboratory spectrograms of vocalizations were generated using RavenPro 1.4 with a 4096-point Fast Fourier Transform (FFT), Hann window (providing 42.7 Hz resolution) and 75% overlap, or the Matlab-based program Osprey (Mellinger, 2007) with the same parameters except using a Hamming window. Recordings were manually reviewed in their entirety and samples were extracted using RavenPro 1.4 (Cornell Laboratory of Ornithology). The signal-to-noise ratio (SNR) of each extracted sample was calculated using the method described by Mellinger and Bradbury (2007). To be included in the analysis, humpback whale vocalizations had to have a SNR of 10 dB or higher (Dunlop et al., 2007; Dunlop et al., 2008; Stimpert et al., 2011; Rekdahl et al., 2013; Fournet, 2014) and have visually and aurally distinguishable start and end points to ensure accurate parameter measurements. Limiting the number of included calls by these criteria limits the likelihood of analyzing calls produced by whales beyond the survey range. Vocalizations were classified based on the methods described in the previous chapter. Analysis was conducted on vocal behavior at the class level in lieu of the call type level to avoid arbitrary separation of calls that appear to exist as a call continuum and to account for individual variation in call production (Parks and Tyack, 2005).

Statistical Analyses

Response variables of interest included calling rates for each vocal class. In the absence of a hydrophone array, localizing callers was not possible; therefore, this study did not directly measure individual behavior. Instead calling rates were defined as the number of calls per minute per whale (calls $\text{ind}^{-1} \cdot \text{min}^{-1}$), and were calculated as the total number vocalizations with a SNR of 10 dB or higher divided by the number of recording minutes, divided by the total number of whales sighted per scan.

The data were fit to a generalized linear model (GLM) using a Poisson Log-Link function to test the effects of whale abundance (number of whales counted) and dispersion (clustered, random, or dispersed) on the total calling rate and calling rates for each vocal class. Model building indicated that an interaction term was non-significant and was therefore not included. In the case of P calls, NC calls and T calls, the variance was

greater than the mean so an overdispersion term was included in the model (Zuur et al., 2009). When appropriate, post-hoc multiple comparisons were made using the Steel-Dwass method (non-parametric version of a Tukey-Kramer Honest Significant Difference test; Hollander and Wolfe, 1999), and non-parametric Spearman Rho correlations were used to test for significant correlations between continuous variables. Surveys containing only a single whale (“Single” states) were not included in models testing for the effect of abundance due to the fact that an abundance of one and single states were perfectly correlated; single states were included in comparisons of vocal behavior by dispersion states.

Vocalizations from each dispersion state were pooled to calculate the Shannon-Weiner Diversity Index (SWI), and to calculate percentage of calls represented by each vocal class. SWI is a popular index used to quantify ecological diversity that accounts for both richness (i.e., number of vocal classes) and evenness (i.e., relative abundance of each vocal class) to generate a single comparable measure, and has been used to quantify vocal complexity in various mammal species (i.e., greater white lined bat *Saccopteryx bilineata*; Davidson and Wilkinson, 2004) and bird species (i.e. bobolink, *Dolichonyx oryzivorus*; Ammer and Capp, 1999). By way of example, when assessing species diversity, a community with a large number of species that are evenly distributed would be considered more diverse and have a higher SWI than a community with a smaller number of overall species and a distribution that favors only one particular species. The in situ measurement of SWI is contingent on the total potential number of unique elements (i.e., vocal classes). The SWI was calculated using the following equation where R equals the total number of unique vocal classes represented, p_i is the proportion of vocalizations belonging to the i th vocal class, and H' equals the Shannon-Weiner diversity index:

$$H' = - \sum_{i=1}^R p_i \ln p_i$$

Vocalizations detected during each unique dispersion state were pooled and the percentage of calls from each vocal class was calculated (e.g., 70% LFH calls, 20% P

calls, 7% NC calls, and 3% T calls). Randomization tests were performed to assess whether the percentage of calls from each vocal class was significantly different from random, and therefore likely or unlikely to have occurred by chance. Randomization tests were conducted by randomly selecting 15 surveys from the total dataset, calculating the percentage of calls from each vocal class from the random selection, and comparing the results to the percentage of calls from each vocal class from the dispersion state of interest. One hundred iterations were performed to calculate the likelihood of obtaining call percentages as extreme as the observed call percentages (p-value). Because the probability of detecting a call, the number of calls detected, and the number of overall vocal classes represented are all necessary components to calculate SWI, randomization tests serve as a proxy for testing the likelihood of obtaining the reported diversity by chance.

Using the same method randomization tests were performed to assess whether the percentage of surveys from each dispersion state that contained vocalizations (i.e., 20% of surveys with whales in a clustered state contained vocalizations) were significantly different from random.

RESULTS

A total of 365 surveys were conducted resulting in 92.6 hours of acoustic recordings. One hundred and eleven scans fit the criteria for inclusion in analysis; whales were observed in every scan. Of those, 35 scans were determined to contain whales in a clustered dispersion state, 51 were determined to contain whales in a randomly distributed dispersion state, 15 were determined to contain whales in an evenly dispersed state, and 10 contained only a single animal (Figure 10). Two hundred and twenty-six whale sightings occurred during clustered states, 260 whale sightings occurred during random states, 66 whale sightings occurred during evenly dispersed states, and 10 whale sightings occurred in surveys containing only a single animal. Mean observed nearest neighbor distance for surveys when whales were clustered was 844 m (\pm 67 m). Mean observed nearest neighbor distance for surveys when whales were randomly dispersed was 2946 m (\pm 191 m). Mean observed nearest neighbor distance for surveys when whales were

evenly dispersed was 7821m (± 808 m). Mean observed nearest neighbor distance for surveys when whales were clustered that also contained vocalizations was 753 m (± 84 m). Mean observed nearest neighbor distance for surveys when whales were randomly dispersed that also contained vocalizations was 2679 m (± 282 m). Mean observed nearest neighbor distance for surveys when whales were evenly dispersed that also contained vocalizations was 8912 m (± 1091 m).

Forty-six scans contained a total of 259 vocalizations (LFH=137, P=60, NC=27, T=35) (Figure 11), whereas sixty-five scans did not contain vocalizations fitting the inclusion criteria. The average calling rate for all scans was 0.017 calls \cdot ind $^{-1}\cdot$ min $^{-1}$ (± 0.004 calls \cdot ind $^{-1}\cdot$ min $^{-1}$). The average number of calls detected was 2.33 calls per scan (± 0.54 calls). Mean calling rates were highest for LFH calls (mean=0.009 calls \cdot ind $^{-1}\cdot$ min $^{-1}$ ± 0.004 calls \cdot ind $^{-1}\cdot$ min $^{-1}$), lower for P calls and T calls (mean=0.004 calls \cdot ind $^{-1}\cdot$ min $^{-1}$ ± 0.001 calls), and lowest for NC calls (mean= 0.001 calls \cdot ind $^{-1}\cdot$ min $^{-1}$ ± 0.001 calls \cdot ind $^{-1}\cdot$ min $^{-1}$) (Figure 12).

There was no evidence that the total calling rate, LFH calling rate, NC calling rate, or T calling rate varied as a function of whale abundance or dispersion (Table 8). There was no evidence of an effect of the number of whales counted on mean P calling rates (Table 8). Results of a Poisson log-linear regression indicated that after accounting for the number of whales counted there is significant evidence that the mean P calling rate varied as a function of dispersion (Table 8). Post-hoc Steel-Dwass tests indicate that mean P calling rates are higher during clustered dispersion states than dispersed states ($p=0.05$) (Table 8 & Figure 13). Additionally, P calling rates were negatively correlated with nearest neighbor distances ($\rho=-0.22$, $p= 0.029$; Figure 14); in the absence of P calls all dispersion states were represented.

Sixty percent of vocalizations were detected during scans containing whales in a clustered state, 37% of vocalizations were detected during scans containing whales in a randomly dispersed state, 6% of vocalizations were detected during scans containing whales in an evenly dispersed state, and less than 1% of vocalizations were detected

during scans containing only a single whale (Table 9). Forty-six percent of surveys containing whales in a clustered state contained vocalizations, 51% of surveys containing whales in a randomly dispersed state contained vocalizations, 13% of surveys containing whales in an evenly dispersed state contained vocalizations, and 20% of surveys containing only a single whale contained vocalizations (Table 9). Mean calling rates and total number of calls for each vocal class varied between dispersion states (Table 10); however, these differences were not statistically significant. Randomizations tests indicate that the percentage of single state and dispersed state surveys that contained vocalizations was lower than would be expected by random chance ($p < 0.01$).

