

ACOUSTIC ECOLOGY OF HUMPBACK WHALES (MEGAPTERA NOVAEANGLIAE)
IN THE HAWAIIAN ARCHIPELAGO

A DISSERTATION SUBMITTED TO THE OFFICE OF GRADUATE EDUCATION OF THE
UNIVERSITY OF HAWAI'I AT MĀNOA IN PARTIAL FULFILLMENT OF THE
REQUIREMENTS FOR THE DEGREE OF

DOCTOR OF PHILOSOPHY

IN

ZOOLOGY (MARINE BIOLOGY)

MAY 2017

By

Jessica Chen

Dissertation Committee:

Whitlow W.L. Au, Chairperson
Marc O. Lammers
Paul E. Nachtigall
Adam A. Pack
Eva-Marie Nosal

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ACKNOWLEDGEMENTS

I would like to thank my advisor, Whitlow Au, for all his support and supervision since my entrance into the graduate program and throughout my doctorate research. It takes a lot of patience to guide a biologist through the field of acoustics, and his assistance was priceless. I would like to thank my dissertation committee, Paul Nachtigall, Adam Pack, Marc Lammers, and Eva-Marie Nosal for their valuable guidance and support. I have learned so much from each of you and could not have made it this far without your advice and cooperation.

My research involved many parts and people, so I wish to thank all who contributed to the research. Many thanks to my colleagues, past and present, in the Marine Mammal Research Program (MMRP) of the Hawai'i Institute of Marine Biology (HIMB) for their guidance and support: Alison Stimpert, Adrienne Copeland, Lee Shannon, Giacomo Giorli, Aude Pacini, Michael Richlen, Alexis Rudd, Adam Smith, Ali Bayliss, Aliza Milette-Winfrey, and Helen Ou. Additional thanks to “honorary labmates” Brendan Rideout, Andy Dewald, and Anne Rosinski. I would also like to thank the many volunteers who came out to assist with fieldwork and data collection: Andrea Bendlin, Chelsie Counsell, Elia Herman, Merrra Howe, Zachary Jambor, Anke Kuegler, Sheldon Plentovich, Mark Royer, Sabena Siddiqui, Hilary Street, Chelsea Szydlowski, Allison Taranto, Grant Thompson, Dana Wilkes, and Eden Zhang. Thanks to Adrienne Copeland and Melanie Abecassis for help with statistical analysis and R scripts. If I have missed anyone, know that you have my gratitude for your help throughout the years.

I could not have carried out my research without the partnership of the Hawaiian Islands Humpback Whale National Marine Sanctuary and Ed Lyman. Their logistical and vessel support was essential for the success of my research. The exemplary captaining skills of Ed Lyman, Joe Carrier, and Carmen DeFazio were priceless. Thanks also to Oceanwide Science Institute and Marc Lammers for vessel support. Bill Burgess always did his best to provide troubleshooting and data analysis support for the Acousonde and Bioacoustic probe tags.

I also want to thank my family and friends for their continued support throughout the years. Their love and encouragement allowed me to persevere through the many academic and research challenges, and complete my PhD.

This research was supported by the University of Hawai‘i (UH) Sea Grant College Program, the UH School of Ocean and Earth Science and Technology, the NOAA Coral Reef Conservation Program, the NOAA/HIMB Northwestern Hawaiian Islands Partnership Program, NOAA’s Pacific Islands Fisheries Science Center - Coral Reef Ecosystem Division, the Hawaiian Islands Humpback Whale National Marine Sanctuary, and the Office of Naval Research. Additional funding was provided by the University of Hawai‘i E. A. Kay Award.

Research was conducted under NOAA National Marine Fisheries Service scientific research permit numbers 14682, 14682-01, and 14585, State of Hawai‘i Special Activity Permit numbers 2014-02, 2014-10, PMAL-2015-204, and PMAL-2017-206, and University of Hawai‘i Institutional Animal Care and Use Committee protocol numbers 13-1769, 13-1769-2, 13-1769-3.

ABSTRACT

Humpback whale songs are some of the most studied of cetacean vocalizations, however some of their other non-song vocalizations are less researched. During the winter breeding season, humpback whales are a consistent source of sound in the waters surrounding Hawaii. This dissertation research focused on quantifying and describing both song and non-song vocalizations at various spatial and temporal scales. Song units from the Main and Northwestern Hawaiian Islands were identified and quantified. The pattern in song unit occurrence suggested that the songs varied geographically but there is no clear divide between the humpback songs from Main and Northwestern Hawaiian Islands, showing instead a gradient of change along the island chain. Sound levels were examined across time of day and over the course of a year for patterns of sound contribution from humpback whales around the island of Kauai. Sound levels were approximately 6 dB higher during the winter season compared to summer, when possible sound sources include humpback whales, wind, and waves. Sound levels were approximately 1 dB higher during the day compared to night during the humpback season. A calf off the coast of Maui was tagged with an Acousonde acoustic and movement recording tag. The tag recorded song from a singing escort and revealed that a calf may be exposed to sound levels from 126 to 158 dB re 1 μ Pa. Additional mother-calf groups were tagged in the Maui area to study the vocalizations and associated behaviors. Twelve call types were identified from tags deployed on mothers and calves, and correlated with travel and surface activity. These studies are important to understanding the way humpback whales communicate and the vocalizations are used in order to understand their use of the environment. As the levels of anthropogenic noise in the ocean increase, this knowledge is important for preserving the acoustic environment of the humpback whales.

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LIST OF ABBREVIATIONS

ANOVA	analysis of variance
DPS	distinct population segment
DTAG	Digital Acoustic Recording Tag
EAR	Ecological Acoustic Recorder
ESA	Endangered Species Act
GAM	generalized additive model
HARP	High-frequency Acoustic Recording Package
HIMB	Hawaii Institute of Marine Biology
MC	mother-calf
MCE	mother-calf-escort
MHI	Main Hawaiian Islands
MMPA	Marine Mammal Protection Act
MMRP	Marine Mammal Research Program (of UH)
NMFS	National Marine Fisheries Service
NOAA	National Oceanic and Atmospheric Administration
NWHI Monument)	Northwestern Hawaiian Islands (Papahānaumokuākea Marine National
PAM	passive acoustic monitoring
pp	peak-to-peak
rms	root-mean-square
SEL	sound exposure level
SL	source level
SNR	signal-to-noise ratio
SOFAR	sound fixing and ranging
SPL	sound pressure level
SPLASH	Structure of Populations, Levels of Abundance and Status of Humpback Whales in the North Pacific
TDR	time-depth recorder
TOD	time of day
UH	University of Hawaii

CHAPTER 1

Introduction

1.1 Acoustics as a tool to study wildlife

Bioacoustics, defined as the area of acoustics relating to the study of sounds produced by or affecting living organisms, have been widely used as a tool for studying various species of wildlife. Acoustic methods have been useful for studying acoustically active species that may be difficult to observe with other methods, and to survey areas for species density and richness (e.g. Riede 1998, Blumstein et al. 2011, Zimmer 2011). For example, the species may be active nocturnally, or live in remote and difficult to access locations, such as deep in mountaintop forests, on remote uninhabited islands, or under sea ice in the Arctic and Antarctic Oceans. These remote areas are not only difficult to access, but also expensive for scientists attempting to study these species. Acoustic recorders can capture sounds produced by animals over large areas, over long periods of time, and can record sounds outside the human audible range thus allowing for study of infrasound and ultrasound. In addition, with the high speed of technological development, recorders are becoming less expensive with the ability to store increasing amounts of data and record for longer periods of time.

Acoustics have been an especially useful tool in studying marine species due to the challenges of working in the marine environment. The ocean is vast and still largely unexplored by humans, and ship time to reach and explore large swathes of the ocean are extremely expensive. Because light does not travel far in water, and sound can travel further and faster in water than in air, many marine species use sound to communicate. Scientists can listen for marine species to determine where they are present and what activities they are engaging in at what time. For example, echolocation clicks produced by odontocetes usually indicate foraging (Au 1993, Tyack & Clark 2000), while other sounds are correlated with breeding (Herman 2016, Rice et al. 2016). Some sounds may be observed for many years before the species producing them are identified (Risch et al. 2014). However, since sound recordings are archived, it will be possible to reanalyze them in the future for new insights.

There are two ways to study the ocean and its organisms using sound: active and passive acoustics. Active acoustics means that sound is transmitted into the ocean and data gathered from the reflected sound waves received back at receivers. Examples of sources include sonars and airguns. These methods can be used, for example, to survey schools of fish (Misund et al. 1995, Kang et al. 2002) and study organisms that are otherwise too deep to observe (Benoit-Bird & Au 2003, Copeland 2016). Passive acoustic methods only record sounds that are present in the environment. In this way, scientists can record the presence or absence of species, diel or seasonal patterns, the activities they are engaged in, and relative abundance (Wiggins et al. 2005, Arranz et al. 2011, Klinck et al. 2012, Au et al. 2014, Rice et al. 2016).

One thing that long-term passive acoustic recordings of sound in the ocean have already revealed is that the ocean is an increasingly noisy place (Andrew et al. 2002, Hildebrand 2009). One major contributor to increased low frequency sound in the ocean is engine noise from commercial shipping vessels. Other sources of anthropogenic, or human made noise include airguns used for seismic and oil exploration, pile driving for construction, and various types of sonars. Animals may react to acute and chronic sources of sound differently. Acute sound sources are relatively short but intense, such as explosions and sonars. These types of sound may cause behavioral changes, temporary or permanent hearing damage (Ketten et al. 1993). Chronic sound sources are long duration, such as the increase due to increased shipping vessels, or construction over a period of months. These sounds may cause long-term effects such as chronic stress or cause the animals to change their behavior over time (Moore & Clarke 2002, Holt et al. 2009, McDonald et al. 2009, Rolland et al. 2012). Several comprehensive reviews about the potential impacts of anthropogenic noise on marine mammals exist (Nowacek et al. 2007, Weilgart 2007, Ellison et al. 2012) and studies continue to attempt to parse out the relationship between anthropogenic noise and marine mammals.

Chapters 2 and 3 will focus on passive acoustic monitoring of humpback whales using autonomous acoustic recorders. These devices are self-contained packages consisting of a hydrophone, computer board to regulate recordings, data storage (e.g. hard drive or flash memory), and batteries. A variety of commercially available as well as custom built recorders are available, such as the Ecological Acoustic Recorder (EAR) (Lammers et al. 2008), High-frequency Acoustic Recording Package (HARP) (Wiggins & Hildebrand 2007) and SongMeter

(<https://www.wildlifeacoustics.com>). They can be programmed to record on a duty cycle, at various sample rates and bandwidths, and to record events meeting pre-programmed parameters. Because the device can be moored and left to record until pickup, it is possible for researchers to cover wide geographic and temporal ranges including remote and inhospitable regions. This method also likely causes less disturbance to the study animals than many direct observational methods, since an obstacle in the water is less likely to cause a behavioral change than a boat following a whale. However, passive acoustic monitoring can be limited by a lack of information at the scale of individuals or by poorly described sounds and novel sounds that prevent identification of sound source.

Identification of the sound source can be aided by acoustic recording tags that are attached directly to an animal. Acoustic recording tags are one of a number of small, animal-borne tags that can be used at the individual level to record the sounds produced or received by that particular animal and its accompanying movements. These are passive acoustic recording tags that also contain sensors such as pressure sensors, accelerometers, magnetometers, light sensors, and other sensors to collect data on the movements of the tagged individual. Examples include the Acousonde and its predecessor the Bioacoustic Probe (Burgess et al. 1998), and the DTAG (Johnson & Tyack 2003). Other types of animal-borne tags may or may not include acoustic recordings, and include video cameras (e.g. Crittercam), satellite location, time-depth recorder (TDR), or “pinger” tags that transmit coded signals to receiver buoys. These systems allow scientists to collect data on the acoustic and movement behavior of underwater species.

1.2 Humpback whales

Humpback whales (*Megaptera novaeangliae*) are one of the most studied baleen whales, also known as mysticetes. They have a worldwide distribution, recently divided into 14 sub-populations or “distinct population segments” (DPS) by the U.S. National Oceanic and Atmospheric Administration (NOAA) National Marine Fisheries Service (NMFS) based on an extensive review of the life history, morphology, and genetic information available (NOAA 2016). All except one DPS migrate annually from high latitude feeding grounds during summer to low latitude breeding grounds during winter. Their migrations take them along coasts and across ocean basins on routes between 4,000 and 10,000 km (Gabriele et al. 1996, Rasmussen et

al. 2007, Stevick et al. 2011). In their high latitude feeding grounds in the North Atlantic, North Pacific, and off Antarctica, humpback whales feed on a range of prey including krill, sand lance, herring, and other small fish (Jurasz & Jurasz 1979, Hain et al. 1982, Hain et al. 1995, Clapham 1996). They may feed individually or in cooperative foraging groups, for example when engaged in bubble net feeding (Jurasz & Jurasz 1979). On the low latitude breeding grounds, whales may exhibit different migration patterns and spatial distribution due to age and sex. Mothers with calves are the only stable social group observed over multiple days, typically close to shore or in relatively shallow waters (e.g. Smultea 1994, Cartwright et al. 2012). Males may join mother-calf (MC) groups as a single escort (MCE group) or to form competitive groups, leave such groups to become lone singers, or accompany another adult (dyad) (e.g. Mobley Jr & Herman 1985, Clapham et al. 1992). Females reach sexual maturity between 4 and 15 years (Clapham 1992, Gabriele et al. 2007), and typically reproduce every two to three years although some individuals have been recorded to have young two or more years in a row (Clapham & Mayo 1990, Glockner-Ferrari & Ferrari 1990, Straley et al. 1994). Calves nurse for and are weaned at approximately 10 months (Chittleborough 1958). Humpback whales may live to be over 45 years old (Gabriele et al. 2017).

Humpback whales use a variety of sounds to communicate. Males are known to sing complex songs that change over time, although songs within a geographic area tend to be very similar at any point in time (e.g. Winn & Winn 1978, Winn et al. 1981, Garland et al. 2011, Garland et al. 2013). The exact method of sound production is still unknown. It is hypothesized that baleen whales produce sound using a laryngeal system similar to humans, with the difference of a closed system using air sacs to recycle air (Reidenberg & Laitman 2007). In addition, it is unknown what frequencies they hear and how they hear, though it is generally agreed that they are able to hear sound they produce. Although the hearing capabilities and pathways have been tested in several odontocete species, mysticetes are too large to be kept in captivity for these tests. Current estimates of mysticete hearing ranges are based on frequencies of produced vocalizations and models based on physical properties of the ears. Humpback whales have been recorded producing song vocalizations from 100 Hz to 4 kHz, with harmonics as high as 24 kHz (Tyack & Clark 2000, Au et al. 2006). Based on models, humpback whales

are estimated to hear from a minimum of 30 Hz to a maximum of 18 kHz (Helweg et al. 2000, Houser et al. 2001).

Humpback whales in the Hawaiian Islands have an interesting history. Though they are a common sight in Hawaii today during winter and draw large numbers of both tourists and scientists to the islands, there is a lack of information about their history prior to the mid-1900s (Herman 1979). Although many whaling ships were based in Hawaii, according to commercial whaling records, very few humpback whales were killed in Hawaiian waters (Herman 1979). Today, thousands of humpback whales migrate to Hawaii annually from their rich feeding waters off Alaska and British Columbia. The North Pacific population is now estimated to be over 21,000 individuals (Barlow et al. 2011) with approximately half migrating to Hawaii and the rest migrating to Mexico, Japan, and the Philippines (Calambokidis et al. 2008, NOAA 2016). While the first whales are usually sighted in October, the humpback whale season is generally considered December through April, with the highest concentrations in February and March (Herman & Antinaja 1977, Darling et al. 1983). Some whales, presumably mature females, apparently do not migrate to lower latitude breeding grounds every year based on lack of sightings between years (Clapham et al. 1993, Brown et al. 1995). One hypothesis is that they take a “rest year” to continue feeding in preparation for breeding the next year. Other possible reasons include a female becoming pregnant on the migration route and turning around before reaching Hawaii, or migrating to a different breeding ground. However, most whales return to the breeding grounds where they were born (Baker et al. 2013).

Humpback whales were first listed under the Endangered Species Act (ESA) as an Endangered species in 1970. The North Pacific population of humpback whales, of which Hawaii’s breeding population is a part, is considered to have recovered well from whaling. The population was estimated to increase at approximately 6% per year (Calambokidis et al. 2008). The Hawaiian humpback whale DPS was delisted from the Endangered Species list in 2016 (NOAA 2016), although it is still protected under the Marine Mammal Protection Act (MMPA). However, the population still faces numerous threats from humans, including pollution (e.g. chemicals, plastic), sound pollution, entanglements, ship strikes, climate change, and hunting. One of the threats gaining attention from the public is acoustic impacts from military sonar sources. Because of the presumed importance of sound to all cetacean species including the

extremely vocal humpback whales, it is important to study the acoustic environment and of, and sounds produced by all ages and sexes of humpback whales while present in Hawaii.

1.3 Humpback whale acoustics

Sailors have written accounts of hearing whales through the wooden boat hulls, and recordings of sounds with unknown sources have existed since hydrophones were put in the ocean. Some sounds are not identified to species until over 50 years later, such as the minke whale (*Balaenoptera acoutorostrata*) “boing” attributed in 2005 (Rankin & Barlow 2005) and the “bio-duck” sound attributed in 2014 (Risch et al. 2014). Humpback whale vocalizations may be some of the earliest noted whale sounds because their frequencies are in the human audible range. Humpback songs were first formally described by Payne and McVay (1971). However, Payne states that the first songs were recorded by Schreiber in 1952 and subsequently identified as humpback whales by Schevill by 1964.

Humpback whale vocalizations, especially songs, are arguably one of the most studied and most recognizable marine mammal sounds. The sounds were termed “song” by Payne and McVay (1971) because of its similarity to bird song. The songs are formed by repeated, fixed patterns of sounds, with the shortest continuous sound termed the “unit”. Only males have been recorded to sing, including both mature and juvenile males (Herman et al. 2013). It is believed to have a function in breeding because most song is recorded during the winter breeding season and on the breeding grounds, although it also occurs to a lesser extent on migration routes and on the feeding grounds (Winn & Winn 1978, Mattila et al. 1987, McSweeney et al. 1989, Clapham & Mattila 1990, Clapham 1996, Smith et al. 2008, Herman 2016). The patterns inherent in song have been used to study population structure because most whales within a breeding population sing approximately the same song (Winn & Winn 1978, Winn et al. 1981, Payne & Guinee 1983, Payne & Payne 1985, Garland et al. 2011). Songs do change over time, however, and researchers have been able to track the cultural transmission of song over multiple years and across ocean basins (Noad et al. 2000, Cerchio et al. 2001, Garland et al. 2011, Garland et al. 2013).

In addition to songs, humpback whales make non-song vocalizations, also termed social sounds. The term “social sound” was first used by Silber (1986) to describe vocalizations that did

not fit in the rhythmic pattern of a song. These sounds are, in contrast, made by individuals of both sexes, all ages, and in feeding areas, along migration routes, and in breeding areas. Studies of non-song vocalizations have been conducted primarily in the Pacific, including on the feeding grounds (D'Vincent et al. 1985, Thompson et al. 1986, Cerchio & Dahlheim 2001, Stimpert et al. 2007, Stimpert et al. 2011, Fournet et al. 2015), migration routes (Dunlop et al. 2007, Dunlop et al. 2008, Dunlop et al. 2013, Rekdahl et al. 2013, Rekdahl et al. 2015), and breeding grounds (Pack et al. 2005, Zoidis et al. 2008, Stimpert 2010, Seger 2016). Non-song vocalizations may be made in the context of feeding, competitive groups of males pursuing females on breeding grounds, and contact or warning calls between individuals of a group.