The percentage of calls from each vocal class detected during clustered dispersion states was 50% LFH calls, 29% P calls, 11% NC calls, and 10% T calls (Table 9 & Figure 15). Of the calls detected during randomly distributed states 56% were LFH calls, 13% were P calls, 10% were NC calls, and 29% were T calls (Table 9 & Figure 15). Comparatively, surveys containing whales in a dispersed state or single state had more highly stratified percentages of calls from each vocal class; the percentage of calls from each vocal class during dispersed states was 80% LFH calls, 0% P calls, 0% NC calls, 20% T calls (Table 9 & Figure 15). The percentage of calls from each vocal class detected during single states was 0% LFH calls, 100% P calls, 0% NC calls, and 0% T calls (Table 9 & Figure 15). Based on random permutation tests, the percentage of calls from each vocal class detected during dispersed states is not likely to have occurred by random chance ($p < 0.01$). Based on random permutation tests, the percentage of calls from each vocal class detected during evenly dispersed states is not likely to have occurred by random chance ($p < 0.01$). Total calling diversity was highest for vocalizations detected when whales were clustered, and slightly lower when whales were randomly dispersed. Vocal diversity of calls detected during evenly dispersed states was lower, and there was no evidence of vocal diversity detected within vocalizations produced by single whales. (Table 9).

Variable changes in observed nearest neighbor distance (m) were observed at low calling rates (Figure 16); as calling rates increased changes in observed nearest neighbor

distances decreased to zero or near zero; however, there was no identifiable correlation between absolute change (absolute value of the change in nearest neighbor distance) and total calling rate ($\rho=-0.2$; $p=0.1$).

DISCUSSION

Unlike on the breeding grounds where vocalizations are heard almost continuously (Winn et al., 1975; Winn et al., 1981), sound production in humpbacks appears relatively infrequently on Southeast Alaskan foraging grounds (Helweg et al., 1992). Only 40.5% of scans fitting the inclusion criteria contained vocalizations, and average calling rates indicate only approximately 1 in 8 whales produced vocalizations during periods of observation. This is lower than calling rates reported for humpbacks migrating out of breeding grounds (Dunlop et al., 2008) or for humpbacks interacting in agonistic groups on breeding grounds (Silber, 1986). Although direct comparison of calling rates is limited given discrepancies in how data were calculated, migrating humpbacks were reported to vocalize consistently for between 5-30 minutes (Dunlop et al., 2008), a phenomenon which was never observed in this study. When recalculated based on criteria described in Dunlop's 2007 publication, calling rates in this study were 11.5 times lower than those reported for migrating humpbacks, and 10 times lower than calling rates reported for humpbacks in competitive groups (Silber, 1986). Based on this evidence it appears that Southeast Alaskan humpbacks were comparatively quiet throughout this study. This is expected, as humpbacks in Southeast Alaska are primarily concentrated on foraging activities that do not necessitate social interaction.

Differences Between Vocal Classes

The humpback whales observed in this study appeared to favor calls from the LFH vocal class over other vocal classes. The acoustic properties of some LFH calls, and of LFH-F-2 calls in particular, namely low-frequency, temporal pattern, terminal upsweep, short durations, have the potential to provide a great deal of information. The low-frequency portion of the sound is capable of travelling great distances, while as the call attenuates the temporal pattern will "smear", and the upsweep will truncate. Dunlop (2008) proposed that the "wop" call, which is equivalent to the LFH-F-2 call by this

classification system, may function in inter- or intra-group communication, or as a contact call between cows and calves. This is supported by anecdotal observations of counter-calling between individuals using this call. Despite this, however, there was no evidence linking the use of LFH calls to either abundance or dispersion, indicating that these calls are used under variable social/spatial contexts. I propose that the absence of calls detected when only a single whale was present is a function more of foraging context – humpback whales often forage alone (Clapham, 1993) – than an argument against long-distance communication. It is clear based on their frequency of occurrence that LFH calls play a significant role in vocal sound production on foraging grounds, but that role may not be directly linked to spatial and behavioral patterns at the scale of this study.

The association of P calls with clustered states (surveys when animals were generally within $\sim .8$ km of one another) suggests that use of these types of calls is higher in periods of increased potential for social interaction, and that P calls may be used for close-range communication. In migrating humpbacks, “grunts”, “groans”, and “barks” - calls that by the current classification system would be considered P calls - were almost exclusively reported in joining groups, when whales were clearly interacting (Dunlop et al., 2008). In avian fission-fusion societies, similar to fission-fusion societies described for humpbacks (Weinrich and Kuhlberg, 1991; Clapham, 1993; Weinrich et al., 2006), the use of acoustic communication to facilitate social contact in a foraging context, has been documented in various systems. Orange-fronted conures (*Aratinga canicularis*) and orange-chinned parakeets (*Brotogeris jugularis*) allegedly exchange specific contact calls with nearby groups of non-kin conspecifics, purportedly to recruit affiliated individuals to foraging sites (Bradbury, 2004); in the marine environment it has been similarly hypothesized that male fin whales produce long stereotyped calls that may function to advertise prey to potential mates (Croll et al., 2002). Large aggregations of foraging humpbacks have been documented, particularly in Southeast Alaska (Jurasz and Jurasz, 1979; Baker and Herman, 1984; D'Vincent et al., 1985; Baker and Herman, 1989; Cerchio and Dalheim, 2001; Sharpe, 2001), and foraging humpbacks are often found travelling in pairs or small groups (Weinrich, 1991; Weinrich and Kuhlberg, 1991;

Clapham, 1993; Ramp et al., 2010) that would require some sort of signal to facilitate. Further, it has been demonstrated that humpback whales in Southeast Alaska cluster around prey patches, and it is likely that the increased proximity of humpbacks utilizing P calls is linked to foraging activities. Based on the results of this study, however, it is not possible to determine whether or not P calls serve to initiate clustering between animals (facilitating the “fusion” portion of humpback whale behavior on foraging grounds), or whether increased P calling rates are a response to increased spatial proximity and function as small scale territorial calls, meant to deter conspecifics from further approach (fulfilling the “fission” portion of humpback whale behavior on foraging grounds).

It is important to note that while an increase in P calling is affiliated with decreasing distances between individuals, P calls were not always represented in clustered scans. While based on this data it could be inferred that with a calling rate of ~ 0.02 calls $\text{ind}^{-1} \cdot \text{min}^{-1}$ that the animals will be in a clustered state, the inverse is not true. Clustered scans did not always contain P calls, indicating that perhaps spatial proximity state drives the use of P calls, and not the inverse.

There was no apparent relationship between T calling rates and abundance or dispersion. The T vocal class contains a single call type, the T-F-1 call type also known as a feeding call, which has been associated with cooperatively foraging humpbacks in Southeast Alaska (Jurasz and Jurasz, 1979; D'Vincent et al., 1985; Cerchio and Dalheim, 2001; Fournet, 2014). The call is believed to coordinate humpbacks during cooperative foraging events (bubble-net foraging) and in combination with bubble blowing, is thought to assist in herding schools of herring (Jurasz and Jurasz, 1979; D'Vincent et al., 1985; Sharpe, 2001; Brown and Corkeron, 2006). This feeding technique was not observed during this study; however, while hydrophones were deployed, vessels transiting within 5-10 miles of the Five Finger Lighthouse anecdotally observed cooperative foraging events. It is likely that this particular call was recorded while the animals were out of view of land-based observers. It should be noted, however, that considerable variability in call gradation was observed between feeding calls. At close range, feeding calls have noticeable harmonics, which are lost as the call attenuates. At least two feeding call

events had high SNR, prevalent harmonic structure, and high received levels. This suggests that these calls were produced at close range. While it is still possible that cooperative foraging was occurring in observer blind spots or beyond visual detection range, it appears possible that this call may be produced in more than one behavioral context, or may be used by solitary foragers. To date no studies have investigated the presence or use of this call in other behavioral contexts. Studies describing the use of the call were focused on cooperatively foraging groups, and whales not participating in bubble net foraging events were underrepresented or omitted. Similar to early hypotheses that humpback calves don't vocalize (Tyack, 1983), or that social calls are primarily a function of competing males (Silber, 1986), it is possible that the lack of documentation of this call in other contexts is a function of sampling effort. While the call to date has been recorded only during cooperative foraging I propose that further investigation (including localization) of passively recorded feeding calls may demonstrate that the call is being used in other foraging contexts.

Similar to the feeding call, calls in the NC vocal class are highly stereotyped and were detected comparatively infrequently during this study. Comparison of spectrograms collected in this study to spectrograms of 2012 song collected in Glacier Bay suggests that some of the call types in the NC vocal class may be song units from the 2012 breeding song (Gabriele, 2013). Along the South Pacific migratory corridor, song-unit social calls were often produced in short repeated phrases, similar to song, but lacking the overall song structure (Dunlop et al., 2008); similarly, short bouts of repeated NC calls resembling song were detected in this study. Based on the presence of song in Southeast Alaska in late summer and early fall, and the anecdotal presence of structure to the social calls in the NC vocal class, it is likely, had this study continued later into the summer or fall, that song would have been observed in the region. NC calls were never produced during dispersed scans or scans containing only a single whale, and, although both dispersed scans and single scans were few, this distribution was highly unlikely to be a function of chance. NC calls, therefore, appeared to occur only during times of increased social interaction. Song allegedly serves a social function, and has been shown to elicit joining responses and approach responses during playback trials (Darling et al., 2006;

Darling et al., 2012). It has been proposed that humpbacks may use song on foraging grounds to entice future mates, despite current unavailability (Charif et al., 2001; Clark and Clapham, 2004). It is possible that song-unit social calls serve a similarly social function, but their limited presence in this data set preclude quantitative inference.

Abundance, Dispersion, and Calling Behavior

Whales in this study did not appear to alter their vocal behavior based on the total number of animals in the area. Presumably, if social calling facilitated group formation calling rates would increase as the opportunities for interactions increased. This phenomenon has been observed in gray whales wintering in the lagoons of San Ignacio, where the daily number of calls increased roughly as the square of the number of animals present (Ponce, 2012). That no trends demonstrating a relationship between abundance and calling behavior emerged in this study may be explained by the regional context under which these vocalizations were recorded. Frederick Sound is an historic foraging ground for humpback whales; presumably most behaviors in the region will be driven by the need to acquire food. Unlike wintering grounds where the primary driver for social interaction is mate selection and/or the parental care, group facilitation may be counterproductive for animals attempting to capture patchily distributed ephemeral prey.

Another explanation for the absence of a relationship between abundance and vocal behavior, however, may be an artifact of this particular research season. There is evidence that whale abundance in the summer of 2012 was comparatively low around the Five Finger Islands. Compared to the results of a 2011 pilot study at the same location and using the same visual sampling protocol – though lacking an acoustic component – total humpback whale sightings, based on equivalent sampling effort, in the month of July were 52% lower in 2012 than in 2011. Further, studies of abundance in the region from 2008 documented a peak in whale abundance in Frederick Sound in late July (Szabo, 2011), while in this study the average number of whales sighted per survey was lowest during that period. Humpback whales in Southeast Alaska utilize multiple foraging grounds, and it has been proposed that emigration into Frederick Sound is driven by prey availability (Baker and Herman, 1989; Baker et al., 1992). At the time of this

study, multiple large aggregations (20-40+) of humpbacks were documented foraging in parts of Southeast Alaska (i.e., Glacier Bay, Icy Strait) that are typically utilized by the same individuals who forage in Frederick Sound (Neilson et al., 2013). This study did not attempt to quantify prey availability in the Five Finger region, nor did it monitor oceanographic conditions that may affect prey abundance; however, reports of colder than average water temperatures were speculated to have affected prey distribution in summer 2012. Notably, there was a large abundance of pteropods in Icy Strait in summer 2012, and humpbacks were observed foraging on pteropods in Chatham Strait in the month of August (Neilson et al. 2013). These combined variables may have impacted the abundance of animals in the study region. Based on this evidence, the vocal behavior documented in this study may best be described as the vocal behavior of foraging humpbacks during periods of reduced abundance.

Clustered, random, evenly dispersed, and single dispersion states were all observed during the study, and broadly describe the mean nearest neighbor distance between animals throughout the survey region. Vocal behavior in this study does appear to vary between dispersion states, indicating that the distance between individuals has an impact on vocal behavior. The majority of vocalizations detected in this study were produced when animals were in closest proximity, typically less than one kilometer (clustered dispersion states); however, less than one-third of all surveys contained whales in clustered states, and based on the total number of whale sightings during clustered states, this was not a function of increased whale presence, indicating that overall vocal behavior was higher when animals were in closer proximity. The total number of vocalizations detected decreased as animals grew more dispersed, with fewer vocalizations detected during randomly dispersed surveys, and fewer still in evenly dispersed and single surveys. Results indicate that this decrease in vocal behavior is not a function of chance, and I propose that overall call use increases with the potential for increased social interaction.

Clustered and random dispersion states were characterized by higher vocal diversity, and were more likely to contain vocalizations than dispersed or single states. Call use was

more diverse when whales were in closer proximity and presumably had increased opportunity to interact, but was not necessarily contingent on animals being in direct proximity to one another (i.e., travelling together as a cohesive group). In contrast, surveys where whales were either evenly distributed – indicating organized spacing and a lack of group travel – or when only a single whale was present – indicating an average nearest neighbor distance greater than the survey area – were characterized by low vocal diversity. This suggests that as the clustering increases that vocal complexity also increases.

Vocal diversity increasing with increased social interaction is a demonstrated phenomenon throughout the animal kingdom in many species, most notably in non-human primates (Bouchet et al., 2013), and may be linked to the need to disseminate greater amounts of information for either cooperation or competition. The same phenomenon has been reported in the marine environment. Southern right whales increase the complexity of acoustic signaling with increasing close range interaction and behavioral complexity (i.e. group size, mating behavior, number of males present) (Clark, 1990), and northern right whales show markedly higher calling rates during social interactions than during foraging interactions (Parks et al., 2011). Humpbacks in this study travelled predominantly alone and calves were rarely sighted; therefore, the ability to assess increasing vocal complexity as a function of group composition was not possible in this study. However, the use of vocalizations during cooperative foraging events in Southeast Alaska, in competitive groups, and in pods of multiple migrating whales, all support the theory of increased vocal behavior with increased social interaction. The decreased calling rates reported in this study, when animals were not travelling in surface active groups or otherwise engaged in highly interactive activities, further supports this theory. I hypothesize that this trend would become evident in Southeast Alaska given further study, particularly when comparing groups of animals engaged in cooperative foraging events and those engaged in solitary foraging events or travel.

Communication

There was a visually evident, though not statistically significant, trend for the absolute change in nearest neighbor distances to decrease as calling rates increases, suggesting that increased calling rates are associated with sustained spatial proximity. Conversely, in the absence of calling, animals appear to cluster or disperse with greater variability. I hypothesize that social calling on foraging grounds functions in part to maintain spatial relationships between individuals. This is consistent with earlier proposals that social calls may facilitate interactions between conspecifics, facilitate joining events, and maintain contact between individuals (Dunlop et al., 2008). It is also consistent with general theories that define communication as the process by which an animal transfers information that increases the probability of a future behavior. The use of communication to maintain animal dispersion is most famously seen in anurans who use calling to maintain distance between male conspecifics during the breeding season (Whitney and Krebs, 1975), and in birds who use song to defend territories and mates (Catchpole, 1982; Todt and Naguib, 2000; Osmun and Mennill, 2011). More pertinently, however, the use of song to maintain spacing between breeding males has been proposed for North Pacific humpback whales on Hawaiian breeding grounds (Frankel et al., 1995) and is therefore already, at least theoretically, a known use of humpback whale vocalizations. It is possible that some vocalizations are used to maintain small-scale separation between animals, similar to even dispersal in frogs and birds, as they forage.

As the body of research on social bonds in baleen whales grows, evidence is accumulating that humpback whales – particularly on foraging grounds – are capable of, and benefit from, stable associations (Weinrich, 1991; Sharpe, 2001; Ramp et al., 2010; Sharpe, 2013). At high latitudes these bonds are often centered on observable foraging events (Baker and Herman, 1984; D'Vincent et al., 1985; Weinrich and Kuhlberg, 1991; Clapham, 1993; Sharpe, 2001; Ramp et al., 2010; Sharpe, 2013), and have been shown to have a positive impact on female reproductive fitness (Ramp et al., 2010). In Southeast Alaska in particular non-kin humpbacks convene to cooperatively forage over multiple years (Sharpe, 2001). If these relationships are mutualistic, it would be supposed that animals would have developed a way to identify individuals, maintain bonds, and reunite

on foraging grounds after a winter's absence. I hypothesize that one function of acoustic communication in the marine environment is to maintain contact with individuals over time and space.