Other non-vocal sounds may also be used in communication between individuals. The sounds from non-vocal impact sounds such as those from a breach, head slap, tail slap, or pectoral flipper slap have been hypothesized to have a communicative function (Deakos 2002, Dunlop et al. 2008, Dunlop et al. 2013). Other species use non-vocal impacts for communications, such as the dusky dolphins (*Lagenorhynchus obscurus*) which are believed to use breaches as a signal in cooperative feeding (Wursig & Wursig 1980). One study correlated pectoral flipper slap behavior in humpback whales with age, sex, and social role while on Hawaiian breeding grounds (Deakos 2002). Other studies examined the social and environmental context of surface active groups on their migration route (Dunlop et al. 2010, Kavanagh et al. 2017). However, the possible functions of surface-activity in humpback whales are still poorly studied.

One area of concern and study for humpback whales and other marine mammals is the effect of anthropogenic noise. The many sound sources present in the ocean were previously discussed. Some studies opportunistically observed effects of sound on various species (e.g. Todd et al. 1996, Frankel & Clark 2000, Dunlop et al. 2010, Rolland et al. 2012). Others conducted experimental playback and controlled exposure experiments to study the responses of animals to known sounds at controlled distances and source levels (e.g. Mobley Jr et al. 1988, Frankel & Clark 1998, Fristrup et al. 2003, Darling et al. 2012, Goldbogen et al. 2013, Friedlaender et al. 2016). Because humpback whales are so vocal, it is important to develop a good understanding of vocal development, sounds produced, and contextual use in order to protect their acoustic environment. The wide variety of sounds and the variability of song

suggests that humpback whale sounds are likely learned to a certain extent, rather than innate. Thus acoustic disturbances may have a greater effect on mother-calf groups than adult animals.

1.4 Research objectives

In order to develop a holistic understanding of the acoustic behavior of Hawaiian humpback whales, a variety of questions about the sounds produced and received by individuals, as well as groups of individuals at larger spatial scales, were examined. These are outlined below for each chapter:

Chapter 2: Humpback whale chorusing behavior around the island of Kauai, Hawaii

- Objective 1: Determine seasonal patterns of chorusing
- Objective 2: Determine if diel patterns of chorusing exist
- Objective 3: Determine if a spatial pattern exists around the island

Chapter 3: Variation in the song units utilized by humpback whales wintering in the Northwestern and Main Hawaiian Islands

- Objective: Compare frequency of song units in NWHI and MHI

Chapter 4: First measurements of the received levels of humpback whale song produced by a singing escort in close proximity to a calf in the Hawaiian breeding grounds

- Objective: Determine sound pressure levels of song received by a calf

Chapter 5: Acoustic characteristics of humpback whale mother and calf vocalizations in the Hawaiian wintering grounds

- Objective 1: Describe non-song vocalizations produced by mothers and calves
- Objective 2: Determine if vocalizations are correlated with behavioral state or movement in the water column

Chapter 6: Conclusions and future directions of research

1.5 Research significance

These studies add to the knowledge about the acoustic ecology of humpback whales in the Hawaiian breeding grounds. Patterns of habitat use around the island of Kauai over long time scales and large spatial scales are elucidated by examining the sound added to the environment by chorusing males. Information about the song units utilized by singing males in

the poorly studied Northwestern Hawaiian Islands area is presented in comparison with songs from the Main Hawaiian Islands. The first direct measurements of song sound levels received by a calf are presented, providing information about the sound levels that developing animals are exposed to by conspecifics. Lastly, the first comprehensive study of non-song vocalizations produced in mother-calf groups in the Hawaiian breeding grounds are discussed in context with behavioral state and dive profiles. The results of this dissertation provide some of the first measurements of song sound levels at individual and island scale, and novel descriptions of the acoustic repertoire of mother-calf groups in the Hawaiian Islands.

CHAPTER 2

Variation in the song units utilized by humpback whales (*Megaptera novaeangliae*) wintering in the Northwestern and Main Hawaiian Islands

2.1 Abstract

A comparison of the humpback whale song in the Northwestern Hawaiian Islands (NWHI) and the Main Hawaiian Islands (MHI) during the 2009 breeding season suggests that humpback whale song may be more variable than previously documented. Data from underwater autonomous acoustic recorders (EARs) deployed at five locations in the NWHI and MHI were analyzed to compare the frequency of occurrence of song units produced by whales at different locations within the island chain. Song units from randomly selected recordings in the data set were classified as one of 21 units and totaled for comparison between sites. There appears to be a gradient of differences in song units throughout the Hawaiian Islands, rather than discrete differences expected between separate breeding populations. Changes in the frequency of occurrence suggest a gradual change in the most abundant units throughout the island chain. While this could be confounded by changes in the song structure and content that occur throughout the season and throughout the ocean basin, it provides information about the prevalence of song units from the Hawaiian Archipelago.

2.2 Introduction

The Main Hawaiian Islands (MHI) are one of the principal breeding and calving grounds for North Pacific humpback whales (*Megaptera novaeangliae*) (Darling & McSweeney 1985, Baker et al. 1986). Based on a North Pacific Ocean survey (SPLASH: Structure of Populations, Levels of Abundance and Status of Humpback Whales in the North Pacific) of individually identified humpback whales between 2004 and 2006, Calambokidis et al. (2008) estimated the North Pacific population of humpbacks between 18,000 and 20,000 and increasing annually by about 6%. Approximately 10,000 of these individuals migrate to Hawaii each winter.

Humpback whales in the North Pacific have three known distinct breeding and wintering areas: Hawaii, Mexico, and Asia, which includes Japan, Taiwan, the Philippines, and the Mariana Islands (Calambokidis et al. 2008). These areas can be broken down further into sub-areas, such as each major island of Hawaii. Whales wintering in Asia feed primarily in Russia and the Bering Sea; whales wintering in Mexico feed in the Gulf of Alaska and California-Oregon coast, and whales that winter in Hawaii tend to feed at South-East Alaska and the Gulf of Alaska. The SPLASH survey identified some individuals feeding primarily in the Aleutian/Bering Sea that were not observed in the known and surveyed wintering areas.

The Northwestern Hawaiian Islands (NWHI) are a remote chain of islands stretching 2000 km to the north and west of the Main Hawaiian Islands (MHI) and make up the Papahānaumokuākea Marine National Monument (PMNM). Marine mammal surveys are difficult to conduct in this remote part of the archipelago in part due to the high cost of personnel and ship time, logistical problems due to the distance from ports, and weather constraints. Typically only National Oceanic and Atmospheric Administration (NOAA) ships have entered PMNM to conduct scientific research. Due to its National Monument designation, strict regulations exist to regulate activities in the PMNM. Most scientific research activities are designated as “regulated” in PMNM and must be reviewed. Humpback whales were not believed to utilize the NWHI as a wintering area until Johnston et al. (2007) used spatial habitat modeling to determine that the NWHI contained large areas of the shallow, warm-water habitat that humpbacks seem to prefer during winter. The study also reported observations of humpback whales in shallow, warm waters in the NWHI using both visual and acoustic methods, supporting the model’s predictions (Johnston et al. 2007). Data obtained subsequently with autonomous acoustic recorders

provided further evidence that humpback whales were present throughout the winter months in the NWHI (Lammers et al. 2011). With this discovery, it was suggested that this part of the Hawaiian Archipelago might be a distinct wintering habitat from the MHI not considered or sampled during the SPLASH study.

One method of examining humpback whale movement and habitat use is by listening for and analyzing the song produced by male humpback whales during the breeding season. Humpback whale song is arguably among the most recognized and charismatic sound produced by cetaceans and has been widely studied since being first described by Payne and McVay (1971). Following the discovery that humpback whales produce ordered sounds in the form of song, many studies have focused on analyzing the structure and characteristics of the song for insight into the species' population structure as well as attempting to discover the reasons why humpback males sing (Winn et al. 1981, Helweg et al. 1998, Cerchio et al. 2001, Green et al. 2007, Parsons et al. 2008, Smith et al. 2008, Cholewiak et al. 2013, Garland et al. 2013, Herman et al. 2013). The smallest component of a song is the 'unit,' the shortest continuous, individually identifiable sound produced by the whale (Payne & McVay 1971). Humpback whale song units typically have fundamental frequencies between 200 Hz and 2,000 Hz (Au et al. 2006). However, some units can have most of their energy as low as 100 Hz or as high as 4,000 Hz, and harmonics have been observed reaching up to 24,000 Hz in recordings made within close proximity to the singer (Au et al. 2006). A number of units in a sequence form a 'phrase', a series of phrases forms a 'theme', and a series of themes is contained in a song (Payne & McVay 1971). A song can also be defined as one cycle of a series of themes. For example, if there are three themes designated 'A, B, and C' and the whale consistently sings ABAC, then this can be defined as a song, which may be repeated multiple times in a song session. A song typically lasts about 15 minutes and is produced during a single dive when the whale sings in a stationary position. However, there is also high behavioral variability between singers; one whale may sing two cycles of the song during one dive, while another individual may consistently surface in the middle of a theme rather than at the end of the song cycle (J. Darling, pers. comm.). This can make the accurate representation of a particular song difficult without multiple continuous recordings.

Male humpback whales are known to sing their songs during the breeding season in winter, although songs have also been recorded on migration routes and in the feeding grounds at the beginning and end of the winter season (Mattila et al. 1987, Clapham & Mattila 1990, Norris et al. 1999, Clark & Clapham 2004, Vu et al. 2012, Magnúsdóttir et al. 2014). It has been found that humpback whales from the same breeding population sing approximately the same song each year (Winn & Winn 1978, Winn et al. 1981, Payne & Guinee 1983, Noad et al. 2000). However, the song does change over time, both between seasons and within seasons (Noad et al. 2000, Cerchio et al. 2001, Eriksen et al. 2005, Garland et al. 2013). Differences in the song produced by whales in different breeding areas can help identify the wintering area from which the song originated, given previous knowledge of songs from that area (Winn et al. 1981, Helweg et al. 1998, Garland et al. 2013). This identification and tracking of songs is usually conducted at the phrase or theme level.

The use of passive acoustic monitoring (PAM) is becoming an increasingly common method for studying the occurrence, behavior, and movements of many marine mammal species, including humpback whales. While more traditional methods used in marine mammal research such as photo identification and genetic sampling are important, PAM data can be collected for long periods of time and over large spatial scales at relatively low cost and effort. This is especially true when compared to, for example, time and manpower intensive visual surveys. PAM provides a long-term data set that can be analyzed in a variety of ways (Zimmer 2011). In addition, the recorded data can be reanalyzed at later dates for other information such as shipping noise or presence of other species. However, a drawback of PAM is that it is currently very difficult or impossible to identify individual animals or determine certain characteristics of the sound source, such as source level or directivity. Unless a time-synchronized recording array is used together with knowledge of local oceanographic conditions, the location of an animal beyond its simple presence or absence in the area cannot be determined. Due to power and data storage constraints, most passive acoustic monitoring devices operate on a programmed duty cycle consisting of periods of recording separated by relatively longer periods of inactivity. Since humpback whale songs usually last about 15 minutes and song sessions may last several hours, full songs are rarely captured on these recorders. Instead, the recordings usually contain seconds or minutes of song in sound clips.

Because humpback whale song recorded on PAM devices rarely includes full songs, making comparison among different locations nearly impossible at the traditional level of song themes. Therefore a comparison of songs at the unit level is proposed. Research has been conducted to examine variations within humpback whale song units (Copeland et al. 2011). Characteristics of units appear relatively consistent, minimizing the chance of misclassifying a unit from a different individual, location, or time. This study reports on an effort to use PAM to examine humpback whale song in the Hawaiian archipelago in order to make comparisons between the songs produced in the MHI and the NWHI. Specifically, the hypothesis that NWHI may constitute a breeding area distinct from the MHI, based on the characteristics of songs recorded at various locations in the archipelago, is tested. Because of the remote location and difficulty in accessing the NWHI, a novel method of analyzing humpback whale song using the individual units recorded from duty-cycled PAM systems is attempted.

2.3 Methods

PAM data were obtained using Ecological Acoustic Recorders (EARs), which are digital underwater acoustic recorders with a programmable recording sample rate and duty cycle (Lammers et al. 2008). The EAR hydrophone has a sensitivity of -193.5 dB with relatively flat (+/- 3 dB) frequency response between 1 Hz and 28 kHz. Humpback whale song recordings were obtained at five locations in the NWHI and MHI (Figure 2.1). The three locations in the NWHI were at Lisianski Island, Maro Reef, and French Frigate Shoals. The two locations in the MHI were both off the island of Oahu at Makapu'u point, at the island's SE corner, and at Makua beach, along the island's NW coast. EARs were moored to the bottom at depths ranged between 12-24 m at the three NWHI sites and Makua beach, and 154 m at Makapu'u point (Table 2.1). Recordings from the NWHI were collected as part of a partnership program between the Hawaii Institute of Marine Biology (HIMB) and National Oceanic and Atmospheric Administration (NOAA) to investigate and monitor marine ecosystems in the PMNM (referred to hereafter as NWHI). Recordings from the MHI were obtained as part of a larger HIMB monitoring effort of marine mammal distribution around the island of Oahu.

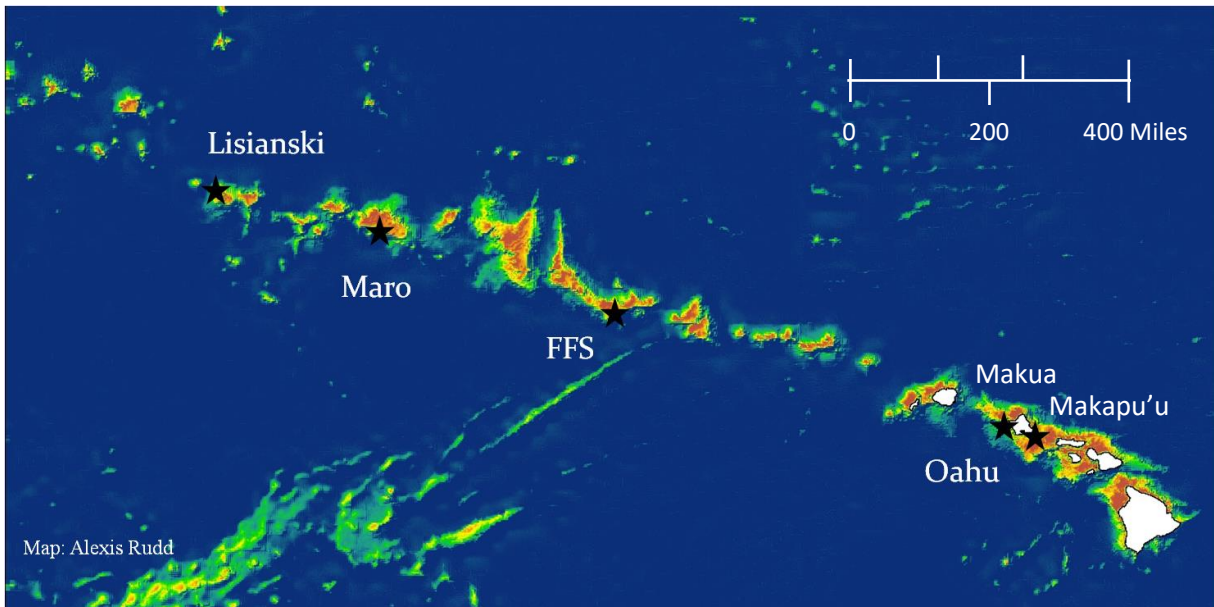


Figure 2.1: Map of EAR deployment locations with stars indicating location of recorders. FFS stands for French Frigate Shoal.

EAR recordings were made at varying sampling rates and recording periods due to the specific project goals of each deployment (Table 2.1). However, the recording bandwidth was sufficiently broad (either 20 kHz to 32 kHz depending on the deployment and sampling rate) to capture the frequency range of humpback whale song in all cases. Recordings were collected from January through May of 2009 at all locations. The Makua beach EAR was recovered once in February for refurbishment and then redeployed, with a loss of recording time of less than a couple days. The EARs were programmed to record on a duty cycle of 30 seconds every five minutes in the MHI where they could be refurbished frequently, and every 15 minutes in the NWHI in order to maximize the deployment period.

Each recording was processed through a custom MATLAB (MathWorks, Inc.) program that calculated the average root-mean-square of the sound pressure level (SPL_{rms}) of the file, the standard deviation, and the percentage of time in the file that tonal signaling was present. These metrics were considered likely indicators of whale song occurrence in the recordings. Of the three metrics calculated, the standard deviation of SPL_{rms} within a recording proved to be the best indicator of the presence of whale song with a high signal-to-noise ratio (SNR). A standard deviation of at least 5.0 dB in SPL_{rms} was set as the threshold for selecting good SNR files for

detailed song analysis. Recorded files were randomly selected from each location for analysis. If a selected file did not contain humpback whale song, it was discarded and another file was randomly selected to replace it. A total of 350 files with whale song were included in this study. All analyzed files were selected so that they were at least 15 minutes apart to prevent choosing recordings from the same part of a song, and to account for the different recording schedules used in the MHI and NWHI so no location was sampled at a higher rate.

Table 2.1: Sampling regime, location, and depth of each Ecological Acoustic Recorder

Location	Sample rate (Hz)	Sample duration (s)	Duty cycle (s)	Latitude	Longitude	Depth (m)
Makapu'u Point, Oahu	64000	30	300	21° 17.678 N	157° 33.392 W	154
Makua beach Oahu	50000	30	300	21° 31.919 N	158° 14.063 W	20
Lisianski, NWHI (LIS)	40000	30	900	26° 06.006 N	-173° 59.879 W	23
Maro Reef, NWHI (MAR)	40000	30	900	25° 25.174 N	-170° 40.148 W	12
French Frigate Shoals, NWHI (FFS2)	40000	30	900	23° 38.104 N	-166° 11.132 W	24

Recordings with high SNR song units were examined visually and aurally using Adobe Audition (Adobe Systems, Inc.) in order to identify and classify the units present. Units were classified based on characteristics such as dominant frequency, frequency modulation, and signal duration. A unit list was compiled by examining a preliminary group of randomly selected files. Out of the files determined to have good SNR, 60 were randomly selected from each NWHI location and 85 files were selected from each MHI location. The number of files selected was primarily due to the limited number of files with good SNR. All units in selected recordings were counted and classified except those cut off at the beginning and end of the file. If more than one whale was singing within a file, the units of the song with the highest SNR were counted by utilizing an experienced listener (J. Chen). All files were examined by one

experienced listener to ensure consistent categorization of units. If one individual's song could not be discriminated from the song of another whale within the file, that file was discarded and replaced by another randomly selected file.

The frequency of occurrence for individual song units was examined for patterns among locations. A cluster analysis was used to examine the relationship of song units between locations using MINITAB 14 (Minitab Inc.).

2.4 Results

The list of discretely identifiable units comprised 21 distinct categories, each given an arbitrarily assigned letter between A and W. All units were between 1 and 3 seconds in duration and the fundamental frequency range was between 100 Hz and 1000 Hz. Large amounts of variation were observed in the frequency of occurrence of units at each location (Table 2.2). The most common units encountered across all locations were units B, D, H, L, N, P, U, and V (Figure 2.2). Some units were rare at all locations. For example, units O and Q comprised less than 1% occurrence at each location. Other units including B and U occurred frequently at all locations comprising 23% and 19% respectively. Some units such as G and F were observed in the MHI but not the NWHI, while units L and P were more common in the NWHI than the MHI. Other units, such as unit N and V, showed differences in frequency of occurrence but no discernable patterns between locations.