Conclusion

The results of this study are that social calling behavior varies between vocal classes, with calls in the LFH vocal class and P vocal class being comparatively more common than calls in the NC or T vocal classes. There was no evidence that calling behavior varied as a function of abundance, but further investigation across longer time periods may reveal trends that were not captured in this study. There is evidence that calling behavior varies as a function of spatial distribution, with increased calling diversity and increased calling behavior observed when animals were within 1-2 km of one another and in either clustered or randomly dispersed states, and decreased calling behavior and lower calling diversity when animals were evenly dispersed throughout the survey area or only a single whale was present. There is evidence to support the hypothesis that vocal complexity may increase as the potential for social interactions increase, though caution should be exercised when attributing this behavior to cooperative interactions. Further, I hypothesize that humpback whales use social calling to make contact with conspecifics, to maintain spatial proximity on foraging grounds, and that as calling rates increase changes in dispersion will decrease. This all supports the hypothesis that humpback whales are using social calling as a form of communication.

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TABLES

Table 8. Results of a Poisson Log-Linear regression testing the effects of abundance and dispersion on calling rates.

Vocal Class	Variable	DF	χ^2	p
Total Calls	Abundance	1	0.04	0.84
	Dispersion	2	0.25	0.88
LFH	Abundance	1	0.002	0.99
	Dispersion	2	0.04	0.98
P	Abundance	1	2.79	0.09
	Dispersion	2	18.74	<0.0001
NC	Abundance	1	0.41	0.52
	Dispersion	2	2.65	0.27
T	Abundance	1	3.19	0.07
	Dispersion	2	3.11	0.21

Table 9. Description of vocal behavior by dispersion state including: total number of surveys of each state containing vocalizations, Shannon-Weiner Index assessing calling diversity of vocalizations detected at each dispersion state (pooled), and number of vocalizations of each vocal class detected in each dispersion state.

	Clustered	Dispersed	Random	Single
Surveys w/ Calls	16	26	2	2
SWI	1.16	0.56	1.15	0
Total Calls	156	5	96	2
LFH Calls	79	4	54	0
P Calls	45	0	13	2
NC Calls	17	0	10	0
T Calls	15	1	19	0

Table 10. Summary statistics for calling rates and counts by dispersion states. Sample size (number of surveys at a given dispersion state) is listed in the heading. Mean calling rates and mean call counts for each vocal class are listed in bold; standard deviations are italicized below.

		Clustered n=35	Dispersed n=15	Random n=51	Single n=10
Total Vocals	Count	4.5	0.3	1.9	0.2
		<i>8.8</i>	<i>1.0</i>	<i>3.9</i>	<i>0.4</i>
	Rate	0.020	0.005	0.02	0.006
		<i>0.036</i>	<i>0.017</i>	<i>0.008</i>	<i>0.004</i>
LFH Calls	Count	2.3	0.3	1.1	0.0
		<i>4.6</i>	<i>0.8</i>	<i>2.7</i>	<i>0.0</i>
	Rate	0.010	0.006	0.013	0.000
		<i>0.016</i>	<i>0.015</i>	<i>0.049</i>	<i>0.000</i>
P Calls	Count	1.3	0.0	0.3	0.2
		<i>2.3</i>	<i>0.0</i>	<i>0.6</i>	<i>0.4</i>
	Rate	0.007	0.000	0.002	0.006
		<i>0.014</i>	<i>0.000</i>	<i>0.005</i>	<i>0.013</i>
NC Calls	Count	0.5	0.0	0.2	0.0
		<i>1.9</i>	<i>0.0</i>	<i>0.9</i>	<i>0.0</i>
	Rate	0.002	0.000	0.001	0.000
		<i>0.006</i>	<i>0.000</i>	<i>0.005</i>	<i>0.000</i>
T Calls	Count	0.4	0.1	0.4	0.0
		<i>1.6</i>	<i>0.3</i>	<i>1.0</i>	<i>0.0</i>
	Rate	0.002	0.001	0.004	0.000
		<i>0.007</i>	<i>0.004</i>	<i>0.019</i>	<i>0.000</i>

FIGURES

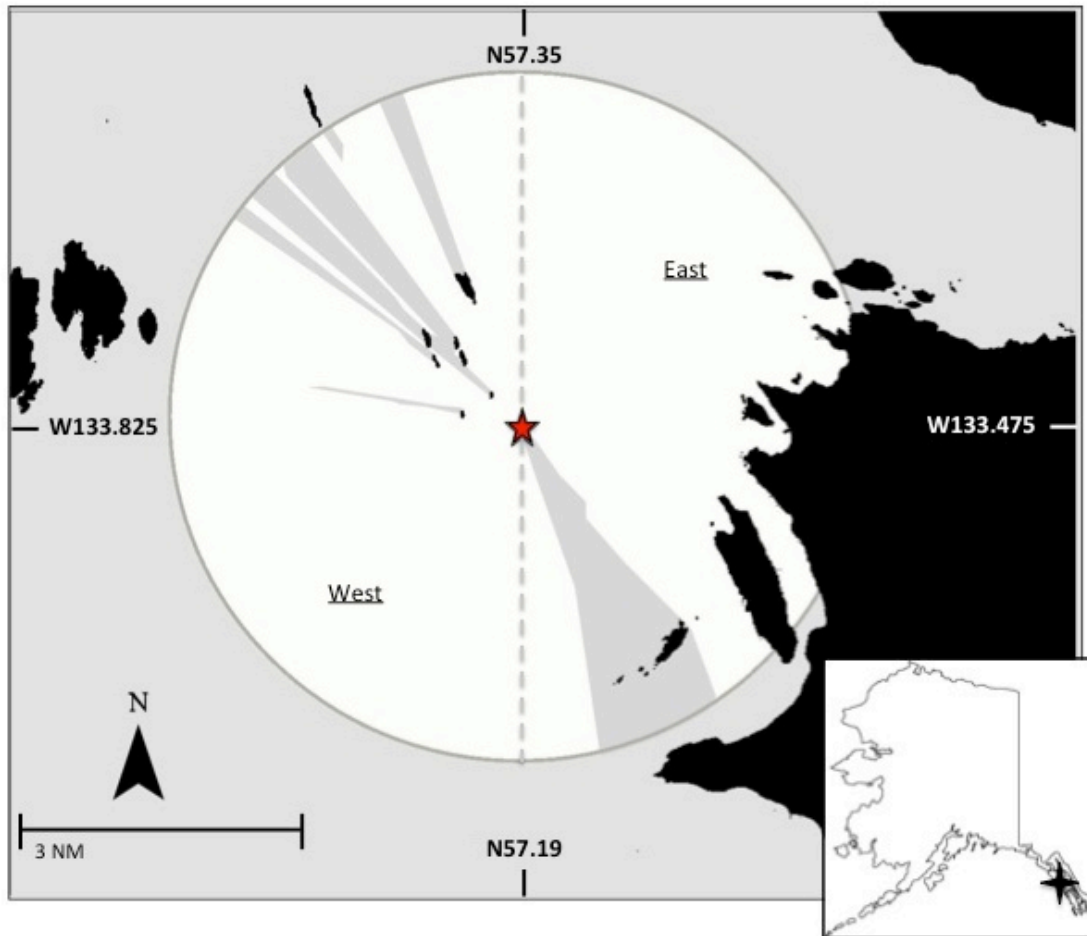


Figure 9. Map showing survey area in Frederick Sound, southeast Alaska. Blind spots and survey area boundaries are shaded in gray. Five Finger Lighthouse observation tower is marked with a star.

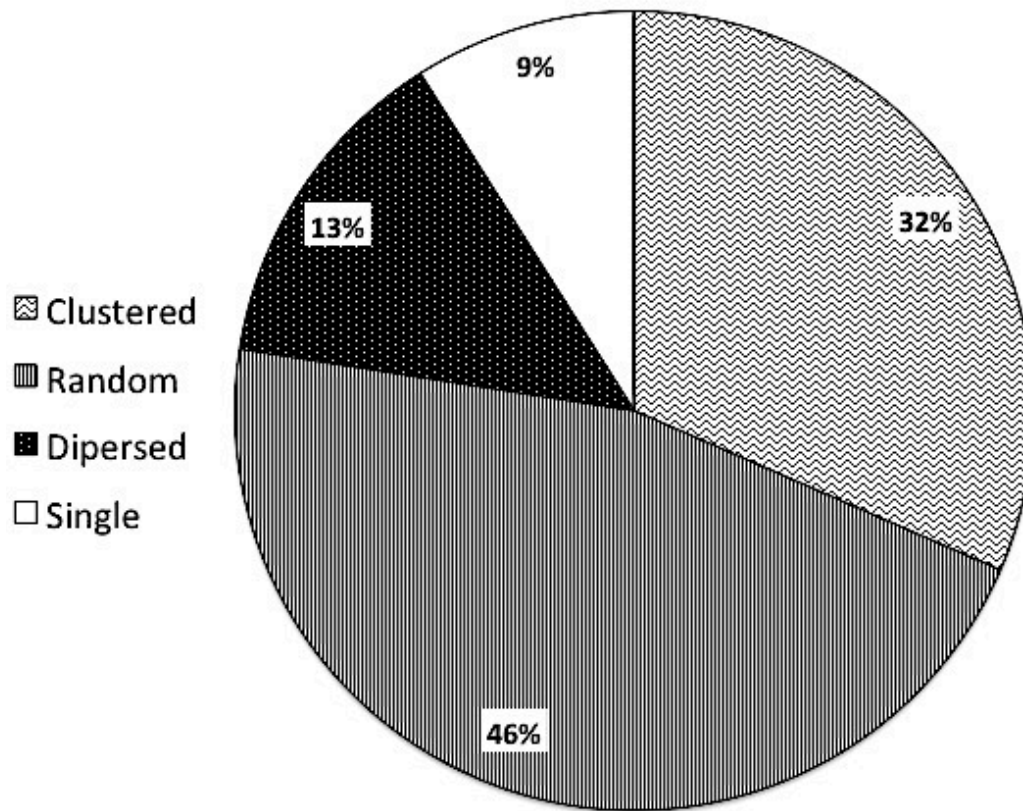


Figure 10. Percentage of total surveys represented by each dispersion state.

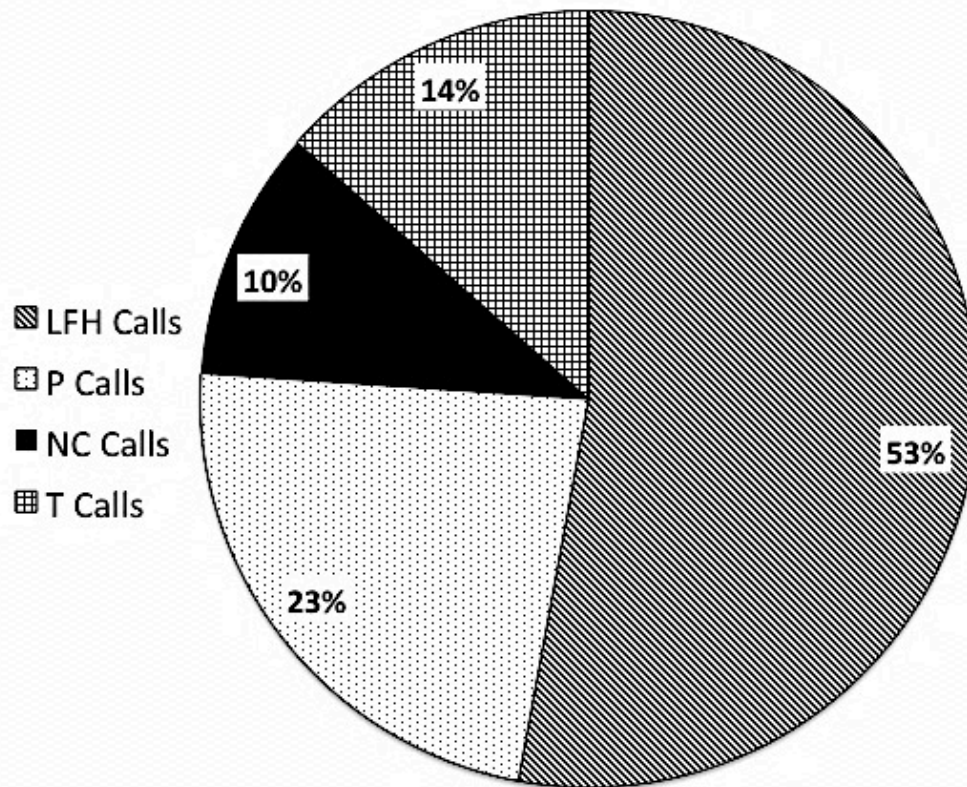


Figure 11. Percentage of total calls represented from each class.

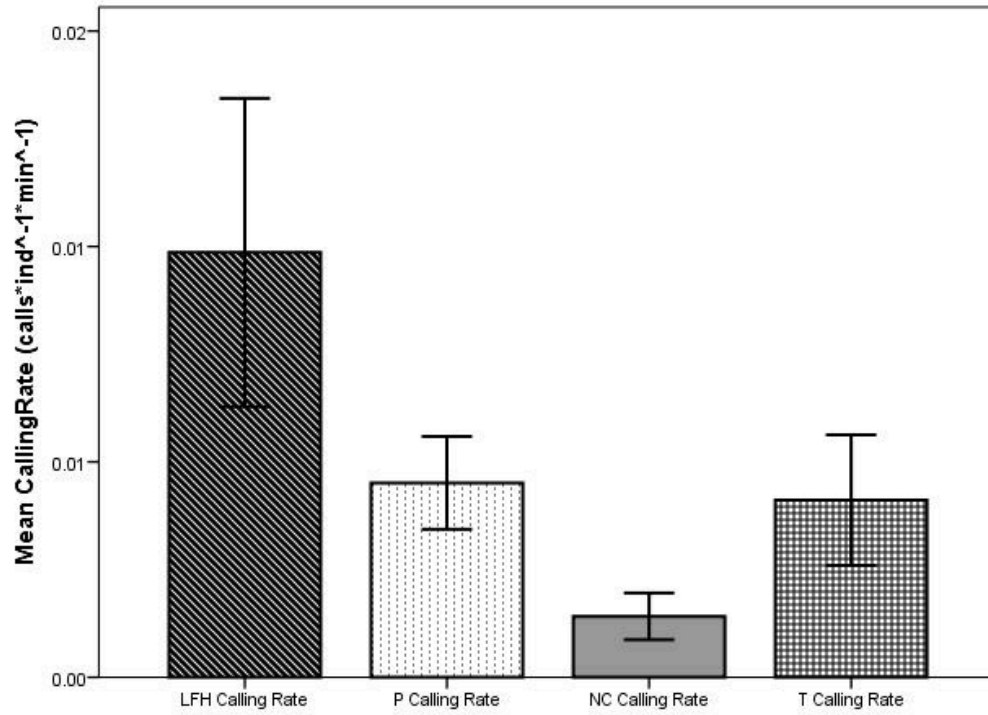


Figure 12. Mean (\pm SEM) calling rates (calls per whale per minute) for each vocal class.