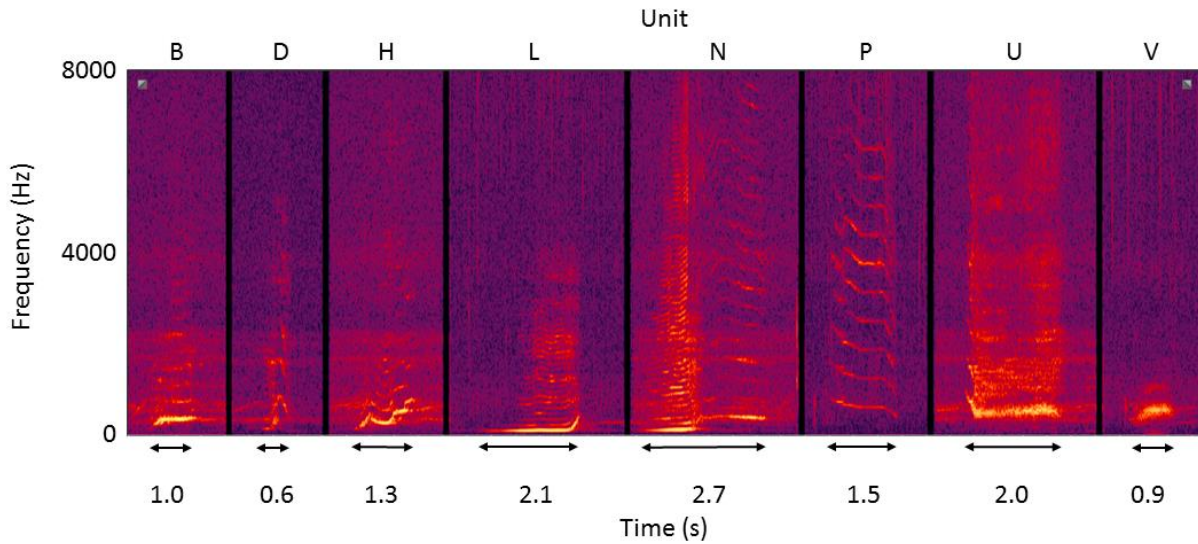


Figure 2.2: Spectrogram of representative examples of the eight most common units in all of the analyzed recordings: B, D, H, L, N, P, U, and V. Length of units is shown on the x-axis, the frequency is shown on the y-axis, and intensity of sound is represented by the brightness of the color.

The commonly occurring units B and D show a pattern of increasing frequency of occurrence when moving from the northwest locations along the archipelago to the southeast. Units L and P shows a contrasting pattern of decreasing occurrence when moving along the same path from northwest to southeast (Figure 2.3).

Table 2.2: Frequency of occurrence of units by location. Unit order is from overall most common to least common.

Unit	NWHI			MHI	
	Lisianski	Maro	FFS2	Makua	Makapu'u
B	14.5%	13.3%	28.1%	26.5%	28.5%
U	18.9%	17.7%	13.2%	19.0%	22.9%
L	26.2%	27.4%	22.6%	10.2%	6.5%
P	13.2%	17.4%	8.3%	5.1%	2.9%
H	3.3%	5.4%	5.0%	4.8%	4.8%
N	2.8%	6.1%	5.5%	6.2%	2.9%
V	8.3%	1.2%	2.6%	5.8%	3.2%
D	0.0%	0.0%	1.5%	5.5%	8.8%
C	0.7%	3.0%	2.6%	2.0%	4.0%
T	4.6%	2.0%	0.2%	0.3%	1.9%
G	0.0%	0.0%	0.0%	3.0%	3.4%
J	1.1%	1.2%	2.2%	1.8%	1.3%
W	3.1%	0.8%	0.8%	2.1%	0.6%
R	0.7%	0.9%	1.8%	1.5%	1.6%
A	0.5%	0.6%	2.3%	1.1%	1.7%
K	0.7%	1.7%	1.0%	1.3%	0.5%
M	1.0%	0.6%	1.7%	0.7%	1.1%
E	0.3%	0.3%	0.2%	1.3%	1.0%
F	0.0%	0.0%	0.0%	1.1%	1.3%
O	0.0%	0.0%	0.3%	0.7%	0.6%
Q	0.3%	0.5%	0.2%	0.1%	0.6%

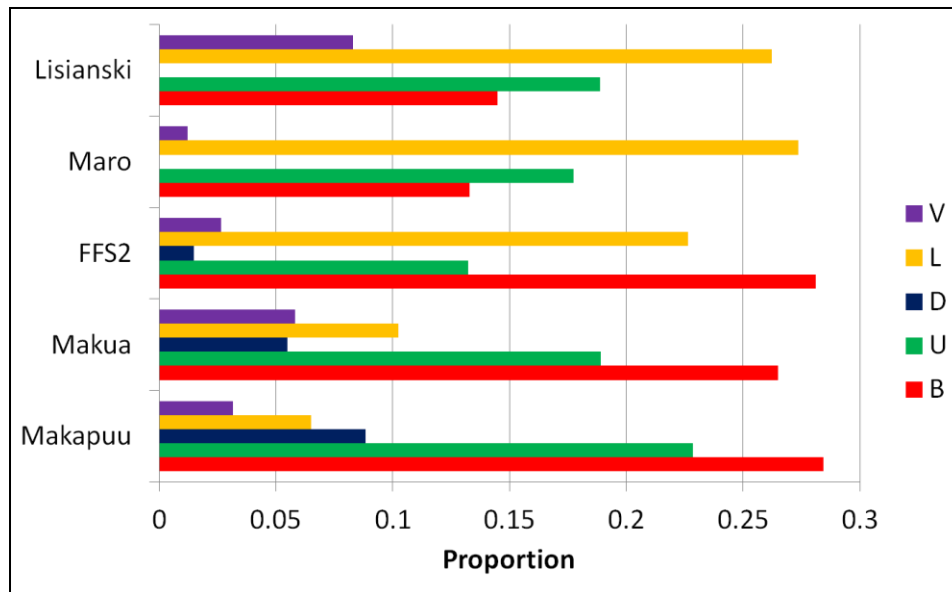
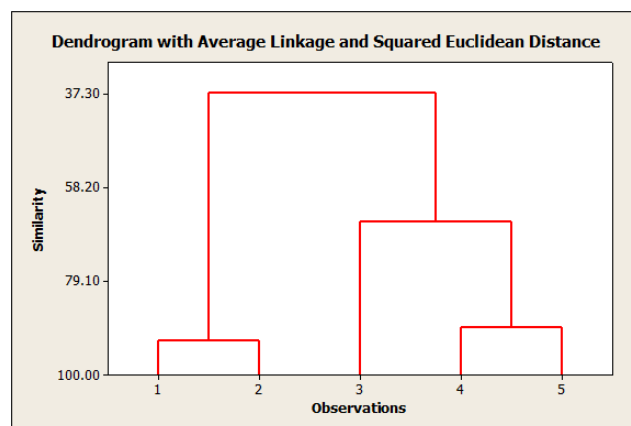


Figure 2.3: Relative frequencies of occurrence of five common song units showing differences between geographic locations. Lisianski is furthest to the northwest, moving geographically to Makapu'u to the southeast.

A cluster analysis was used to compare the song unit frequency of occurrence between the five locations. The dendrogram of results show that the two MHI locations are most similar. The three NWHI locations also group together, with Lisianski Island and Maro reef most similar, followed by French Frigate Shoals, before connecting to the MHI locations (Figure 2.4).

Figure 2.4: Dendrogram showing average linkage and squared Euclidean distance: 1- Makapu'u point (MHI), 2-Makua beach (MHI), 3-French Frigate Shoals (NWHI), 4- Maro reef (NWHI), 5-Lisianski Island (NWHI).



2.5 Discussion

These results, based on the more common units, suggest that there may be a geographical gradient in the frequency of occurrence of song units produced by male humpback whales in the MHI and NWHI during the winter of 2009. This indicates that there may be differentiation between the songs sung by whales in the MHI compared to the NWHI. Observed differences appear to occur along a geographic gradient, with increasing or decreasing unit frequency of occurrence from the MHI to NWHI or vice versa, and show no distinctive major differences between locations. As such, the results may suggest a population large enough to contain a large amount of variation in song units while not comprising of two separate breeding populations. Two populations would be expected to show more distinct differences in the frequencies of units utilized by the singers.

The large number of units identified and the high amount of variation in frequency of occurrence between units make it difficult to compare among locations. This may be due to the inherent flexibility of humpback whale songs. Humpback whale song is known to change throughout the breeding season at varying rates each year (Noad et al. 2000, Cerchio et al. 2001, Garland et al. 2013). No full songs from the 2009 season were obtained during this study, nor were they available from other researchers at these sampling locations. Therefore, it is unknown if the song changed drastically in content over the course of the season. While the data analyzed here spanned from January to May 2009, a temporal analysis to examine changes over time was not conducted due to the limited number of recordings with high SNR in the data set. If, for example, the song changed faster in the NWHI and slower in the MHI and ended with different songs, the difference in rate of change could not have been captured in the analysis. The analysis could be strengthened if the data set could be subdivided into smaller time periods to reduce variability due to temporal changes in song. In addition, because no full songs were recorded, there is no way to determine if the song units were well represented by the analysis. The identity of singing individuals cannot be determined from the data collected. Since the data set characterizes song for the local population as a whole, this should not present a problem. In addition, due to the frequent movement of male humpback whales between islands, it is unlikely that recordings of song from a particular individual could dominate the song analyzed for a

particular location. There is also no way to determine if the NWHI are utilized as a migration corridor rather than a wintering ground, and therefore possibly capturing songs different from those sung in the wintering grounds. As acoustic analysis technology improves, it may be possible in the future to identify individuals based on their sound characteristics.

One of the challenges of the study was the labor intensive and subjective nature of identifying units. Analysis tools for automatic detection and classification of signals have made significant progress in the last few years (Rickwood & Taylor 2008, Helble et al. 2012, Helble et al. 2013, Ou et al. 2013). However, significant challenges still remain; in order for these programs to run effectively, they require not only high SNR, but also work best when a single individual is recorded. Ou et al. (2013) tested the automated detector and classifier on a subset of these recordings, and it was able to identify approximately the same number of units with some adjustment of the parameters. Some units identified separately in this study were grouped together by the detector. However, the detector had trouble in some instances where two humpbacks were singing simultaneously, causing one unit to overlap; the detector classified this as a novel unit while the listener was able to identify it as two separate units. This data set contains a large amount of chorusing in the background, which may prevent it from being a good candidate for analysis using current automated detectors.

The results presented here suggest that there is a need for additional genetic and/or photo identification studies to determine the population structure of humpback whales in the Hawaiian Archipelago. For a better understanding of the variations in song between North Pacific wintering areas, data from other populations in the same season are needed.

In conclusion, the results of this study suggest that the humpback whales wintering in the Northwestern and Main Hawaiian Islands are part of a continuous population that is actively undergoing song evolution. Though humpbacks have not been observed to travel between the NWHI and MHI, the similarity in song units suggest a connection between the locations. However, this hypothesis requires further testing to more conclusively determine whether the differences observed in song are confounded by sampling artifacts or represent natural local variations. If the Hawaiian humpback whales are traveling among the islands in one direction consistently, for example from the MHI up through the NWHI before returning north to Alaska, this could conceivably result in differences seen in song unit frequencies. This would depend on

a gradual change in the song over the course of the breeding season. However, if individuals consistently travel in both directions along the archipelago using the NWHI as a migration corridor as suggested by Cerchio et al. (1998), the pattern is less likely to be observed because this type of movement would presumably lead to the frequency of units averaging out among locations over the breeding season. Due to lack of historical records about humpback whale movements and the extreme remoteness of the NWHI, there is a dearth of information on key aspects of humpback whale habitat use in the NWHI. It is unknown if whales give birth in the area, how long they may stay, or the male to female ratio. This study presents a novel method of gaining preliminary information about humpback whale song in remote areas. Ideally, it will be used in conjunction with other methods such as genetic, photo-identification, or tracking studies to provide a more complete picture of the whales' behavior and movements in the NWHI. In addition, future studies should prioritize the recording of full songs for comparison between the MHI and NWHI as well as the other breeding grounds of Mexico and Philippines in the North Pacific.

CHAPTER 3

Spatial and temporal changes in soundscape around the island of Kauai, Hawaii

3.1 Abstract

Humpback whales are prevalent throughout the Hawaiian Archipelago during the winter season. Five autonomous recorders were deployed around the island of Kauai over the course of about two years. The recordings were analyzed to determine the amount of sound present during the humpback whale season and non-season, and differences between day and night. Results for the five locations showed an average of 6 dB increase in sound levels while humpback whales were present during the winter season, as opposed to during summer. Four out of five locations also showed a diurnal pattern in sound pressure levels, with sound levels during the daytime significantly higher than at nighttime during the winter season. The daytime hourly peak sound levels varied across locations with variable amounts of increase. The increased sound levels during humpback season may be caused in part by humpback whale chorusing. The diel pattern may reflect daily movement inshore during the night and movement offshore during the daytime by the whales.

3.2 Introduction

Humpback whales (*Megaptera novaeangliae*) are a cosmopolitan species that migrate annually between feeding grounds in the high latitudes and breeding grounds in the low latitudes (Baker et al. 1986, Clapham 1996, Smith et al. 1999, Calambokidis et al. 2008, Schmitt et al. 2014). The North Pacific population of humpback whales feed in the nutrient rich waters of Alaska, British Columbia, Russia, and the United States West Coast from Washington to California in the summer and breed and calve in the warm waters off Hawaii, Japan, Mexico, and Philippines (Darling & McSweeney 1985, Calambokidis et al. 2001, Calambokidis et al. 2008). Of the North Pacific population, approximately half are estimated to overwinter in the Hawaiian breeding grounds (Calambokidis et al. 2008).

While in the breeding grounds, humpback whales tend to separate into groups based on behavior and sex. This chapter focuses on the distribution of male singers, which are usually alone but may also accompany a mother-calf pair (Tyack 1981, 1983, Darling et al. 2006) and tend to utilize near-shore areas more than deeper areas (Frankel et al. 1995a). The distribution of singers has not been studied as intensively as maternal females with calves, which usually isolate themselves and their newborn calves in shallow waters (Smultea 1994, Craig & Herman 2000, Ersts & Rosenbaum 2003, Félix & Botero-Acosta 2011, Craig et al. 2014). These mother-calf groups may be joined by a single male escort or joined by multiple escorts creating a competitive group (Mobley Jr & Herman 1985, Smultea 1994, Félix & Botero-Acosta 2011, Craig et al. 2014). Other types of groups include competitive or surface active groups in deeper waters where mature females are pursued by males presumably for mating opportunities (Tyack & Whitehead 1983, Baker & Herman 1984, Mobley Jr & Herman 1985, Clapham et al. 1992, Smultea 1994, Clapham 1996), and dyads composed of two adult whales, either a male-male or male-female pair (Mattila & Clapham 1989, Clapham et al. 1992, Herman et al. 2011).

Humpback whales produce a variety of sounds on their wintering grounds, feeding grounds, and along migration routes. These include non-vocal sounds from impacts such as breaching and tail slaps (Thompson et al. 1986, Dunlop et al. 2008, Dunlop et al. 2013), as well as non-song vocalizations called “social sounds” (e.g. Silber 1986, Thompson et al. 1986, Dunlop et al. 2007, Zoidis et al. 2008). The most thoroughly studied sounds are male humpback whales’ complex “songs.” First described by Payne and McVay (1971), songs consist of a loud,

structured, and ordered series of hierarchically organized vocalizations that may be repeated by individuals for hours (Winn & Winn 1978, Helweg et al. 1992, Helweg et al. 1998). Humpback whales were recorded singing in Alaskan waters starting in November, prior to their migration to their wintering grounds (Mattila et al. 1987, McSweeney et al. 1989). Much of the early work on humpback whale song was devoted to describing the structure and comparing between breeding grounds (e.g. Payne & McVay 1971, Winn & Winn 1978, Winn et al. 1981, Payne & Guinee 1983, Payne & Payne 1985, McSweeney et al. 1989). Since then, research on humpback whale song has expanded from continuing studies on the evolution of song (Garland et al. 2013, Darling et al. 2014), to describing song on feeding grounds (Stimpert et al. 2012b, Vu et al. 2012, Magnúsdóttir et al. 2015), and developing automated detection and classification algorithms (Abbot et al. 2012, Helble et al. 2013, Ou et al. 2013, Helble et al. 2015).

The unit is defined as the shortest continuous sound in a song as distinguished by the human ear (Payne & McVay 1971) and patterned repetitions of units form the song. Source levels (SL) of song units have been directly measured relatively recently (Frankel 1994, Au et al. 2006). Au et al. (2006) reported song unit SL between 144 and 173 dB re 1 μ Pa using a hydrophone array deployed in front of a singing whale. Frankel (1994) reported SL from 140 to 170 dB re 1 μ Pa using an array of hydrophones with whales 2 to 8 km away. These songs can be heard many kilometers away depending on the sound propagation conditions (Frankel 1994, Clark & Clapham 2004, Helble et al. 2015). While in the breeding grounds, it is common for multiple males both mature and immature to sing asynchronously day and night, and this cacophony of song has been termed “chorusing” (Helweg & Herman 1994, Au et al. 2000, Herman et al. 2013). Due to the large number of singing humpback whales, the chorusing contributes a significant amount of sound to the acoustic environment in the breeding grounds (Au et al. 2000) and has been suggested as a method to estimate relative abundance of male humpbacks.

Other species of cetaceans, such as the migratory blue and fin whales, also demonstrate seasonal patterns of sound production (e.g. Wiggins et al. 2005, Mellinger et al. 2007, Oleson et al. 2007, Stafford et al. 2007, Munger et al. 2008). Some species also show diel patterns of sound production that may be linked to foraging and socializing activity (e.g. Goold 2000, Carlström 2005, Wiggins et al. 2005, Mellinger et al. 2007, Arranz et al. 2011). Recordings of

cetacean vocalizations can be used to track habitat use by providing information about foraging activity (Carlström 2005, Arranz et al. 2011, Au et al. 2013, Au et al. 2014), presence in an area including migration routes (e.g. Dawbin & Gill 1991, Dunlop et al. 2007, Stafford et al. 2007, Munger et al. 2008), and to estimate population density (McDonald & Fox 1999, Marques et al. 2009, Kyhn et al. 2012). Though population density estimation is beyond the scope of this paper, the distribution of singing humpback whales is examined using sound levels of humpback whale song recorded around the island of Kauai. The objective is to determine if there is a diel or spatial pattern in humpback whale song chorusing around Kauai. This will increase knowledge about habitat use by singers around one of the less-studied islands (most studies have been conducted off Maui and the Island of Hawaii), including the less studied windward side of the island. This provides a better understanding of areas important to male humpback whales, which may be different from biologically important areas for maternal females and their calves.

3.3 Methods

3.3.1 Deployments

Ecological Acoustic Recorders (EARs) (Lammers et al. 2008) were deployed around the island of Kauai, Hawaii at five locations labeled N, NE, NW, SE, and SW (Figure 3.1) at approximately 600 to 700 m depth with the exception of location N deployed at approximately 400 m depth. The EARs recorded data during five non-continuous deployments between February 2009 and January 2011 (Table 3.1). Not all locations and months are represented equally due to equipment malfunction or a loss of equipment at sea (Table 3.1).

EAR recorders were programmed to record for 30 seconds in each sampling period of 300 seconds (5 minutes). The sample rate (SR) of deployments 1 and 2 was 64 kHz and the sample rate of deployment 3, 4, and 5 was 80 kHz. The high sample rate was selected for the purpose of studying odontocete habitat use and the difference in SR occurred following an update in software. In order to eliminate high frequency energy from other species and environmental noise, and to standardize the sample rate, all data files were decimated (down-sampled) to a 4 kHz sample rate using a custom script in MATLABTM program. This sample rate was chosen so most acoustic energy from humpback whale vocalizations would be included while minimizing other sound sources.

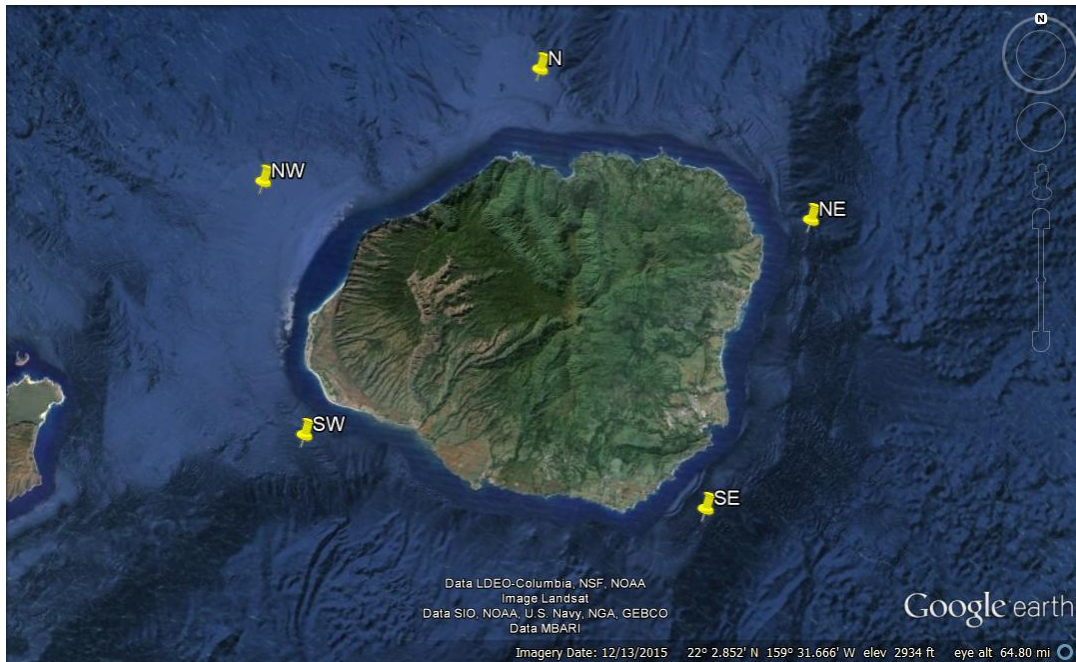


Figure 3.1: Map of the five Ecological Acoustic Recorder (EAR) deployment locations around the island of Kauai, Hawaii. Locations named N, NW, NE, SW, and SE. Five deployments occurred from 2009 to 2011.

3.3.2 Analysis

A custom MATLAB™ program converted the binary files from voltage to pressure and calculated the root mean square sound pressure level (SPLrms) for each file. The SPLrms was calculated using the following equation, where n is the number of points (samples) in the file and p is the pressure in μPa at each sample point in the file:

$$SPL_{rms} = 20 \log_{10} \sqrt{\frac{1}{n} \sum p^2}$$

An average of the SPLrms values within each hour was calculated so that one value was provided for each hour of each day. This was done so the averaged levels represent the SPL in each hour and in an effort to minimize the effects of transient sound sources such as boats passing by. The humpback whales were expected to be a consistent sound source accounting for a significant amount of the recorded SPL during humpback whale season. For the purposes of

this study and after a preliminary look at the data, humpback whale season was considered to occur from January through April in Hawaii.

All statistical tests were conducted using R 3.2.3 (R Core Team 2015). A generalized additive model (GAM) tested the relationship between date and daily average SPL by location using the “mgcv” package (Wood 2006). The relationship is defined in the following equation, where α is the intercept, i corresponds to the five locations (N, NE, NW, SE, SW), and ϵ is the error:

$$\text{SPL.Mean}_i = \alpha + f_1(\text{Julian.date}_i) \times \text{Location}_i + \text{Location}_i + \text{Year}_i + \epsilon_i$$

An analysis of variance (ANOVA) from the “car” package in R (Fox & Weisberg 2011) was used to test the difference in SPL during humpback season and non-humpback season by location. The month of March was used to represent humpback season and August represented non-humpback season to avoid the gradual change in SPL between seasons and to minimize effects from different sample sizes.

From a closer examination of SPL during humpback season, the months of February and March were selected to test for differences between daytime and nighttime. These months were selected because not all location contained data from January and all locations showed different patterns of increase or decrease in SPL during January and April as whales arrived and departed. Since it was suspected that sound levels change in a cyclical manner over the course of a day, the relationship between location and hour of day was tested in R using a GAM as previously described. The relationship is defined by the following equation, where α is the intercept, i corresponds to the five locations (N, NE, NW, SE, SW), and ϵ is the error:

$$\text{SPL}_i = \alpha + f_1(\text{hour}_i) \times \text{Location}_i + \text{Location}_i + \text{Year}_i + \epsilon_i$$

The effect of time of day (TOD), categorized as “day” or “night” during the humpback season and non-season (day=7:00 through 18:00, night=0:00 through 6:00 and 19:00 through 23:00), was tested for each location using an ANOVA. A mean SPL was calculated for “day” and “night” for each day and location. In order to avoid the transition hours at sunrise and sunset, an ANOVA was also conducted with “day” being hours 10:00 through 15:00 and “night” being the hours 0:00 through 3:00 and 22:00 through 23:00.

3.4 Results

EARs recorded data during five non-continuous deployments between February 2009 and January 2011 (Table 3.1). Due to an equipment malfunction, the SW EAR failed to record during deployment 2 between June and September 2009. EAR N failed to return to the surface after deployment 3 in May 2010 and was not replaced after being lost at sea. Therefore no data was collected at location N after September 2009. EAR NW failed to return to the surface after deployment 5 in January 2011, so no data were collected after September 2010. The deployments resulted in a total of 564071 recordings. The SPL for each hour was averaged for a total of 47034 observations across all locations and deployments.

Table 3.1: EAR deployment location, start date and time, and end date and time. EARs that failed to record or were not recovered are noted.

Deployment	Location	Start Date	Start time	End Date	End Time
1	N	2/10/2009	12:00:00	6/6/2009	3:35:01
1	NE	2/10/2009	12:00:00	5/19/2009	7:00:02
1	NW	2/10/2009	12:00:00	5/24/2009	12:50:02
1	SE	2/10/2009	12:00:00	3/6/2009	14:20:02
1	SW	2/10/2009	12:00:00	5/28/2009	11:10:02
2	N	6/9/2009	16:00:00	9/24/2009	8:05:02
2	NE	6/9/2009	13:00:00	9/29/2009	1:20:02
2	NW	6/9/2009	19:00:00	9/22/2009	18:35:03
2	SE	6/10/2009	12:00:00	9/25/2009	14:40:02
2	SW	malfunction, did not record			
3	N	did not release/return to surface – no replacement			
3	NE	1/25/2010	0:00:01	5/3/2010	9:16:50
3	NW	1/25/2010	0:00:01	5/3/2010	8:45:04
3	SE	1/26/2010	0:00:01	5/4/2010	9:10:04
3	SW	1/26/2010	0:00:02	5/4/2010	9:10:04
4	NE	6/13/2010	0:00:01	9/19/2010	5:20:02
4	NW	6/14/2010	0:00:00	9/20/2010	8:15:03
4	SE	6/13/2010	0:00:01	9/19/2010	8:30:02
4	SW	6/14/2010	0:00:00	9/20/2010	8:15:03
5	NE	10/20/2010	0:00:01	1/26/2011	2:20:03
5	NW	did not release/return to surface			
5	SE	10/21/2010	0:00:02	1/27/2011	9:00:04
5	SW	10/20/2010	0:00:01	1/26/2011	8:30:03

3.4.1 Seasonal effects

The generalized additive model (GAM) showed that daily average SPL was predicted by Julian date at each location ($F = 213$, $p < 0.001$) but not year ($F = 4$, $p = 0.06$), and that the smoothers for all locations significantly explained 70.5% of the variation. The smoothers for each location were significant (N: $F = 101$, $p < 0.001$; NE: $F = 57$, $p < 0.001$; NW: $F = 113$, $p < 0.001$; SE: $F = 19$, $p < 0.001$; SW: $F = 77$, $p < 0.001$) and showed similar though not identical patterns of change throughout the year. An overall pattern of higher SPL during the humpback season from January through April and lower SPL during May through December is visible, with the exception of NE and SE (Figure 3.2). Locations SE and NE each have a subset of data showing SPL during summer at higher levels, though the SPL shows little variation during those time periods. A possible explanation for this will be provided in the discussion. Of interest is the gradual increase in SPL during December for the SW location and during January for NE. All locations showed a decrease in SPL starting in April, though the rate of decrease varies across locations.

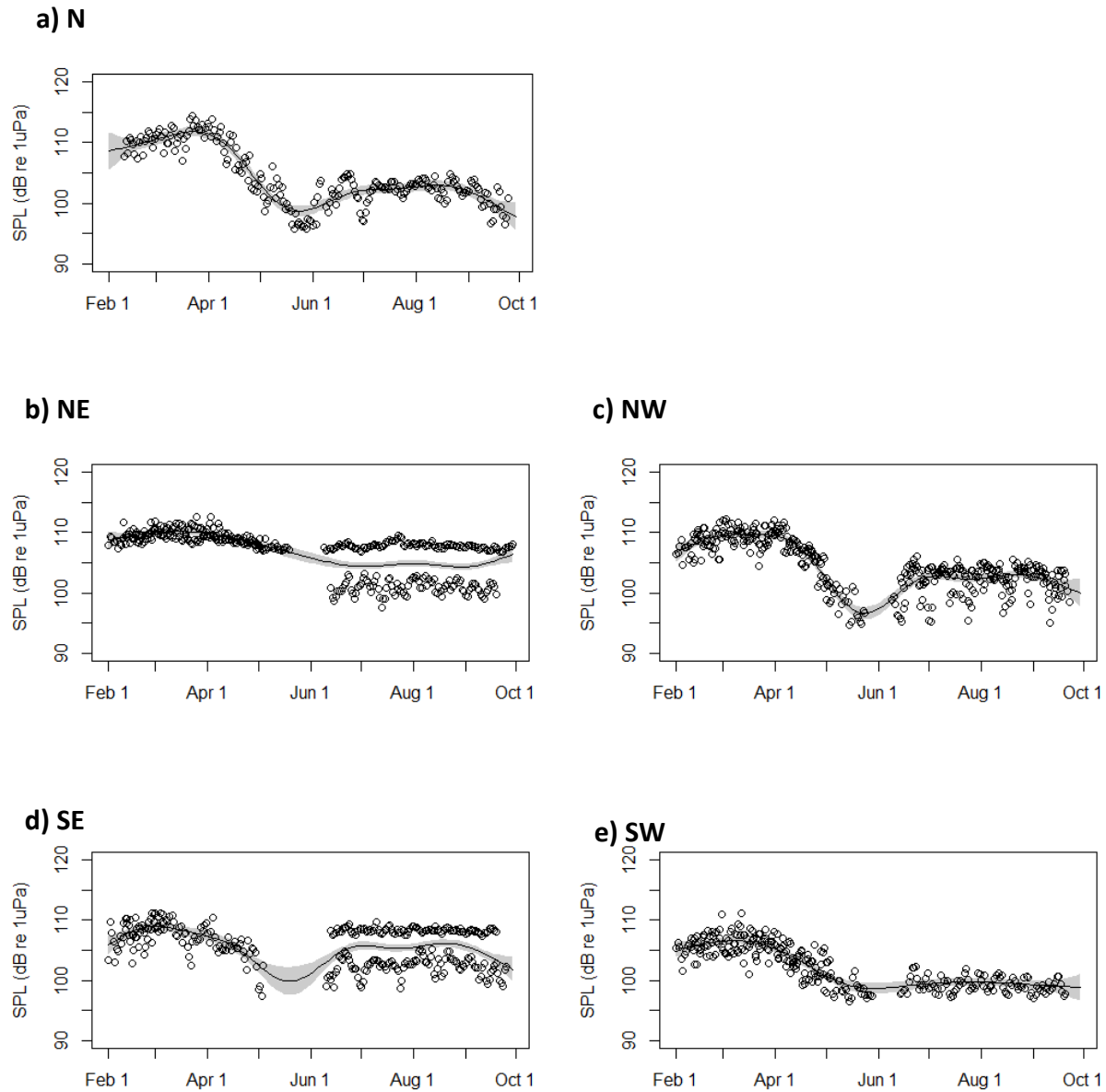


Figure 3.2: Plots of generalized additive model (GAM) smoothers showing the daily average SPL in dB re $1\mu\text{Pa}$ throughout the year for each location: a) N, b) NE, c) NW, d) SE, and e) SW. Smoothers for all locations are significant (Table 2). Grey shading represents two times the standard error for each smoother and the points represent the residuals.

Table 3.2: Generalized additive model (GAM) smoothers for the daily average SPL against date by locations N, NE, NW, SE, and SW. The table includes the estimated degrees of freedom for the model terms (edf), the F-value, and associated p-value. Significant p-values are defined as $p < 0.05$.

Smoother for date	edf	F value	p-value
Location N	7.946	100.57	<0.001
Location NE	7.110	57.00	<0.001
Location NW	8.734	113.01	<0.001
Location SE	8.649	18.88	<0.001
Location SW	6.225	76.50	<0.001

Using March and August as representative months for humpback season and non-season, an ANOVA was conducted to test for differences in SPL between season and location. The season ($F(1, 492) = 985.931, p < 0.001$), location ($F(4, 492) = 78.102, p < 0.001$), and the interaction between location and season ($F(4, 492) = 24.434, p < 0.001$) were all significant, therefore the SPL was significantly different between seasons and between locations. The average difference between season and non-season was 6 dB (Figure 3.3). During humpback season, higher SPLs were generally recorded to the north of Kauai than to the south and a post-hoc Tukey test showed that N, NE, and NW locations were significantly different from the SE and SW locations ($p < 0.01$) with the exception of NW-SE ($p = 0.16$). No pattern was discerned during non-humpback season, and the pattern is obscured when examining SPL at the locations when season and non-season SPL are combined (Figure 3.4). This may be due to the large variance seen in locations NE and SE, possibly due to different deployments. The difference between the means for season and non-season varied by location, ranging from a minimum of 2.6 dB at the SE location to a maximum of 8.7 dB at N location (Figure 3.5).

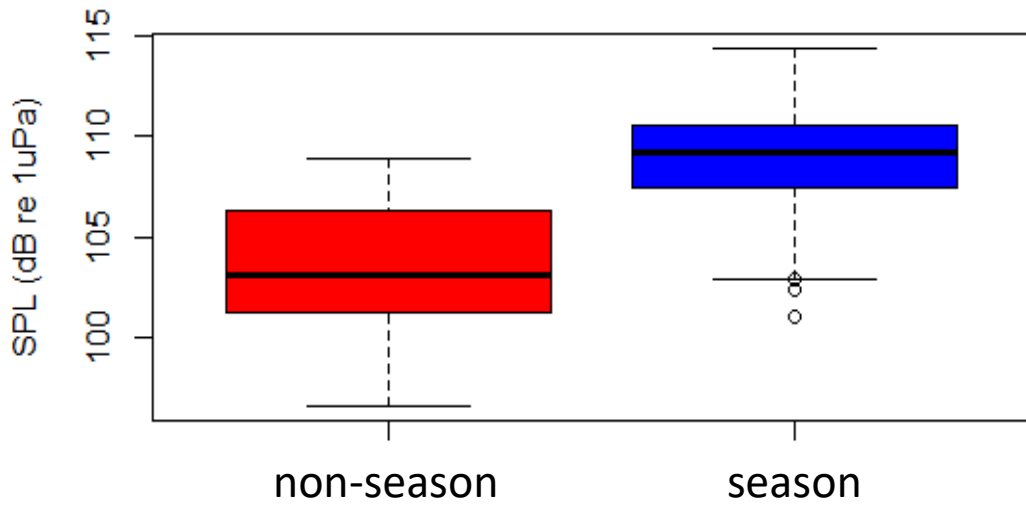


Figure 3.3: Box plot of sound pressure level (SPL) at all locations during humpback season (March) and non-humpback season (August). Brackets are 25% and 75% quartiles.

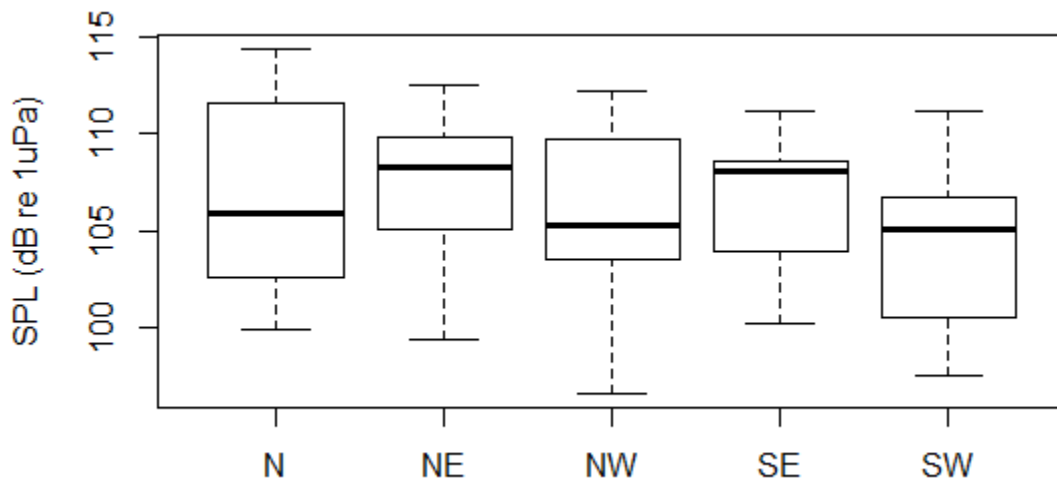


Figure 3.4: Box plot of sound pressure level (SPL) at each location during combined humpback and non-humpback season. Brackets are 25% and 75% quartiles

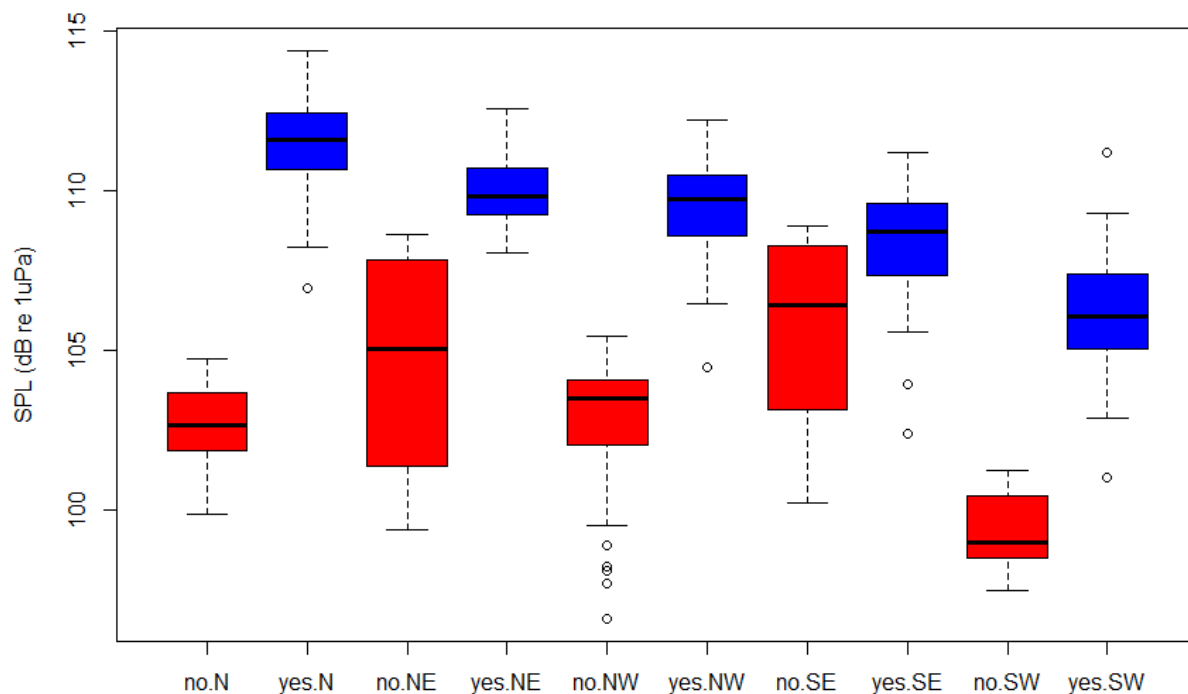


Figure 3.5: Box plot of sound pressure level (SPL) at each location during March (“yes” humpback season) and August (“no” humpback season). Brackets are 25% and 75% quartiles. Red boxes represent August and blue boxes represent March.