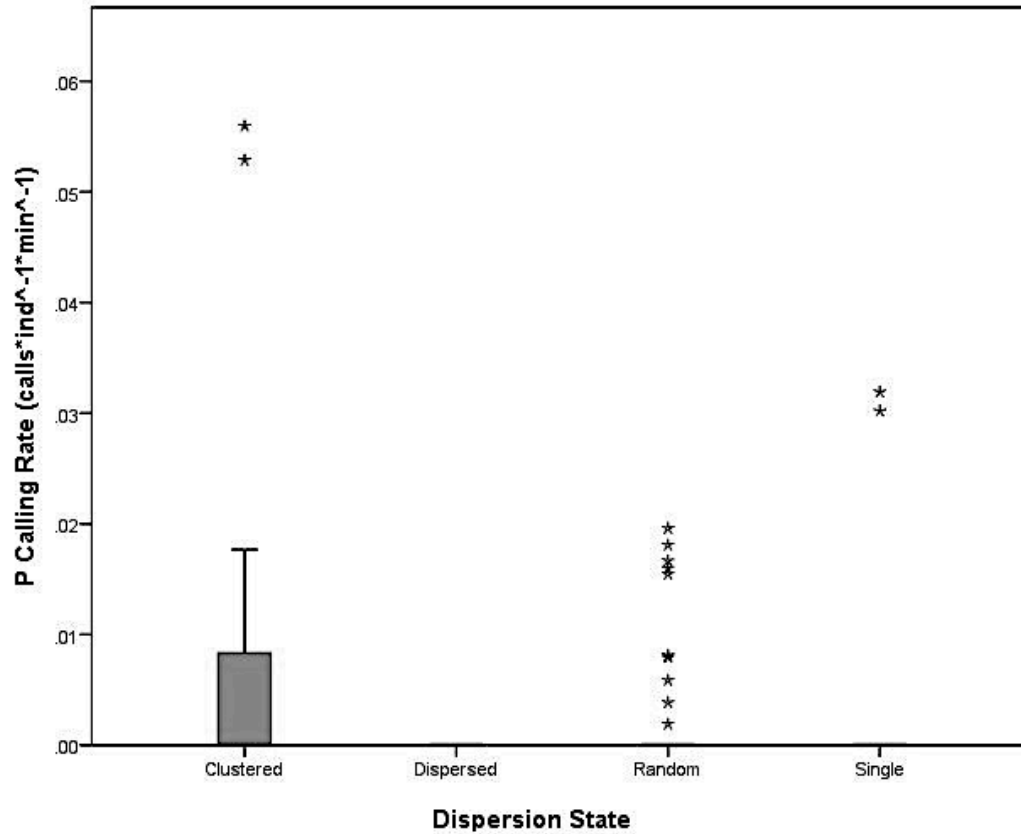


Figure 13. Outlier box plot of Pulsed (P) call production (calls per whale per minute) in four different dispersion states: clustered, random, dispersed, and single. Asterisks indicate outliers.

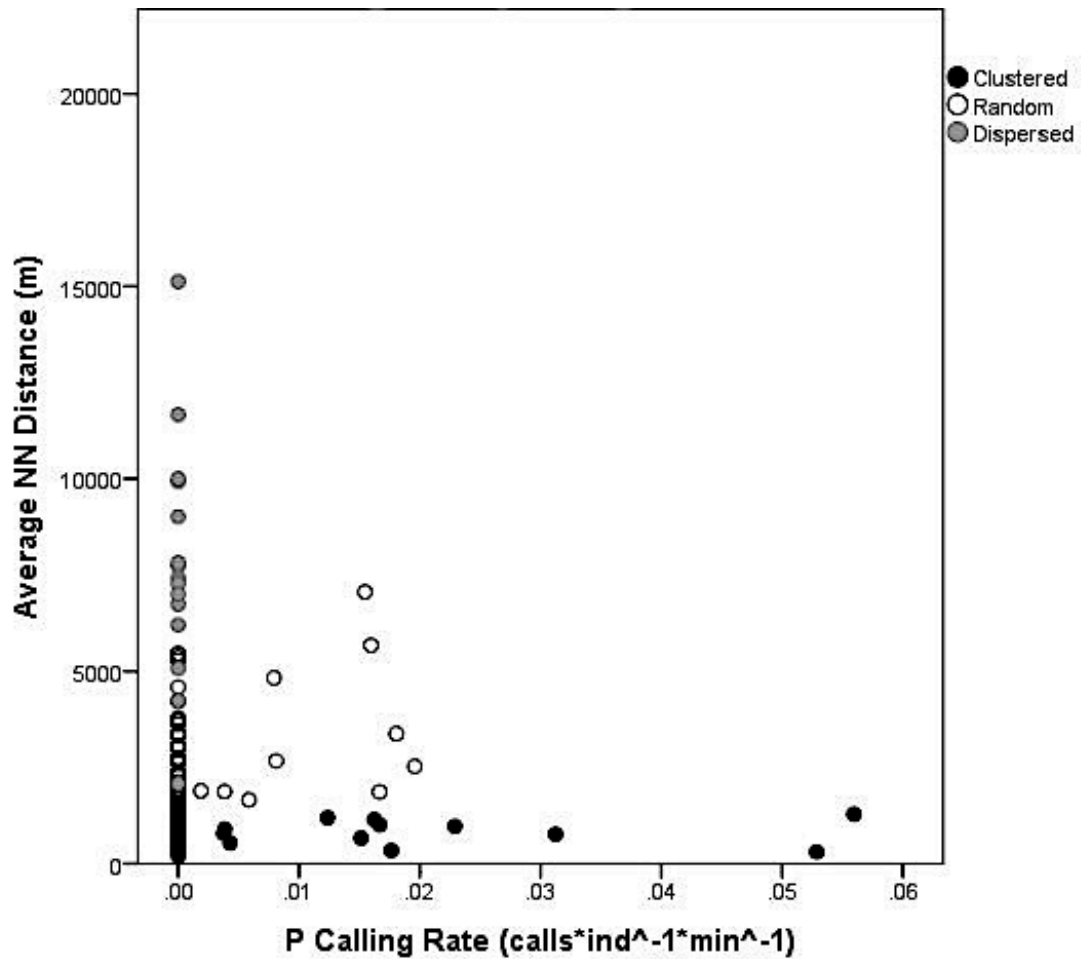


Figure 14. Pulsed (P) calling rate of production (P calls per minute per whale) plotted against average nearest neighbor distance (m) and coded by dispersion state. Solid circles represent clustered dispersion states, hollow circles represent random dispersion states, and gray circles represent dispersed states.

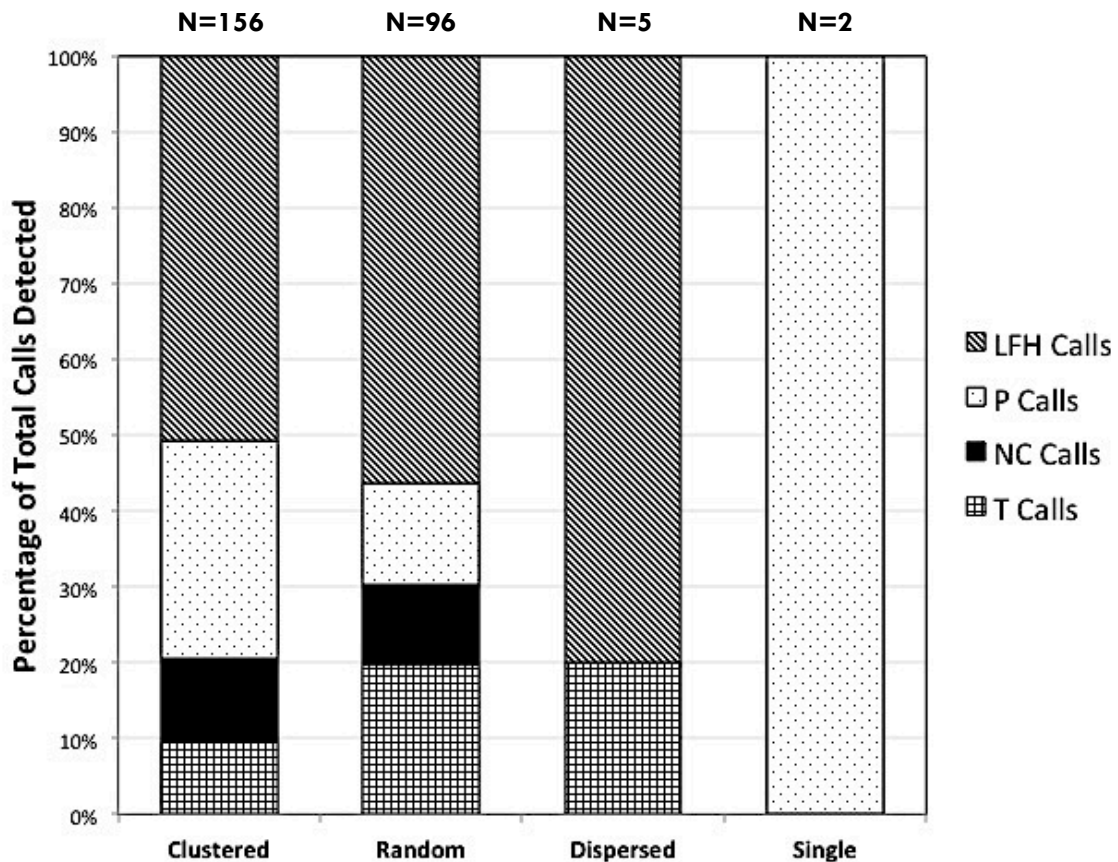


Figure 15. Percentage of calls represented from each vocal class (LFH, P, NC, and T) at each dispersion state (clustered, random, dispersed, and single). Dispersion state is calculated on a per survey basis; calls from all surveys of a given state are pooled to calculate percentage of calls from each vocal class for each dispersion state. Sample size (number of total vocalizations detected at a given dispersion state) is note above the x-axis.