3.4.2 Time of day effects

Based on results presented above and previous studies, humpback whales and song are most prevalent from February to March. Therefore, in order to examine differences between day and night due to humpback chorusing, the months of January and April were excluded to reduce the possible confounding effects of fewer whales contributing to SPL in January and April. The GAM results showed that the change in SPL over time was predicted by hour of day for each location (N: $F = 18.89$, $p < 0.001$; NE: $F = 18.81$, $p < 0.001$; NW: $F = 24.62$, $p < 0.001$; SE: $F = 6.19$, $p < 0.001$; SW: $F = 107.43$, $p < 0.001$) and location ($F = 896.1$, $p < 0.001$), with smoothers explaining 31.7% of the deviance. The smoothers for every location were significant at $p < 0.001$ (Table 3.3). Each location, however, showed different patterns of change across hour (Figure 3.6). All locations except SE showed an increase in SPL during the daytime hours although the change is small at the NE location. The SE location showed two periods of increased SPL around hours 7 and 8. SPL was highest at location N while the lowest SPL was at

location SW. The maximum hourly SPL occurred at different times of day at each location. Location N peaked at approximately hour 8, location NE at hour 10, location NW was highest at hour 7 and hour 18, location SE at hour 7, and location SW at hour 14.

Table 3.3: Generalized additive model (GAM) smoothers for the change in sound pressure level (SPL) by hour and locations N, NE, NW, SE, and SW during humpback season. The table includes the estimated degrees of freedom for the model terms (edf), the F-value, and associated p-value. Significant p-values are defined as $p < 0.05$.

Smoother for hour	edf	F value	p-value
Location N	7.602	18.889	<0.001
Location NE	4.715	18.810	<0.001
Location NW	7.038	24.627	<0.001
Location SE	7.227	6.187	<0.001
Location SW	8.255	107.430	<0.001

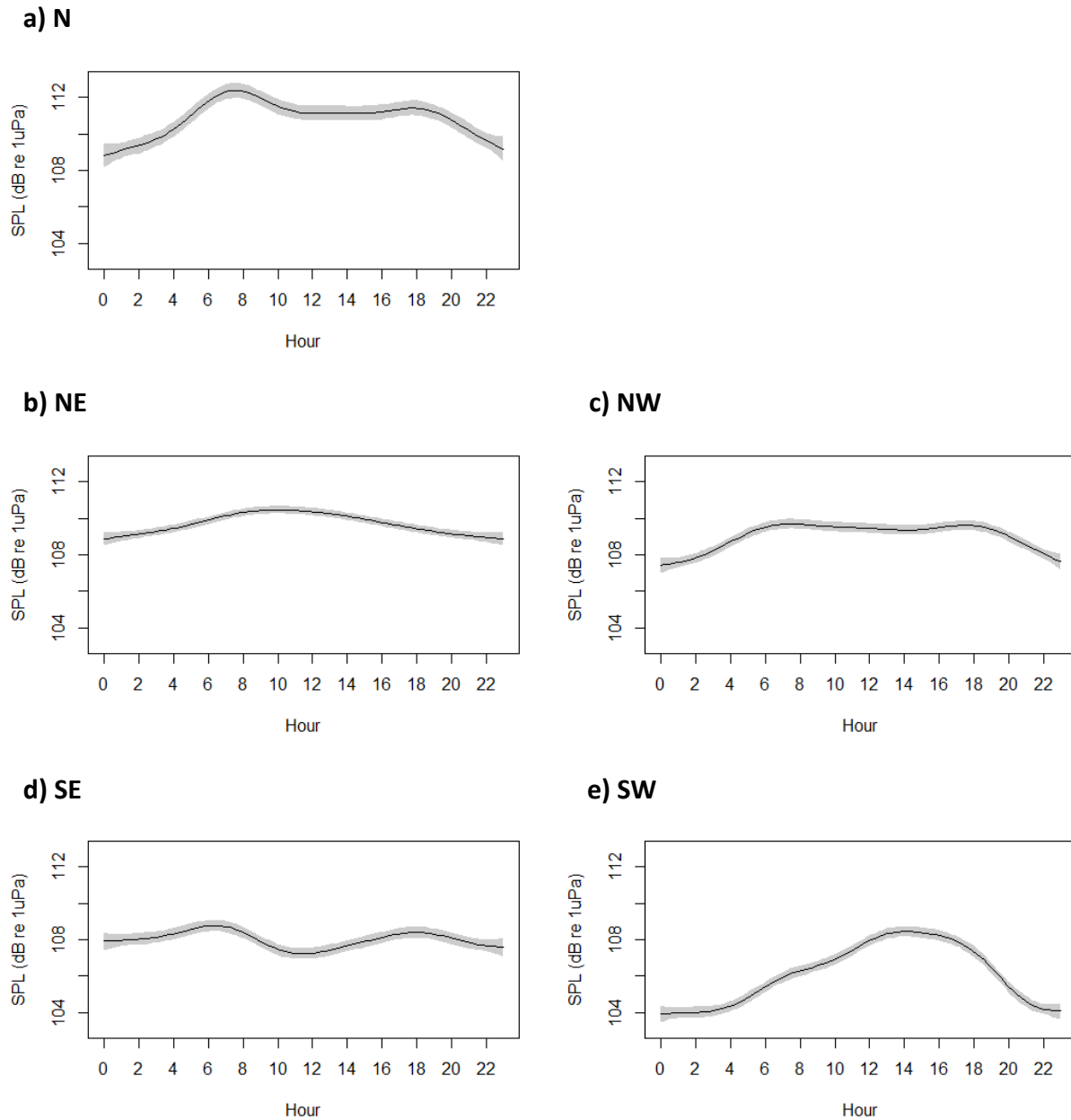


Figure 3.6: Plots of generalized additive model (GAM) smoothers showing the hourly SPL in dB re 1µPa throughout the hours of the day for each location during February and March for humpback season: a) N, b) NE, c) NW, d) SE, e) SW. Smoothers for all locations are significant. Grey shading represents standard error for each smoother.

An ANOVA was used to test for differences in SPL due to time of day (TOD) and location. TOD ($F(1,912) = 106.178$; $p < 0.001$), location ($F(4, 912) = 154.126$; $p < 0.001$), and the interaction between TOD and location ($F(4, 912) = 17.279$; $p < 0.001$) were all significant. The mean SPL was higher during “day” (hours 7:00 to 18:00) than night (hours 0:00 to 6:00 and 19:00 to 23:00) for each location except SE which had higher SPL during the nighttime (Table 3.4). A post-hoc Tukey test reveals that day and night differences are significant for every location except SE (N $p = 0.009$, NE $p = 0.01$, NW $p < 0.001$, SE $p = 0.999$, SW $p < 0.001$). The range of values is relatively large compared to the difference in means, likely due to the gradual change in SPL over the hours (Figure 3.6). However the standard error is small resulting in significant results when testing for difference between day and night (Table 3.4).

The same test was run with “day” restricted to hours 10:00 to 15:00 and “night” restricted to hours 22:00 to 3:00 to avoid the transition hours of sunrise and sunset and the same results were obtained. TOD ($F(1, 912) = 140.427$; $p < 0.001$), location ($F(4, 912) = 105.899$; $p < 0.001$), and the interaction between TOD and location ($F(4, 912) = 25.687$; $p < 0.001$) are all significant. The mean SPL shows similar patterns to the previous test with all hours included. The post-hoc Tukey test also shows the same result, with significant difference between day and night at each location except SE (N $p = 0.001$, NE $p = 0.002$, NW $p < 0.001$, SE $p = 0.878$, SW $p < 0.001$). Overall sound levels are higher to the north side of Kauai and lowest in the SW.

Table 3.4: List of mean sound pressure level (SPL) re 1 μ Pa and standard error (se) for each location during humpback season. Mean is the top number and se the bottom number in each box, with daytime (hours 7:00 through 18:00) in the left column and nighttime (hours 0:00 through 6:00 and 19:00 through 23:00) on the right column.

Location	Mean SPL (dB re 1 μ Pa) day \pm se	Mean SPL (dB re 1 μ Pa) night \pm se
N	111.4519 0.3438758	110.0558 0.220354
NE	110.1226 0.1407685	109.1879 0.08849092
NW	109.5035 0.1937572	108.4165 0.1645163
SE	107.9155 0.2698494	108.1157 0.2241973
SW	107.4989 0.211363	104.5830 0.1789931

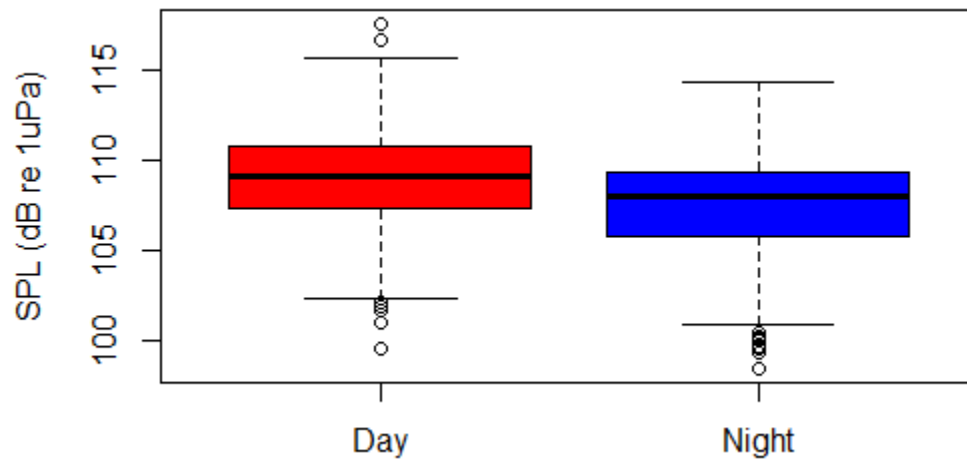


Figure 3.7: Box plot of mean sound pressure level (SPL) of all locations during day and night of humpback season. Brackets are 25% and 75% quartiles.

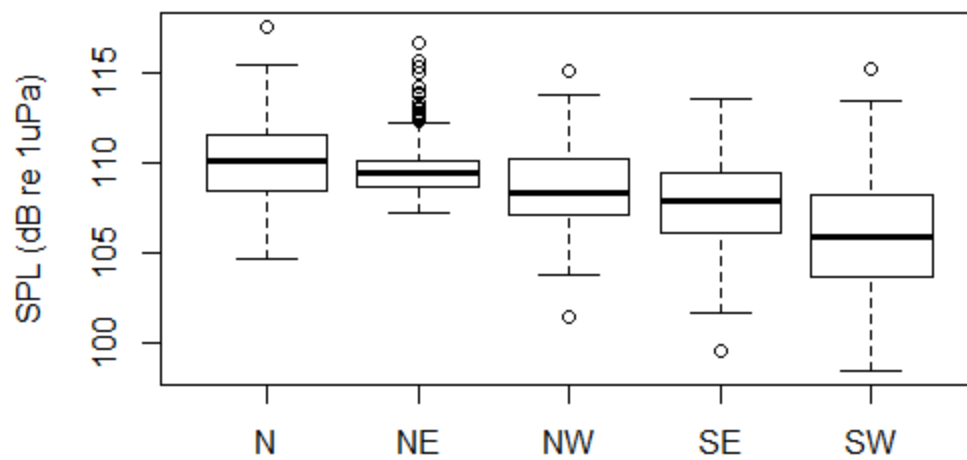


Figure 3.8: Box plot of mean sound pressure level (SPL) at each location during all hours of humpback season. Brackets are 25% and 75% quartiles.

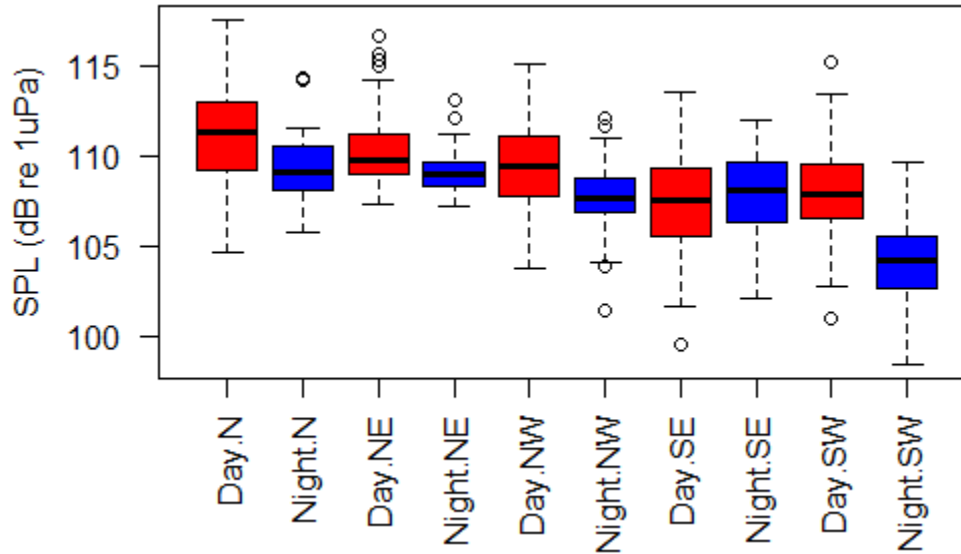


Figure 3.9: Box plot of sound pressure level (SPL) at each location during “day” (hours 10:00 through 15:00) and “night” (hours 0:00 through 3:00 and 22:00 through 23:00) during humpback season. Day SPL are higher than night SPL except for location SE. Brackets are 25% and 75% quartiles. Red boxes represent day and blue boxes represent night.

During the non-humpback season, represented by July and August, there was no significant difference in SPL between day and night. The GAM smoothers explained 33.1% of the deviance, and locations were significant in predicting SPL ($F = 1315$, $p < 0.01$). The smoothers for every location except NE ($p = 0.12$) were significant at $p < 0.001$ (Table 3.5). Locations NW and SW showed changes in SPL across hours, while the remaining locations showed little change in SPL (Figure 3.10).

Table 3.5: Generalized additive model (GAM) smoothers for the change in sound pressure level (SPL) by hour and locations N, NE, NW, SE, and SW during non-humpback season. The table includes the estimated degrees of freedom for the model terms (edf), the F-value, and associated p-value. Significant p-values are defined as $p < 0.05$.

Smoother for hour	edf	F value	p-value
Location N	2.876	6.279	<0.001
Location NE	3.903	1.640	0.120
Location NW	5.222	52.190	<0.001
Location SE	1.000	7.627	<0.006
Location SW	8.741	24.208	<0.001

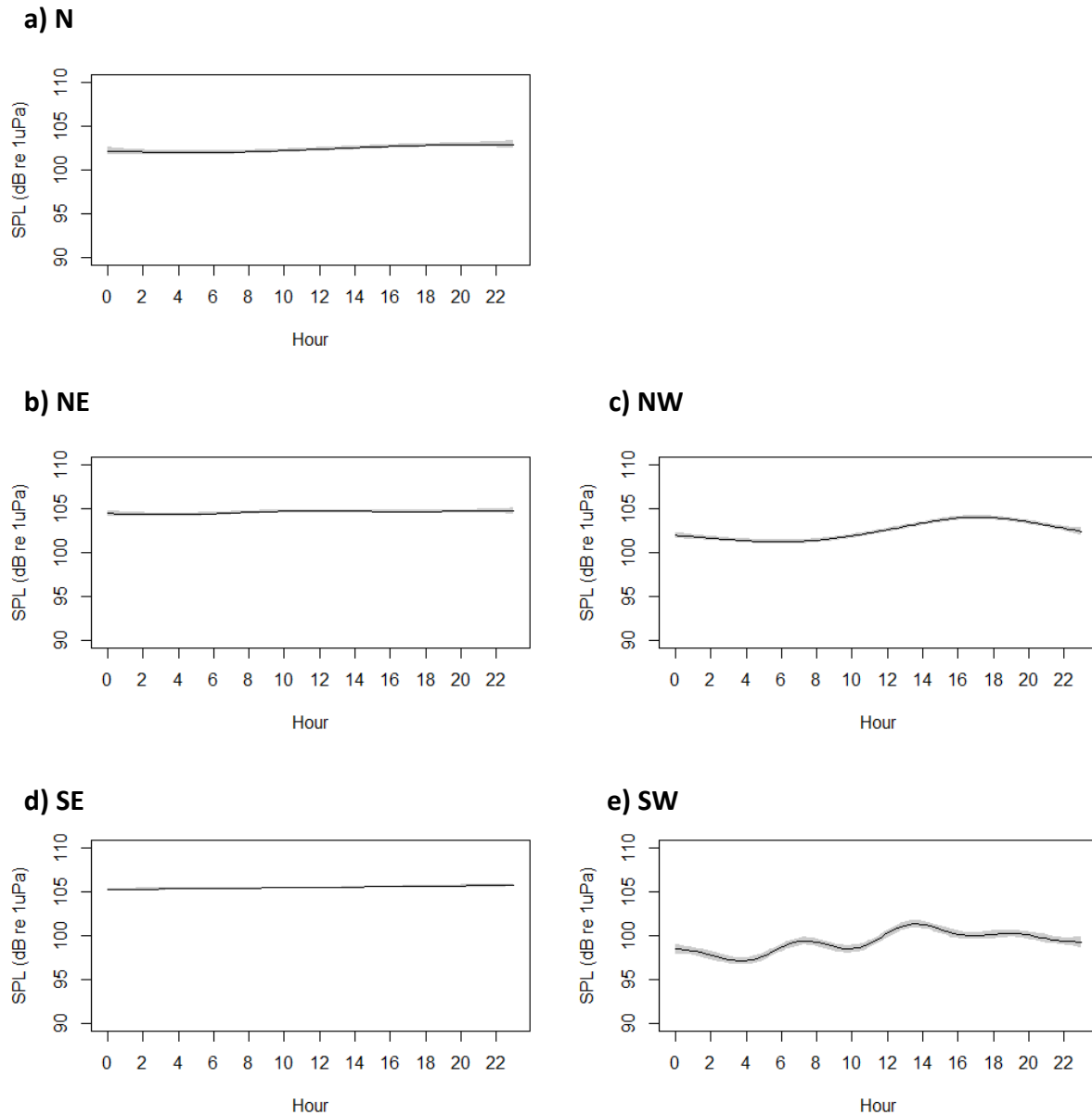


Figure 3.10: Plots of generalized additive model (GAM) smoothers showing the hourly SPL in dB re 1µPa throughout the hours of the day for each location during July and August for non-humpback season: a) N, b) NE, c) NW, d) SE, e) SW. Smoothers for all locations except NE are significant. Grey shading represents standard error for each smoother.

An ANOVA tested for differences in SPL due to time of day (TOD) and location during the non-humpback season. TOD ($F(1,982) = 5.713$; $p=0.02$) and location ($F(4, 982) = 130.890$; $p<0.001$) were significantly different from each other, but the interaction between TOD and location was not significant ($F(4, 982) = 1.480$; $p=0.206$). However, a post-hoc Tukey test revealed that within locations, day and night SPL were not significantly different.

Table 3.6: List of mean sound pressure level (SPL) re 1 μ Pa and standard error (se) for each location during non-humpback season. Mean is the top number and se the bottom number in each box, with daytime (hours 7:00 through 18:00) in the left column and nighttime (hours 0:00 through 6:00 and 19:00 through 23:00) on the right column.

Location	Mean SPL (dB re 1 μ Pa) day \pm se	Mean SPL (dB re 1 μ Pa) night \pm se
N	102.42454 0.1655701	102.34795 0.2026526
NE	104.65684 0.3339984	104.48645 0.3047942
NW	102.73202 0.2412011	102.17388 0.1753831
SE	105.55226 0.2679081	105.38163 0.2794115
SW	99.98256 0.1689407	98.56126 0.1698449

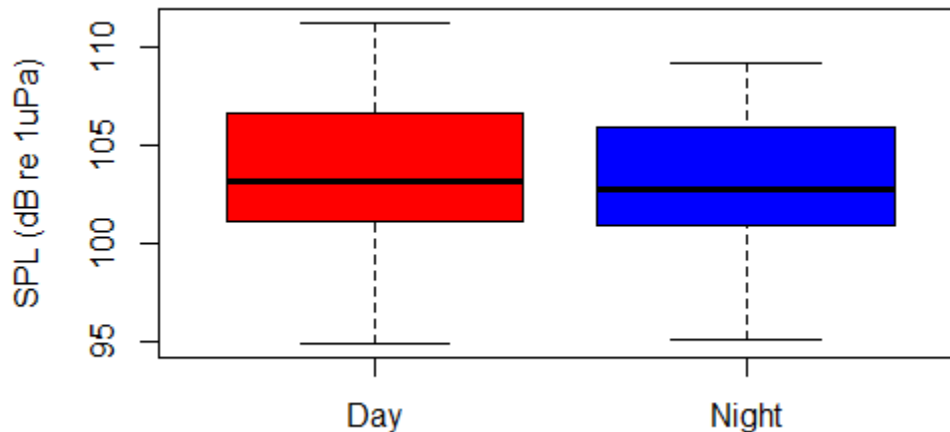


Figure 3.11: Box plot of mean sound pressure level (SPL) of all locations during day and night of non-humpback season. SPL were not significantly different. Brackets are 25% and 75% quartiles.

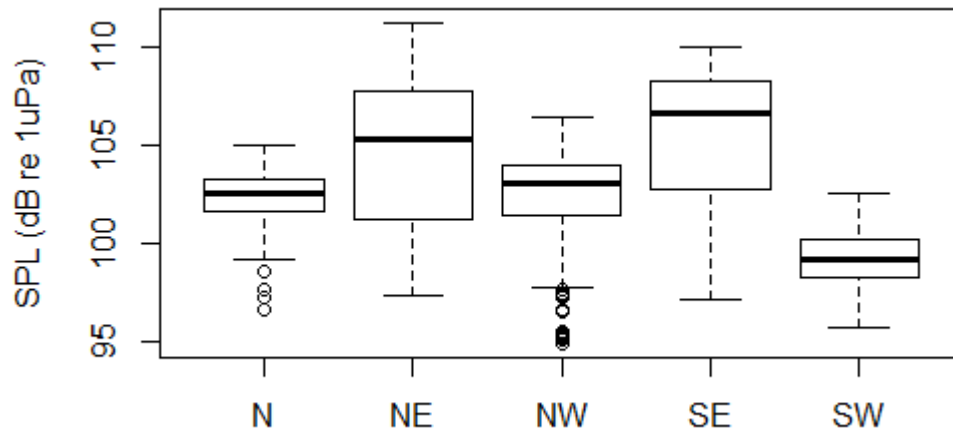


Figure 3.12: Box plot of mean sound pressure level (SPL) at each location during all hours of non-humpback season. Brackets are 25% and 75% quartiles.

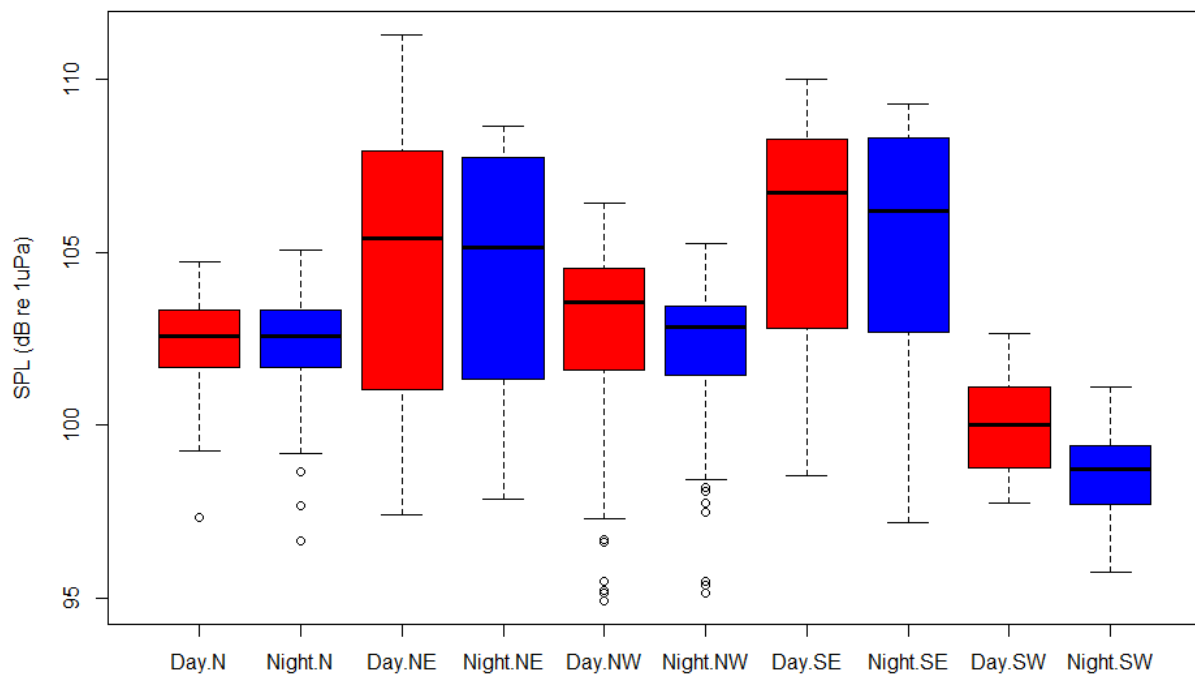


Figure 3.13: Box plot of sound pressure level (SPL) at each location during “day” (hours 10:00 through 15:00) and “night” (hours 0:00 through 3:00 and 22:00 through 23:00) during non-humpback season. Day SPL are not significantly different from night SPL. Brackets are 25% and 75% quartiles. Red boxes represent day and blue boxes represent night.

3.5 Discussion and Conclusions

3.5.1 Seasonal effects

A similar trend in the SPL was seen at the five locations around Kauai, with a few exceptions. In the comparison between humpback season and non-humpback season, the overall SPL was higher by approximately 6 dB during the humpback season than during non-season. Each location increased by different levels, with diverse timings. For example, SPL began increasing in December for the SW location while the NE location showed the increase in January. All locations showed a decrease in SPL during April. At two locations, N and NW, there appeared to be a period of minimal SPL in May.

The locations NE and SE showed a subset of the data (from certain deployments) had a higher SPL than other deployments during the same time period. There are no clear explanations for this. A quick look at a subset of the data showed some files appeared to contain higher levels of background noise from an unidentified source. Since the data set covers two years and multiple deployments, it may be that ocean conditions changed or the exact location during some deployments affected the recorded SPL (e.g. close to a consistent sound source or the SOFAR channel). Another possible explanation is that one EAR had a glitch causing noise or increased gain, although electronic noise was not evident in the manually sampled files. One EAR was deployed at location NE for deployments 1-3 and moved to location SE for deployments 4-5. If this particular EAR recorded higher SPL than the other instruments, it could have led to the pattern seen in figure 3.2. The EARs were not re-calibrated between deployments and no records are available for calibration of those particular instruments before or after these deployments.

3.5.2 Time of day effects

During peak humpback season, the months of February and March, SPL is significantly higher during the daytime than at night at each location except for location SE. The difference is small, approximately 1 dB difference at N, NE, and NW locations, approximately 3 dB difference at SW, and no significant difference at SE. The difference is slightly larger if the transition hours are excluded. The standard error is small, on the order of 0.1 to 0.4 dB. Although statistically significant, the small difference in SPL between day and night may or may

not be biologically relevant. However it suggests that at all locations except the SE location, singing humpback whales have a greater presence or are more vocally active during the day, or there is another major sound source that is more active during the day than at night. The most likely alternative source of sound is the boat engine, which was also a prominent sound source from the manually checked files. Other possible sources include wind and waves which may increase during the day. However, no diel pattern was observed during non-humpback season, suggesting a more seasonal cause for the diel pattern rather than boat engines. The lack of a significant difference in SPL at the SE location may be due to its proximity to Nawiliwili Harbor and its boat traffic, as discussed below.

If the pattern of increased SPL during the daytime is due to humpback whale song, then it is in direct opposition to the pattern observed by Au et al. (2000) off Maui close to shore where SPL increased at night. Au et al. (2000) speculated that the increase in SPL at night was caused by individual whales singing louder at night, more whales singing at night, or whales moving closer to shore at night. Assuming singing humpback whales exhibit the same behavior off Maui and Kauai, the increased SPL during the day off Kauai is unlikely due to whales singing louder at certain hours or changes in the number of singing whales around the islands. The recorders for this study were deployed between 400 and 700 m, at distances of approximately 5 to 14 km from shore while the recorder used by Au et al. (2000) was deployed approximately 0.8 km from shore in 13 m of water. This suggests that singing humpback whales may move inshore at night and offshore during the day. The smaller difference in SPL between day and night in this study may be due to a) less whales being present off Kauai as opposed to the Maui Nui area, b) a greater area to spread out while offshore of Kauai, or c) fewer whales singing during the day over a larger area off Kauai if some are engaged in competitive groups.

3.5.3 Discussion

Overall, SPL were higher at locations to the north of Kauai and lower to the south side of the island. Possible contributing factors may include less human presence leading to increased biological activity, or differences in ocean conditions. The northern or windward side of Kauai is exposed to heavy surf during fall and winter months, increasing the sound from wind and waves, minimizing human presence on the water during humpback season and possibly

attracting soniferous species displaced by human activity elsewhere. In contrast, the SE EAR was close to the entrance to Nawiliwili Harbor. A small subset of files from each location were manually examined and most sound energy below 2 kHz was produced either by humpback whales or boats. However, changes in background noise levels due to wind and waves were not noted during the manual examination of selected files. Though boat engines were recorded at all sites, they appeared intermittent at all locations except at location SE. Many of the files from the SE location included boat engine noise, so it is possible that SPL from SE are derived more from boat engines rather than humpback whales. This could explain the difference in SPL across days and hours between location SE from all other locations. The increased SPL around 6:00 and 18:00 supports this hypothesis, since many fishing boats depart at sunrise and return at sunset. In addition, humpback whales may avoid the area due to increased human activity as seen and suggested off Maui (Cartwright et al. 2012). The SW location may also have a high level of human presence compared to the northern locations because it is close to the Pacific Missile Range Facility where the Navy conducts exercises with multiple vessels, including the use of sonar, over a bottom-mounted array of hydrophones. The presence of vessels and use of sonar may discourage humpback whales and other soniferous species from inhabiting the area and may displace them to areas with less human presence on the northern side of the island. Further analysis is necessary to determine the exact contributors to increased SPL, and the amount of sound contributed by humpback whales, boats, and wind and waves to the soundscape around Kauai.

If humpback whales are confirmed to be the source of increased SPL during humpback season, then the hypothesis that singing humpback whales move offshore during the day and inshore during night could be supported by the results of this study and Au et al. (2000). The whales may be moving inshore during the night in an effort to reduce predation risk, or for the calmer waters if they are resting during this time. The singers may then move offshore during the day to better display themselves and to maintain spacing from each other (Frankel et al. 1995a). This hypothesis cannot be definitively tested in this study, but could be tested in the future if simultaneous paired recordings are conducted in the same area to compare recordings from close to shore to offshore.

This study shows that SPL in waters off Kauai during the wintering season increase on average by 6 dB re 1 μ Pa compared to the summer. In addition, the recorded SPL exhibits a diel pattern around Kauai during the winter humpback season that is not present during the summer. The most likely drivers for these changes in SPL are humpback whales and seasonal wind and waves. If the diel pattern is due to movement toward shore and offshore by singing humpback whales, it could be useful for managers attempting to define important habitat for the whales or prevent collisions. For example, it could help vessels avoid humpbacks by transiting further offshore to avoid collisions during night when visual observers are ineffective. It would be of interest to determine if similar patterns exist at other islands in the Hawaiian Archipelago. Because visual sightings form the basis of knowledge for humpback whale habitat use in Hawaii, there are few studies examining their behavior at night. If there is daily movement toward shore and offshore by singers, then other group types may also exhibit diel patterns. If the SPL changes are due to wind and waves, the study illuminates the amount of sound environmental conditions may add to the soundscape, an area often ignored in favor of examining the sounds produced by study organisms or anthropogenic sources. This study shows how passive acoustic monitoring over large spatial and temporal scales can help scientists and managers better understand the soundscape of humpback whales on their Hawaiian wintering grounds.

CHAPTER 4

First measurements of the received levels of humpback whale song produced by a singing escort in close proximity to a calf in the Hawaiian breeding grounds

This chapter was published in slightly different form as:

Chen, J., A.A. Pack, W.W.L. Au, and A.K. Stimpert. (2016). Measurements of humpback whale song sound levels received by a calf in association with a singer. *Journal of the Acoustical Society of America*, 140(5), 4010-4015.

4.1 Abstract

Current NOAA regulations on received noise levels at a marine mammal are based on limited studies conducted on only a few species. For the regulations to be effective, it is important to first understand the hearing of whales for different species and age classes and the levels of sound to which they are naturally exposed. In the winter breeding grounds, male humpback whales produce loud structured patterns of vocalizations termed “songs.” Although singers are often alone, occasionally a male sings while escorting a mother-calf pair, exposing the pair to near-continuous vocalizations. We measured for the first time sound pressure levels of humpback whale song received at a humpback whale calf in close proximity to the singer in the waters off Maui, Hawaii. Out of seven tags deployed in mother-calf groups, only one contained a singing escort. A calf was tagged with an Acousonde acoustic and data recording tag that captured vocalizations from a singing male escort in close physical association with the calf and its mother. Received sound levels ranged from 126 to 159 dB re 1 μ Pa. These data represent the first direct measurements of sound levels that a humpback whale calf may be exposed to from a singing escort.

4.2 Introduction

Concern about the effects of anthropogenic noise on marine mammals was first spotlighted by the 1991 Heard Island Feasibility test in which an intense acoustic signal was transmitted from the waters off Heard Island in the South Indian Ocean, and received by stations around the world and as far north as Whidbey Island off Washington State (Munk et al. 1994). Since then there has been growing concern about the effects of anthropogenic noise in the oceans on large whales that rely heavily on sound production and reception (Richardson et al. 1995, Southall et al. 2007, Tyack 2009a, Tyack 2009b, Ellison et al. 2012). This concern has prompted research that seeks a better understanding of the sound production and hearing capabilities of all large whales.

Current United States National Oceanic and Atmospheric Administration (NOAA) regulations on received noise levels as well as the Draft Guidance for Assessing the Effect of Anthropogenic Sound on Marine Mammal Hearing (NOAA 2015) estimated allowable sound exposure levels for marine mammal species based on anatomical models of the ear and skull (Ketten 2000, Houser et al. 2001, Parks et al. 2007b), recorded vocalization ranges (e.g. Au et al. 2006), and extrapolations from other better studied species (Clark 1991, Ridgway & Carder 2001, Mooney et al. 2009). Behavioral response studies of cetaceans to anthropogenic sounds have shown considerable variation in response to different sounds, sometimes within the same species, making it difficult for regulators to determine a single sound exposure level limit for cetacean species. For example, cetacean responses to anthropogenic sounds included increased calling rate (Miller et al. 2000, Di Iorio & Clark 2010), increased call intensity (Scheifele et al. 2005, Holt et al. 2009), changed call frequency (Parks et al. 2007a, McDonald et al. 2009), reduced or halted calling (Parks et al. 2007a, Tyack et al. 2011, DeRuiter et al. 2013), or movement away from the sound source (Tyack et al. 2011, Castellote et al. 2012). Even harder to quantify are possible long-term effects of stress caused by noise (Bejder et al. 2006, Rolland et al. 2012). Experiments on captive odontocetes have established sound exposure levels that cause temporary threshold shifts in hearing (Schlundt et al. 2000, Nachtigall et al. 2004, Finneran et al. 2005, Finneran 2015). However, no studies have been conducted on mysticetes. In synthesizing these and other findings, various review papers have attempted to generalize behavioral responses to different acoustic signals and identify topics in need of additional research

(Nowacek et al. 2007, Southall et al. 2007, Weilgart 2007, Ellison et al. 2012). One fundamental area of research required to better understand the impact of anthropogenic noise on cetaceans are empirical studies to determine baseline levels of what individuals of different age classes of a species are exposed to naturally. Understanding the received levels and types of conspecific sounds that calves are exposed to may provide information on changes in hearing and vocal development. If a calf is regularly exposed to sound levels from conspecifics that models expect to cause harm, they may have an undiscovered way to minimize damage. Yet, relatively little research has been conducted on the sound levels a cetacean may be exposed to by conspecifics in a natural setting. Studies have been limited to a few recordings of sounds from nearby conspecifics such as on tagged long-finned pilot whales (Alves et al. 2014), Blainville's and Cuvier's beaked whales (Johnson et al. 2004), and minke whales (Risch et al. 2014). Even fewer studies have addressed received levels directly at the animal, although estimates of received sound levels may be made from source level calculations. In this study, we measured received levels of humpback whale song at a calf in close proximity to a singer to determine what sound levels a calf may be exposed to when newly born.

Humpback whales (*Megaptera novaeangliae*) are a migratory species with distinct feeding and breeding areas (Baker et al. 1986, Calambokidis et al. 2008). Summer and fall months are spent in high latitudes feeding on krill and small schooling fish, and winter and spring months are spent in low latitudes engaged in activities related to calving and mating (Clapham 1996). While in the breeding grounds, maternal female humpbacks do not associate with other females and tend to isolate themselves and their newborn calves in shallow waters (Herman & Antinaja 1977, Smultea 1994, Félix & Haase 1997, Ersts & Rosenbaum 2003), partially to avoid harassment by male humpbacks seeking mating opportunities, which can be energetically costly (Craig et al. 2014). Despite this segregation by maternal females in the breeding grounds, calves are exposed to a variety of conspecific sounds, including songs. For example, social sounds have been recorded within "competitive groups" (Silber 1986) consisting of a female with or without a calf and two or more males competing for physical access to the female (Tyack & Whitehead 1983, Baker & Herman 1984, Clapham et al. 1992, Spitz et al. 2002). Social sounds have also been recorded from calves (Pack et al. 2005, Zoidis et al. 2008) and presumably they hear well within the range of these vocalizations. Arguably, the most

intense and longest duration conspecific sounds to which calves are exposed are those from male humpback whale song, a structured and ordered series of hierarchically organized vocalizations that may be repeated by individuals for hours (Payne & McVay 1971, Winn & Winn 1978, Helweg et al. 1992, Darling et al. 2006, Parsons et al. 2008). These vocalizations are referred to as song units and have been reported to have different root mean square source levels (SLrms) for different song units from 149 to 169 dB re 1 μ Pa, and peak-to-peak (SLpp) levels 17 to 20 dB greater than SLrms, depending on the unit type and individual whale (Au et al. 2006). While in the breeding grounds, it is common for multiple males, both mature and immature, to sing asynchronously day and night (Helweg & Herman 1994, Au et al. 2000, Herman et al. 2013). The continued presence of male song in the breeding grounds indicates that this behavior is related to the whales' mating system, which some have likened to a "lek" system (Herman & Tavolga 1980, Clapham 1996), although the exact nature of the function or functions of song remains debatable (Herman & Tavolga 1980, Clapham 1996, Darling et al. 2006, Smith et al. 2008, Herman et al. 2013). Although most males sing alone, adopting a stereotypic stationary posture with head tilted downward (Au et al. 2006), some singers sing while traveling (Frankel et al. 1995a) and some sing while escorting a mother-calf pair (Herman & Tavolga 1980, Baker & Herman 1984, Helweg et al. 1992, Darling et al. 2006, Smith et al. 2008).