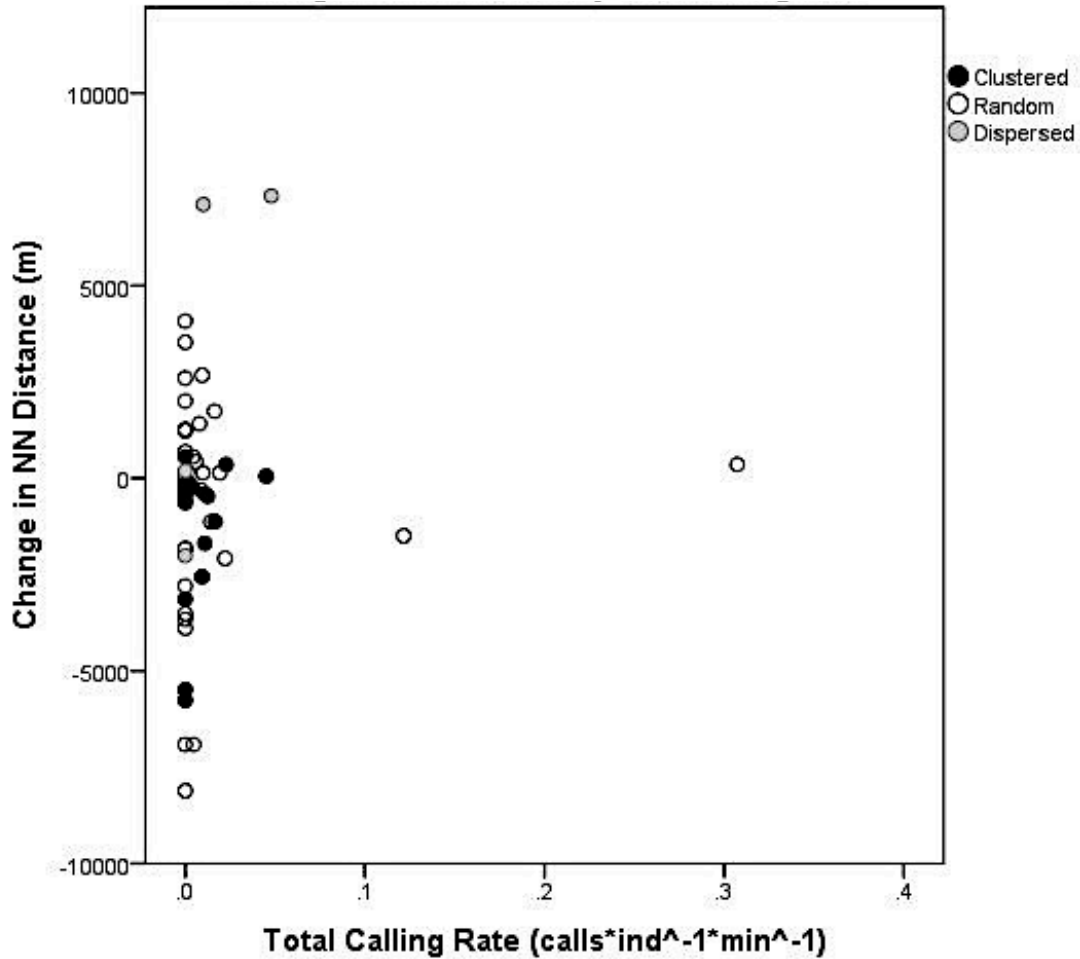


Figure 16. Rate of total call production (total calls per whale per minute) plotted against the change in average nearest neighbor distance (m). Change is measured as the average nearest neighbor distance observed in a given survey minus the average nearest neighbor distance of the survey directly previous. Solid circles represent clustered dispersion states, hollow circles represent randomly distributed dispersion states, and gray circles represent dispersed states.

CHAPTER FOUR: General Conclusions and Future Directions

The goals of this thesis were to describe the social calling structure of Southeast Alaskan humpback whales and investigate vocal sound production as it related to social context and communication. Combining passive acoustic monitoring with visual observations made it possible to attribute detected vocalizations to humpback whales with a high degree of confidence, and facilitated the classification of calls and an investigation of the spatial-behavioral context under which calls from the different vocal classes were utilized. The analyses in this thesis resulted in a quantitative description of humpback whale social calling structure and a catalog of social call types (Chapter 2), and a summary of vocal behavior as it relates to social-spatial context (Chapter 3). These pieces combined indicate that humpback whales have a more diverse repertoire than previously documented in Southeast Alaska, that humpback whales are using social calls discriminately between social contexts, and that sound production may serve a communicative function.

PRIMARY FINDINGS AND CONTRIBUTIONS

My analysis in Chapter 2 classified social calls within a hierarchical structure that consisted of 4 vocal classes, 7 vocal subclasses, and 16 unique call types. The four vocal classes – low-frequency-harmonic (LFH), pulsed (P), noisy/complex (NC), and tonal (T) – were distinguished by a human observer and corroborated through hierarchical agglomerative cluster analysis and discriminant function analysis. The high degree of agreement between classification methods at all levels (vocal class, vocal subclass, and call type) indicates that the proposed hierarchical structure describes a true organizational system. Results of this classification system also suggest that not all humpback whale social calls are discrete; some social calls appear to form a vocal continuum. I hypothesize that discrete calls may be more clearly linked to well-defined functions.

In Chapter 3 I found that call use varied between vocal classes, and in some cases (P calls) calling rates were linked to particular dispersion states. Additionally, results indicated that generally vocal behavior varies based on the distance between animals, with higher vocal diversity occurring when whales were in closest proximity to one another. Further, I found that in this study vocal behavior was not linked to abundance, though I propose that whale abundance during the 2012 field season may have been low. I propose that as social complexity increases, vocal complexity may also increase. This was demonstrated by an increase in calling diversity as spatial proximity decreased, and poorer call representation during evenly dispersed and single states than could be attributed to random chance. That vocal classes were disproportionately represented in the data indicates that not all vocalizations are suitable to all situations. I propose that each vocal class is used under specific social situations, and that stereotyped calls versus calls that comprise a vocal continuum may serve separate behavioral functions.

This research presents multiple novelties regarding humpback whale vocal behavior and its role in social communication. Numerous call types described in this thesis have been previously undocumented and/or unattributed to humpback whales. The resulting catalog of social call types is available as a resource for passive acoustic monitoring efforts in the North Pacific, and may be particularly useful for assigning previously unidentified vocalizations to humpback whale callers. This catalog also provides important baseline acoustic measurements necessary to assess management and conservation concerns, including vocal masking and shifting vocal behavior in the face of a changing soundscape.

Although the elusive question of *why* humpbacks vocalize has yet to be answered, the results of this thesis provide a framework for investigating call function and behavioral interactions between conspecifics in Southeast Alaska. Establishing call function is an iterative process. By demonstrating that vocal behavior is context-specific, is associated with particular behavioral conditions, and proposing calling behavior is associated with the maintenance of animal dispersion states, it can be inferred that social calls do in fact

serve a communicative function. The results of this thesis mark a first step in understanding the role of social calling in foraging humpbacks.

FUTURE RESEARCH

As is often the case, this thesis has generated as many questions as it set out to answer. While I am confident that the structure of social calling has been adequately described, neither the call catalog nor the descriptions of vocal behavior are comprehensive. The vocal behavior documented in this thesis occurred in months that I believe were indicative of relatively low abundance conditions, and thus may not be wholly representative of species repertoire or vocal behavior. Continued collection of humpback whale vocalizations concurrent with visual observations would allow for a more comprehensive catalog to be constructed. Additionally, this research would have been greatly benefited from the ability to localize calling animals. Critical acoustic measurements, including source levels, are currently unknown for humpback whales. The ability to localize callers would enable researchers to calculate these levels. Individual caller identification would enable finer-scaled behavioral analysis to be correlated with particular call types, and would allow for investigation of specific call functions that could not be addressed with the equipment used in this study. Further, the use of playbacks would greatly expand the results in this study, as they would allow for hypothesis testing related to particular vocal classes and/or behavioral states.

Lastly, this study was initially envisioned with the greater goal of addressing the impact of vessel noise on humpback whale calling behavior. While that particular goal was never realized, it is my hope that the results of this study will augment studies addressing the impact of anthropogenic sound on humpback whale vocal behavior and social communication. As ocean noise levels increase the risk of vocal masking grows. If social calling facilitates significant interactions between humpback whales, then masking may have deleterious effects on behavior and the transmission of cultural information within populations. The results of this thesis provide baseline information against which future studies can be compared for evidence of adaptation in the face of change.

Continued research on call function, humpback whale sound source levels, masking potential, and behavioral plasticity is a natural future direction founded in the research presented here.

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APPENDIX

POTENTIAL CALL TYPES (PRELIMINARY)

Based on the inclusion criteria set forth in the classification study, only call types that were detected on a minimum of two non-consecutive sampling days and had a SNR of 10 dB or better were included in analysis and the subsequent call catalog. However, an additional five potential call types that did not fit the criteria were preliminarily identified through aural-visual (AV) analysis, and merit further consideration. Acoustic parameters for the preliminary call types and justifications for their omission are listed in Table 11; spectrograms of potential call types can be found in Figure 17. The call types have been named according to the aforementioned naming system, though their placement into vocal classes and subclasses was determined solely through AV analysis, and thus should be considered preliminary at best.

Table 11. Selected acoustic parameters for potential call types. Call types were classified based on aural-visual analysis alone. Means are presented in bold, standard error are below in italics.

Call Type	P-F-5 (Bullet) n=2	NC-F-8 (Creek*) n=2	NC-F-6 (Creaky) n=3	NC-F-7 (Shake) n=2	LFH-F-7 (H. Moan) n=1
Bout (n)	1 <i>0</i>	1 <i>0</i>	1.14 <i>0.14</i>	2 <i>1</i>	1
Peak (Hz)	155.77 <i>32.63</i>	1404.7 <i>0.07</i>	1403.2 <i>225.08</i>	1291.86 <i>455.23</i>	111.53
Lower (Hz)	123.82 <i>53.83</i>	1227.39 <i>48.45</i>	1109.73 <i>195.64</i>	732.13 <i>197.67</i>	37.68
Upper (Hz)	678.3 <i>392.98</i>	3617.58 <i>296.08</i>	3510.68 <i>585.4</i>	2417.1 <i>565.58</i>	371.45
Duration(s)	0.59 <i>0.13</i>	1.65 <i>0.02</i>	1.03 <i>0.15</i>	0.92 <i>0.03</i>	0.77
Band(Hz)	554.48 <i>339.15</i>	2390.19 <i>344.53</i>	2400.95 <i>507.34</i>	1684.97 <i>391.9</i>	333.76
Median (Hz)	198.4 <i>94.23</i>	1868.82 <i>3.81</i>	1753.67 <i>238.08</i>	1250.78 <i>350.48</i>	104.99
Freq. Q. (Hz)	163.09 <i>125.88</i>	572.16 <i>22.42</i>	927.81 <i>163.24</i>	592.1 <i>120.96</i>	159.87
AM	3.54 <i>0.76</i>	1.21 <i>0.02</i>	2.64 <i>1.66</i>	1.65 <i>0.33</i>	1.31
FM	4.62 <i>1.84</i>	0.61 <i>0.01</i>	2.36 <i>0.76</i>	1.09 <i>0.03</i>	1.31
Upsweep	6.86 <i>9.24</i>	-2.02 <i>1.37</i>	-5.87 <i>5.13</i>	-8.51 <i>3.26</i>	-0.87
Start (Hz)	87.45 <i>8.05</i>	950.9 <i>6.2</i>	1312.54 <i>238.85</i>	903.93 <i>233</i>	101.3
End (Hz)	84.55 <i>8.55</i>	826.6 <i>6.2</i>	1157.06 <i>200.72</i>	932.9 <i>206.63</i>	116.5

Table 12. Justification for omitting potential call types.

Potential Call Type	Reason for Omission
Bullet	Samples detected in a single day
Creek	Insufficient Sample Size
Creaky	Samples did not meet SNR criteria
Shake	Sample did not meet SNR criteria
Harmonic Moan	Sample detected in a single day

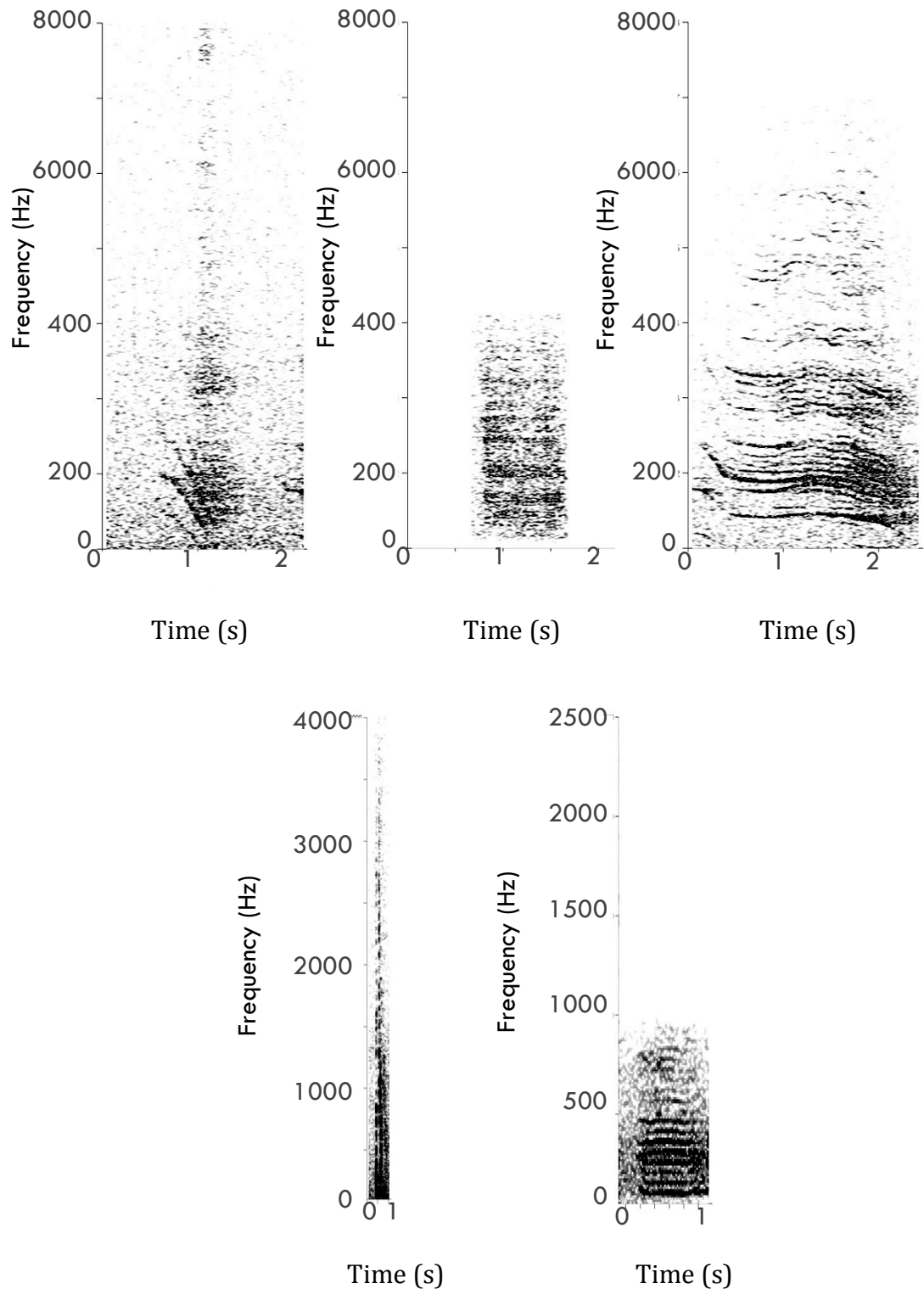


Figure 17. Potential call types, preliminarily identified through AV classification. L-R from top: NC-F-6 (Creaky), NC-F-7 (Shake), NC-F-8 (Creek*), P-F-5 *Bullet), LFH-F-7 (Harmonic Moan). Naming precedents set by Dunlop et al. 2007 are denoted with an asterisk. Note differences in frequency scale.