Although much early work on humpback whale song was devoted to describing its structure and dynamics (Payne & McVay 1971, Winn & Winn 1978, Guinee et al. 1983, Payne & Guinee 1983, Payne & Payne 1985, Mercado et al. 2003), it is only relatively recently that SL have been directly measured for various song units (Au et al. 2006). Au et al. (2006) recorded maximum SLrms of 173 dB re 1 μ Pa. In terms of the sounds humpback whales can hear, several playback studies have demonstrated individual humpbacks responding to social sounds (Tyack 1983, Mobley Jr et al. 1988), an Alaskan feeding call (Mobley Jr et al. 1988), and familiar and unfamiliar song (Mobley Jr et al. 1988, Darling et al. 2012). Humpbacks have been reported to respond to feeding calls as low as 102 dB re 1 μ Pa (Frankel et al. 1995b).

To date, no studies have reported the levels of sounds produced by conspecifics that are received by humpback whale calves because acoustic recording tags have rarely been deployed on calves. In the present study, we determined the received levels of humpback whale song on a calf in close proximity to a singer by deploying an archival acoustic and data recording suction

cup tag on a calf that was accompanied by its mother as well as a singing escort. Of the seven mother-calf groups tagged over two years, an escort accompanied four and one of these escorts sang during the tag deployment.

4.3 Methods

4.3.1 Study Area

Humpback whales were studied in the Hawaiian Islands, the principal wintering grounds of the North Pacific population (Calambokidis et al. 2008). Tagging activities took place in the Au'au channel off West Maui during March 2014 (Figure 4.1). This area contains one of the highest concentrations of humpback whales in the Hawaiian Islands and is a preferred location for mother-calf pairs (Herman & Tavolga 1980, Mobley et al. 1999, Craig et al. 2014).

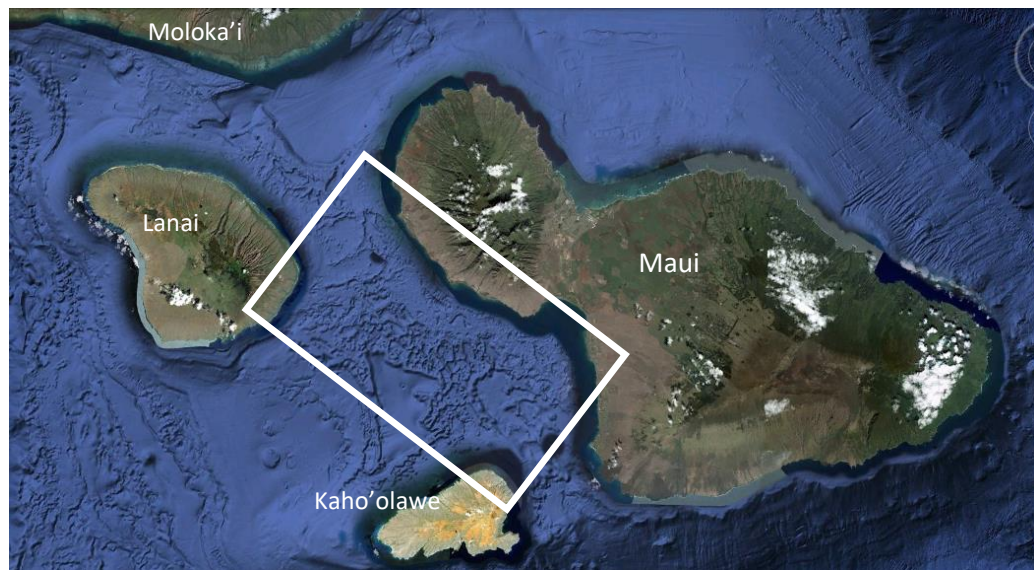


Figure 4.1: Map of study area (indicated by box)

4.3.2 Equipment and Procedures

A suction cup archival acoustic recording and data logging tag “Acousonde 3B” (www.acousonde.com) was deployed on a humpback whale calf as part of a larger study to understand the acoustic communications between mother-calf pairs during the calf’s early development in Hawaiian waters. The Acousonde contains one low frequency and one high

frequency hydrophone (one-channel recording), a pressure sensor, 3-axis accelerometers, 3-axis magnetometers, light sensor, and temperature sensor in addition to solid-state memory and battery housing. This package is connected to a foam float to which a VHF transmitter is attached for tracking purposes. This 22.5 cm tag is attached to a whale with four suction cups. The deployed tag recorded acoustics at a 10.1 kHz sample rate, the accelerometers at 800 Hz, the magnetometers at 40 Hz, the pressure at 10 Hz, and light and temperature at 5 Hz. The acoustic recording was made with a 20 dB gain.

Tagging was conducted from an 11-meter rigid-hull inflatable boat equipped with dual outboard engines launched from Ma'alaea Harbor. The tag was deployed using a 7.4-meter handheld carbon fiber pole following methods presented in Stimpert et al. (2012a). Prior to any tagging, the crew visually searched for potential candidate mother-calf groups including those with a single escort. Groups were observed from a distance and approached once it was determined they were a candidate for tagging.

At 11:06 am on March 4, 2014, a stationary mother-calf pair in the company of an escort was sighted by observers aboard the boat at 20° 45.454' N, 156 ° 30.925' W. The tag was deployed on the calf while it was logging at the surface. Following tag deployment, the crew heard loud humpback whale song transmitting through the hull of the boat. A second escort temporarily joined the group for approximately 15 minutes before leaving. At 50 minutes after tag attachment the group was stationary and a snorkeler was deployed to confirm that the escort was singing and determine the sex of the calf by examining the ventral surface for the presence (in females) or absence (in males) of a hemispheric lobe just caudal to the genital slit (Glockner & Venus 1983). The tag was retrieved by the snorkeler when it detached at 12:13 pm, at 20° 46.677' N, 156° 30.625' W.

4.3.3 Analysis

The acoustic signals recorded by the tag were converted into a .wav file using custom MATLAB scripts along with software provided by the tag manufacturer. The .wav file was visualized in Adobe Audition with a spectrogram (Blackmann-Harris window, FFT size 512, 50% overlap). Vocalizations were identified manually, and song units were isolated and classified subjectively by an experienced listener (JC). Song units with elevated background

noise from the calf's surfacing activity or increased flow noise were excluded from the analysis. A custom MATLAB script calculated the root-mean-square sound pressure level (SPLrms), peak-to-peak sound pressure level (SPLpp), and the sound exposure level (SEL).

The equation used to calculate SPLrms is as follows, where n is the number of samples in the signal and p is the pressure at each sample point in the signal:

$$SPL_{rms} = 20 \log_{10} \sqrt{\frac{1}{n} \sum p^2}$$

The equation used to calculate SPLpp is as follows, where p_{max} is the maximum pressure level in the signal and p_{min} is the minimum pressure level in the signal:

$$SPL_{pp} = 20 \log_{10}(p_{max} + |p_{min}|)$$

The equation used to calculate SEL is as follows, where t is the length of signal in seconds (Tyack 2009b):

$$SEL = SPL_{rms} + 10 \log_{10} (t)$$

4.4 Results

The tag remained attached to the calf for 65 minutes. The recording included three sections of song including repeated phrases from the singing escort. These were separated by periods of travel with high flow noise or absence of prominent song units. The tag also recorded sounds including background chorusing, non-song sounds that may have been produced by either the calf or mother, and occasional boat engine noise, although song was more audible and visible in the spectrogram than any of these other sound types.

Within one minute of tag deployment, song units distinct from the background chorusing were recorded. Approximately 10 minutes after deployment, a second escort temporarily affiliated with the group for approximately 15 minutes, during which the original escort stopped singing (i.e. no song was recorded on the tag other than background chorusing). During this time, the mother performed one head slap, the calf performed one breach, and one of the escorts performed a head lunge and high-arch dive. The escort behaviors are typical of those associated with male humpbacks competing over a female (e.g. Baker & Herman 1984). Singing resumed

shortly after the second escort disaffiliated (separated) from the group. Approximately 5 minutes after the original escort resumed singing, the flow noise increased while the group travelled for 10 minutes in variable directions. The flow noise masked most of the ambient sounds, although the escort appeared to continue singing, based on higher frequency harmonics and calls recorded above the noise. Once the group stopped travelling, the snorkeler entered the water. The snorkeler identified the calf as female and confirmed the escort was the singer based on attenuation of song when the singer surfaced. The tag detached from the calf while the snorkeler was in the water, and was recovered.

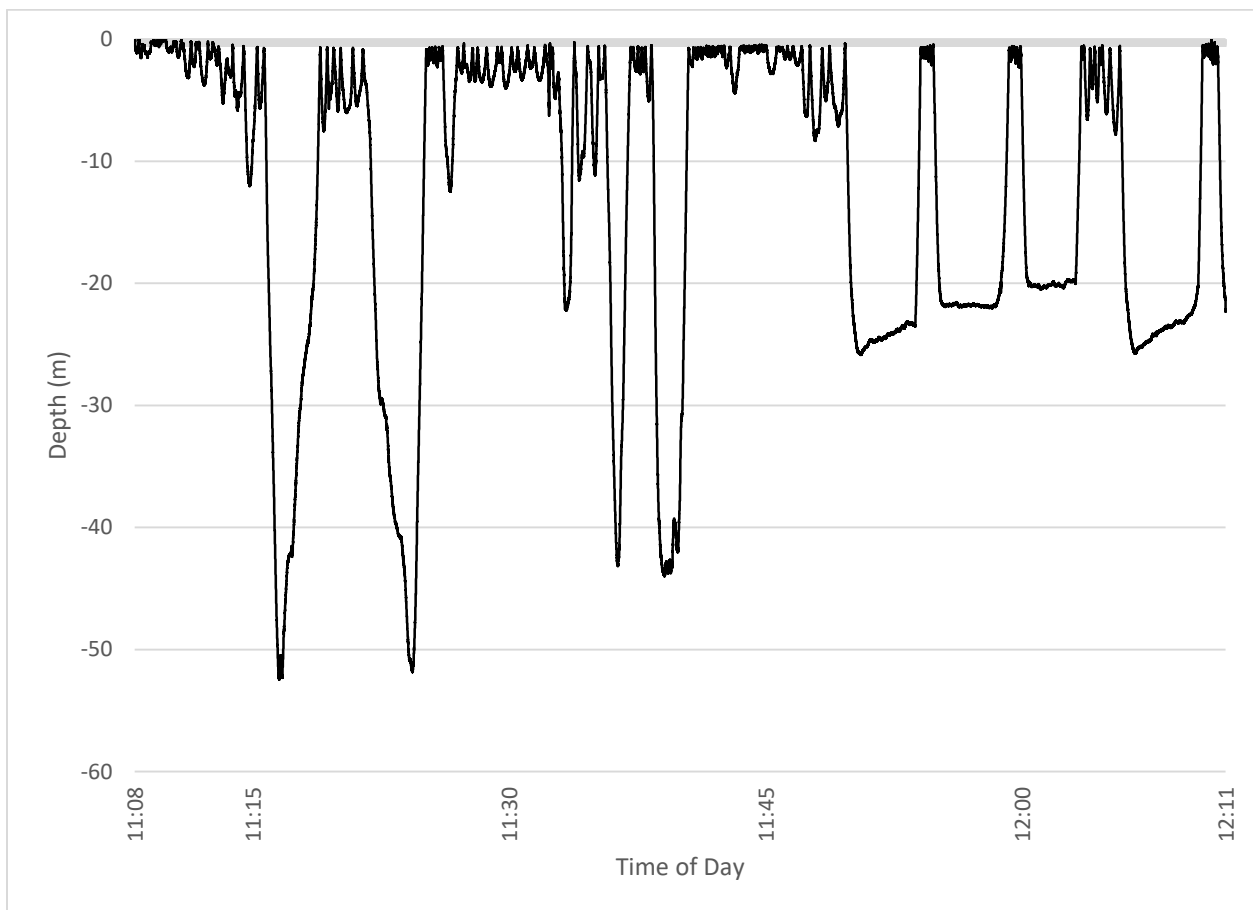


Figure 4.2: Dive profile of tagged calf with depth (m) versus time (min). Deepest dives were to approximately 52 m.

A total of 695 song units were extracted from the Acousonde recording. Of these, 548 units were used in the analysis (see methods). Fourteen unit types were present in the song. The

duration and received levels of each unit are reported in Table 4.1, and representative examples of the six most common units are shown in Figure 4.1. The most common unit was designated Unit A, a short 0.3 to 0.8 second long, frequency modulated (upsweep) sound. Unit N showed the most variation in signal duration. Mean, minimum, and maximum levels across all unit types as received at the calf are reported in Table 4.2. Song unit durations ranged from 0.18 s to 7.02 s, and the mean duration of a song unit was 1.23 ± 0.79 s.

Table 4.1: Details the unit name, mean length of unit, SPLrms, SPLpp, SEL, and number of units used in analysis for each unit type. Only units with good SNR and low flow noise are reported.

Unit	Length (s)	SPLrms (dB re 1 μ Pa)	SPLpp (dB re 1 μ Pa)	SEL (dB re 1 μ Pa ² s)	# units used of total
A	0.42 \pm 0.12	135 \pm 5	153 \pm 6	131 \pm 6	151 of 180
B	1.28 \pm 0.25	133 \pm 3	150 \pm 3	134 \pm 3	73 of 99
C	1.37 \pm 0.29	136 \pm 4	154 \pm 5	137 \pm 5	55 of 64
E	1.31 \pm 0.28	137 \pm 3	155 \pm 4	138 \pm 4	5 of 5
H	1.89	134	150	137	1 of 1
K	1.33 \pm 0.38	134 \pm 4	149 \pm 4	135 \pm 5	13 of 20
L	0.90 \pm 0.20	131 \pm 2	147 \pm 3	130 \pm 2	16 of 19
M	1.43 \pm 0.18	142 \pm 5	159 \pm 4	143 \pm 5	105 of 131
N	2.49 \pm 1.31	139 \pm 4	159 \pm 3	142 \pm 3	8 of 8
P	1.56 \pm 0.27	137 \pm 4	155 \pm 3	139 \pm 4	47 of 54
U	1.67 \pm 0.67	132 \pm 2	152 \pm 2	134 \pm 2	18 of 29
V	2.41 \pm 1.04	133 \pm 4	152 \pm 5	136 \pm 5	38 of 53
X	1.45 \pm 1.07	133 \pm 3	151 \pm 6	133 \pm 4	16 of 29
Y	6.77 \pm 0.35	132 \pm 1	153 \pm 1	140 \pm 1	2 of 3

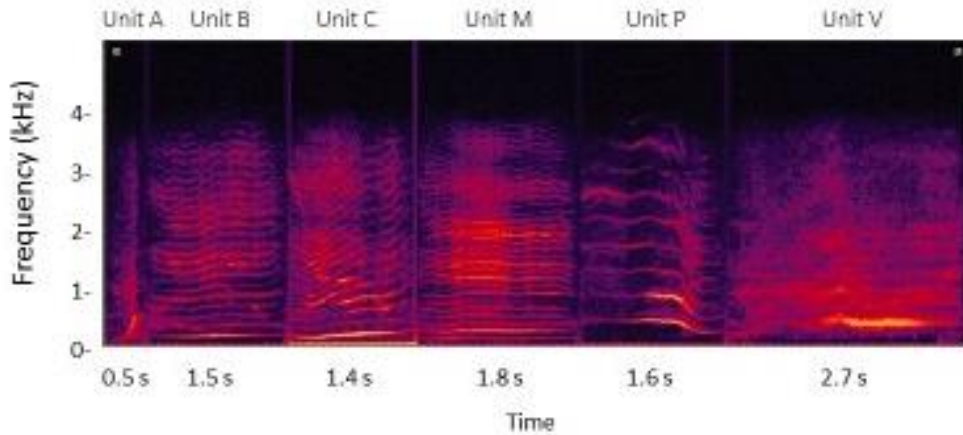


Figure 4.3: Spectrogram of six most common units recorded with the duration of the units given on the x-axis and frequency (kHz) of the units provided on the y-axis. Each unit is labeled above the spectrogram.

The minimum SPLrms received was 126 dB re 1 μ Pa (Table 4.2). The maximum SPLrms was 158 dB re 1 μ Pa. The mean SPLrms for the 548 units was 136 ± 5 dB re 1 μ Pa. The SPLpp was 10 to 20 dB higher than the SPLrms for all unit types, as expected when length of the unit is taken into account for SPLrms, with an overall mean of 153 ± 6 dB re 1 μ Pa pp. Sound exposure level (SEL) varied from a minimum of 120 dB re 1 μ Pa²s to a maximum of 155 dB re 1 μ Pa²s, with a mean of 136 ± 6 dB re 1 μ Pa²s. Song unit lengths ranged from 0.18 s to 7.02 s, with some units showing a consistent length while others had a variation of over a second in signal length. The mean duration of a song unit was 1.23 ± 0.79 s.

Table 4.2: Mean, minimum, and maximum received sound levels (SPLrms, SPLpp, and SEL) of song from a singing escort at the calf, averaged over all unit types.

	Mean (dB re 1 μ Pa)	Min (dB re 1 μ Pa)	Max (dB re 1 μ Pa)
SPLrms	136 ± 5	126	158
SPLpp	153 ± 6	138	171
SEL (1 s)	136 ± 6	120	155

The pressure sensor was used to determine dive profile of the calf (Figure 4.2). The two deepest dives made by the calf were approximately 52 m deep, likely to the bottom based on location and depth charts. They occurred when a second escort was observed interacting with

the group, when the primary escort was not singing. Since the primary escort sang for most of the duration of the deployment with the exception of the aforementioned times, the calf was exposed to the song no matter where it was in the water column. Of the 65-minute tag deployment, 36 minutes were spent within 10 m of the surface on shallow dives and to breathe, and 29 minutes were spent between 10 and 60 m. Of the nine deeper dives below 20 m, five dives had a v-shaped profile where the calf descended down to 52 m, then immediately ascended. Four dives had a u-shaped profile where the calf descended down to 30 m, stayed at depth for approximately 3 minutes, then ascended to the surface.

4.5 Discussion

These results are the first direct measurements of sound levels at a humpback whale calf exposed to a singing conspecific in its natural environment. The measured received SPLrms are consistent with what might be modeled for a calf a short distance from the singing escort. If we assume the male escort is between 1 and 60 m away from the calf, the approximate distance from the surface to the bottom, transmission loss is estimated at 0 to 36 dB assuming spherical spreading. Assuming cylindrical spreading, the transmission loss is estimated between 0 and 18 dB. Realistically, the transmission loss would be somewhere between spherical and cylindrical spreading. Assuming an rms source level from the escort of 149 to 169 dB re 1 μ Pa (Au et al. 2006) and spherical spreading for transmission loss between 1 and 60 m, the received levels at the calf would be expected to fall between 113 and 169 dB re 1 μ Pa, which is consistent with the calculated levels of 126 to 158 dB re 1 μ Pa rms at the calf.

These are novel data, important to understanding the natural acoustic conditions to which a humpback whale calf is exposed. However, care must be taken when using these data to inform regulatory agencies about sound levels tolerated by humpback whales. Because one tag was deployed only on the calf, there is no concurrent record of the mother or escort for comparison of dive behavior. The exact distance of the calf from the singing escort cannot be determined, only estimated based on assumptions of the whales' positions. It is also unknown what shading effect the calf's body may have had on the recording or its own hearing since the tag was located on the back and the escort was usually located below the calf.

Because there have been no measurements of mysticete whale hearing, the only estimates of sound levels required to induce TTS or PTS are based on models that are themselves based on models of mysticete hearing abilities, and/or data from odontocete studies (Gedamke et al. 2011, NOAA 2015). NOAA (2015) gives an estimate of 188 dB re 1 $\mu\text{Pa}^2\text{s}$ cumulative sound exposure level to induce TTS in mysticetes. In the present study, the calf was exposed to an estimated maximum sound level from single song units of SEL 155 dB re 1 μPa , and RLrms 158 dB re 1 μPa . Although not calculated here, exposure to a long song session would result in exposure to higher cumulative sound levels. It is fairly common to find singing escorts on the wintering grounds (Baker & Herman 1984, Darling et al. 2006, Herman et al. 2013) and on migratory routes (Smith et al. 2008). It is possible that the ears of humpback whales have evolved in such a way that near-continuous exposure to conspecific song is not harmful, and/or have physiological mechanisms to prevent permanent hearing damage in these naturally occurring conditions. Such adaptations are of course not only beneficial to individuals in close proximity to a singer, but to the singer itself who may be receiving the most intense levels of these sounds.

CHAPTER 5

Acoustic characteristics of humpback whale (*Megaptera novaeangliae*) mother and calf vocalizations in the Hawaiian wintering grounds

5.1 Abstract

Humpback whale mother-calf groups in the winter breeding grounds produce a variety of vocalizations. The spectral characteristics of some calf vocalizations have been described, but few studies have been conducted on the breeding grounds. There is also a lack of general information on vocalizations produced by mothers. To address these issues, we deployed suction cup acoustic and movement recording tags on humpback whale calves and mothers on the Hawaiian breeding grounds to record vocalizations and percussive sounds. Deployments took place in waters off West Maui over three winter seasons. Tags were deployed on 7 humpback whale mothers and 3 calves for a total of approximately 44 hours of recordings. Calling rates of tagged animals were relatively low compared to song, with individual's means ranging from 0 to 16 vocalizations per hour. Most calls occurred singly or in bouts, with long periods of silence before the next vocalization or set of vocalizations. These included sounds resembling previously reported non-calf social sounds as well as single song units, with durations up to 2 seconds and fundamental frequencies below 1.5 kHz. Our findings provide information that is important to understanding vocal development in humpback whale calves and the sounds produced by adult females.

5.2 Introduction

Humpback whales (*Megaptera novaeangliae*) produce a variety of sounds including song, non-song vocalizations, and percussive sounds. The songs produced by male humpback whales primarily during the winter breeding season have been extensively studied since they were first comprehensively described by Payne and McVay (1971). Descriptions of song, comparisons between years and locations, and efforts to determine the function of song have occurred during studies from breeding grounds, migration routes, and feeding grounds (e.g. Payne & McVay 1971, Winn et al. 1981, Clapham & Mattila 1990, Au et al. 2006, Garland et al. 2013, Herman et al. 2013, Magnúsdóttir et al. 2015). Less well studied are non-song vocalizations and non-vocal surface-generated or percussive sounds. The term “social sounds” was utilized by Silber (1986) to describe vocalizations that did not fit within “the rhythmic and continuous patterning of song.” Social sounds also include non-vocal, surface generated percussive sounds such as from breaches, pectoral flipper slaps, and tail slaps (Tyack 1983, Dunlop et al. 2008).

Social sounds in humpback whales have been described in a variety of locations and contexts. They are produced by males, females, and calves (e.g. Dunlop et al. 2008, Zoidis et al. 2008). The sounds are most often produced in social groups, though single individuals also produce social sounds (Dunlop et al. 2008), perhaps as a contact call searching for other individuals. Early work by Thompson et al. (1986) described non-song vocalizations, blowhole-associated sounds, and surface impacts from humpback whales in their feeding grounds off Alaska. More recently, a comprehensive study of non-song vocalizations produced by humpback whales in Southeast Alaska described 16 call types (Fournet et al. 2015). Eight groups of social call types produced by humpback whales on the North Atlantic feeding grounds were described by Stimpert et al. (2011). In addition, vocalizations identified as related to foraging, the “feeding call” and the “megapclick,” were described from Alaska and the North Atlantic feeding grounds (D’Vincent et al. 1985, Cerchio & Dahlheim 2001, Stimpert et al. 2007).

Social sounds have also been relatively well studied and described off the east coast of Australia along a migration corridor (Dunlop et al. 2007, Dunlop et al. 2008, Dunlop et al. 2013, Rekdahl et al. 2013, Rekdahl et al. 2015). Dunlop et al. (2007) described 34 separate call types,

some of which were the same as individual song units, but used outside the pattern of song. The call catalog was increased to 46 call types by Rekdahl et al. (2013). These studies included calls recorded from mother-calf groups, but were unable to determine which individual produced the vocalization. While on the migration, the sounds are unlikely to be used in a feeding context, but may be used to communicate in the context of male-to-male competition for a female, for maintaining contact between individuals and groups along the migration route, or to warn of predators. Specialized calls between mothers and their offspring to find and identify each other, recall, warn, and elicit feeding exist in a variety of species such as mallard ducks (Miller & Gottlieb 1978), cats (Szenczi et al. 2016), white-tailed deer (Atkeson et al. 1988), Antarctic fur seals (Aubin et al. 2015), cattle (de la Torre et al. 2016) and bottlenose dolphin (King et al. 2016). Because humpback whale mothers provide care for their calves for about one year, it is reasonable to assume that they have mother-calf specific calls in addition to other intraspecific non-song calls.

Fewer studies have focused on social sounds produced by humpback whales on the breeding grounds. Pack et al. (2005) first reported that calves in the Hawaiian breeding grounds produced vocalizations. Calf vocalizations from Hawaii were described as amplitude modulated, frequency modulated, or pulsed (Zoidis et al. 2008). Seger (2016) described social calls used by humpback whales in the Los Cabos region of Mexico by group type. Non-song vocalizations produced in the breeding grounds are most often attributed as contact or alarm calls between mother and calf (Zoidis et al. 2008) or sounds produced by competitive groups (Seger 2016). However, Darling (2015) recently described low-frequency pulse trains in the Hawaiian breeding grounds from a surface active group and a male-female pair. Darling (2015) speculated that these pulse trains may be related to breeding behavior.

A large portion of the North Pacific humpback whale population migrates to Hawaii during the winter to breed and give birth to calves. Mothers with newly born calves tend to have slightly longer residence times compared to other group types, likely to allow the calf to grow as much as possible before beginning the migration north (Clapham 1996, Craig et al. 2003). The calf stays with the mother for approximately one year (Clapham 1996). While on the breeding grounds, the calf stays in close proximity to the mother (Glockner & Venus 1983, Cartwright & Sullivan 2009) and mother-calf groups favor shallow waters less than 50 m (Ersts & Rosenbaum

2003, Félix & Botero-Acosta 2011). When young, the calf must leave the mother to surface and breathe at shorter intervals. As the calf grows older, its surfacing intervals become longer as it improves its breath holding capability and becomes more independent, moving further from the mother for longer periods of time (Cartwright & Sullivan 2009). The calf's growing independence may develop simultaneously with non-song vocalizations as it necessitates a way to keep in contact or to call for help. However, as the sample size of vocalizations produced by mothers and calves on the breeding grounds and recorded by researchers is small, there are as yet no studies on development of the vocal repertoire of young humpback whale calves.

There are only a few studies of non-song vocalizations in the breeding grounds, therefore the full range of sound produced by mothers and calves has likely not yet been described. In addition, previously described non-song vocalizations include calls with shorter and lower frequencies than song units. These may be more susceptible to masking from anthropogenic noise as well as singing conspecifics. Information about the vocalizations of mothers-calf groups is necessary to understand and therefore better protect the acoustic environment of these more vulnerable groups. The goal of this chapter is to describe the non-song vocalizations produced by mother-calf groups in the breeding grounds off Maui.

5.3 Methods

5.3.1 Study Area

Humpback whale acoustic tagging activities took place in the Hawaiian Islands in the Au'au channel off West Maui over 3 seasons. Fieldwork occurred March 2 to 10, 2014, March 8 to 22, 2015, and February 28 to March 19, 2016. The area contains one of the highest concentrations of humpback whales in the Hawaiian Islands and is a preferred location for mother-calf pairs (Mobley et al. 1999, Craig & Herman 2000).

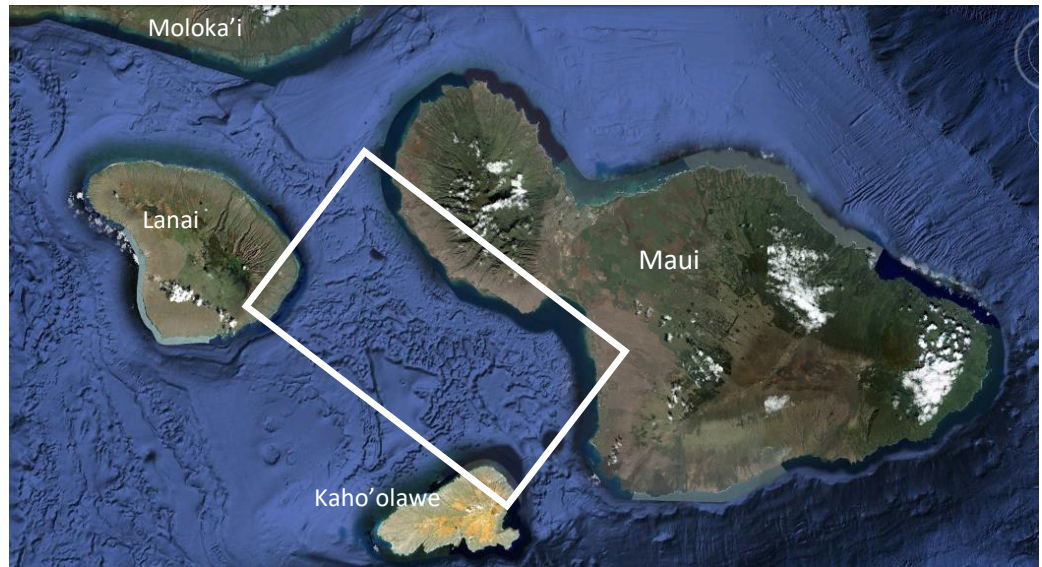


Figure 5.1: Map of study area in the Maui Nui area with tagging activities conducted primarily in the boxed area.

5.3.2 Equipment and Procedures

Two types of suction cup archival acoustic recording and data logging tags were used in this study, the Acousonde 3B (acousonde.com), and the Bioacoustic probe (Burgess et al. 1998). The Bioacoustic probe is an older version of the Acousonde. Both tags include a sound recording hydrophone, a pressure sensor, and a temperature sensor. The Bioacoustic probe also includes 2-axis accelerometers, while the Acousonde includes 3-axis accelerometers, 3-axis magnetometers, and a light sensor. These tags were deployed on humpback whale mothers and calves in order to study the acoustic communications between mother-calf pairs.

The Acousonde was deployed on mothers and calves in 2014, 2015, and 2016. Sound was recorded using the low frequency hydrophone with a sensitivity of -187.2 dB re 1 V/ μ Pa. The tag recorded sound data at a 10.1 kHz sample rate (SR) with 20 dB gain for one tag in 2014 and 0 dB gain for all other tags deployed in 2014 and 2015, and recorded at 12.2 kHz sample rate with 0 dB gain in 2016. Auxiliary sensors recorded pressure at 10 Hz, 3-axis accelerometers at 800 Hz, 3-axis magnetometers at 40 Hz, and light and temperature at 5 Hz sample rates. The analog to digital converter (A/D converter) was 16 bits. Tag data files were recorded in a proprietary .mt file format.

The Bioacoustic probe was deployed on one mother in 2016. The Bioacoustic probe uses a HTI 96 min hydrophone with a sensitivity of -172.7 dB after pre-amplification. Sounds were recorded at 12 kHz sample rate with 0 dB gain. Auxiliary channels for pressure, temperature, and 2D accelerometer were recorded at 4 Hz. The A/D converter was 16 bits.

Tagging was conducted from one of two small boats with dual outboard engines. The tag was deployed using a 7.4-meter handheld carbon fiber pole following methods presented in Stimpert et al. (2012a). Prior to any tagging, whale groups were observed from a distance greater than 100 yards. If the group was a candidate for tagging by experienced researchers, the boat slowly approached. Groups of interest included mother-calf pairs (MC) and mother-calf pairs with a single male escort (MCE). The calf also had to be at least one month old, which was determined by confirming that the calf's dorsal fin was erect, indicating it was a non-neonate (Cartwright & Sullivan 2009). Candidate groups included those that were stationary or traveling slowly. If major avoidance behaviors or aggressive behaviors occurred on approach, the boat backed away and moved on to search for another group.

5.3.3 Analysis

The acoustic and auxiliary data files were recorded by the Acousonde and Bioacoustic probe tags in proprietary .mt file format. These .mt files were read using manufacturer-provided MATLAB™ script MTread.m. Acoustic data were converted into .wav files using a custom written MATLAB™ script. Wav files were reviewed by an experienced listener (JC) both visually and aurally, and events were annotated in RavenPro 1.4 (Bioacoustics Research Program 2011). The .wav file was visualized as a spectrogram (Hann window, FFT window size 1024, 70% overlap) for review. The bandwidth was 5 or 6 kHz depending on sample rate. Data from the pressure sensor were also examined by reading the .mt files into MATLAB™.

Identification of calls was conservative in an effort to avoid identifying one of the pervasive song units as a social call. In the context of this chapter, a call is a non-song vocalization and excludes both song units and surface generated percussive sounds. Calls were excluded if they resembled song units and were repeated in a song pattern, defined as more than one of the same call within 30 seconds and repeated in song rhythm with other song units. A call was counted in the total but excluded from calculations of call parameters if it was definitively

identified as a non-song vocalization, but overlapped with a song unit or other prominent acoustic event (e.g. surfacing, high flow noise) such that the beginning, ending, minimum frequency, or maximum frequency were visually obscured. Accurate measurements of the call parameters would have been difficult to obtain for these obscured calls. Behavioral state of group during the calls were identified as stationary, traveling, or surface active.

Statistical tests were conducted in R (R Core Team 2015). A linear model and 1-way ANOVA was conducted to test if tags on mothers or calves recorded more vocalizations, and if mother-calf (MC) or mother-calf-escort (MCE) groups vocalized at higher rates. Identified vocalizations were classified as one of 13 call types. The following parameters were described for each call type: duration (s), minimum frequency (Hz), maximum frequency (Hz), and bandwidth (Hz).

5.4 Results

Ten tags were deployed over three field seasons from 2014 through 2016. Three were placed on calves and seven were placed on mothers. Tags were deployed for a total for 44 hours and 14 minutes of recordings (Table 5.1). The Bioacoustic probe was deployed on one mother in 2016; all other deployments were with the Acousonde. The majority of recordings occurred during daylight hours. One deployment (tag 20160317) stayed on the mother into the night, detaching at about midnight. That tag had an exceptionally long duration of about 12 hours. All other deployments lasted six hours or less. The shortest duration a tag was on an animal was about 25 minutes.

Table 5.1: Tag deployment information for each of the 10 deployments, including the individual that was tagged, the group composition, the time of deployment and detachment from animal, number of vocalizations identified, number of hours the tag was on the animal, vocalization rate, and maximum depth recorded by the tag.

Tag	Tagged individual	Group	Time deployed	Time retrieved	# calls	# hours	Calls per hour	Max depth (m)
20140304	calf	MCE	11:08:27	12:13:03	17	1.08	15.74	52
20150318	calf	MCE	14:54:19	16:51:50	8	1.95	4.10	108
20150319	calf	MC	12:29:16	18:30:55	92	6.02	15.28	108
20140306	mother	MC	10:30:19	15:20:36	4	4.83	0.83	19
20150310	mother	MCE	9:28:44	15:26:02	63	5.95	10.59	69
20150311	mother	MCE	12:26:11	18:13:12	91	5.78	15.74	109
20150315	mother	MC	10:47:10	14:20:08	0	3.55	0.00	69
20160313	mother	MCE	10:04:25	10:31:54	2	0.45	4.44	65
20160317	mother	MCE	12:18:54	0:21:26	73	12.05	6.06	92
20160318	mother	MCE	10:15:00	12:39:05	31	2.4	12.92	70

Calling rates of tagged animals were relatively low compared to the constant repetitive song units, where males produce song units a few seconds apart over long periods of time. Social calls recorded from these mother-calf (MC) and mother-calf-escort (MCE) groups usually occurred singly or in bouts, with long periods of silence before the next call or call bout. Individual vocalization rates ranged from 0 to about 16 calls per hour. The mean number of calls per hour was 8.5 (sd 6.2). An ANOVA was used to determine that although tags on calves recorded almost five calls per hour more than tags on mothers, there was no statistically significant difference in number of calls per hour. Similarly, tags in MCE groups recorded almost five calls per hour more than MC groups though there was no statistically significant difference between group types. This may be because of the small sample size of a total of 10 tags deployed.

A total of 381 vocalizations were detected. These were categorized into 13 call types (Table 5.2, Figure 5.2). Most call types resembled single song units or social sounds reported from previous studies. The ‘cry’ and ‘lf cry’ were frequency modulated calls that increased in

frequency then decreased in frequency, with the ‘cry’ at higher frequencies and the ‘lf cry’ at lower frequencies. Downsweeps were calls that decreased in frequency. ‘Downsweep1’ appeared more broadband than ‘downsweep3.’ ‘Downsweep2’ was short in duration. The ‘groan’ was a broadband call with center frequency around 1 kHz. The ‘lf mod’ was a frequency modulated call with multiple inflection points. The ‘mp’ appeared to have two parts, beginning with pulses that transformed into a tonal upsweep. ‘Pulsed’ calls included multiple parts that were very close, less than 0.5 s apart. The pulses could be the same frequency or change across the bout. ‘Squeaks’ were high frequency, between 3 and 4 kHz, and very short duration. Upsweeps were calls that increased in frequency. ‘Upsweep1’ appeared somewhat broadband. ‘Upsweep3’ was more narrowband and often had many harmonics visible. ‘Upsweep2’ resembled a short version of ‘upsweep3’.

After excluding obscured calls as described in the methods, there remained 298 calls of 12 call types. The mean and standard deviation was calculated for each of the following parameters: signal duration (s), minimum frequency (Hz), maximum frequency (Hz), bandwidth (Hz). For ‘pulsed’ calls, the number of pulses was also calculated (Table 2). The most common call types were ‘upsweep2’ (n=92), ‘upsweep1’ (n=79), and ‘pulsed’ (n=64). Several call types were uncommon and occurred less than five times after excluding obscured calls (‘cry’=4, ‘downsweep1’=4, ‘groan’=1, ‘lf mod’=0, ‘mp’=1, ‘squeak’=2). Mean call durations ranged from 0.14 s to 2.95 s. Frequency ranges were wide, with low frequency call minimum down to 35.5 Hz and high frequency call maximum at 3,676 Hz. ‘Pulsed’ calls included many 2-pulse calls, and a number of 10 to 20 pulse calls.

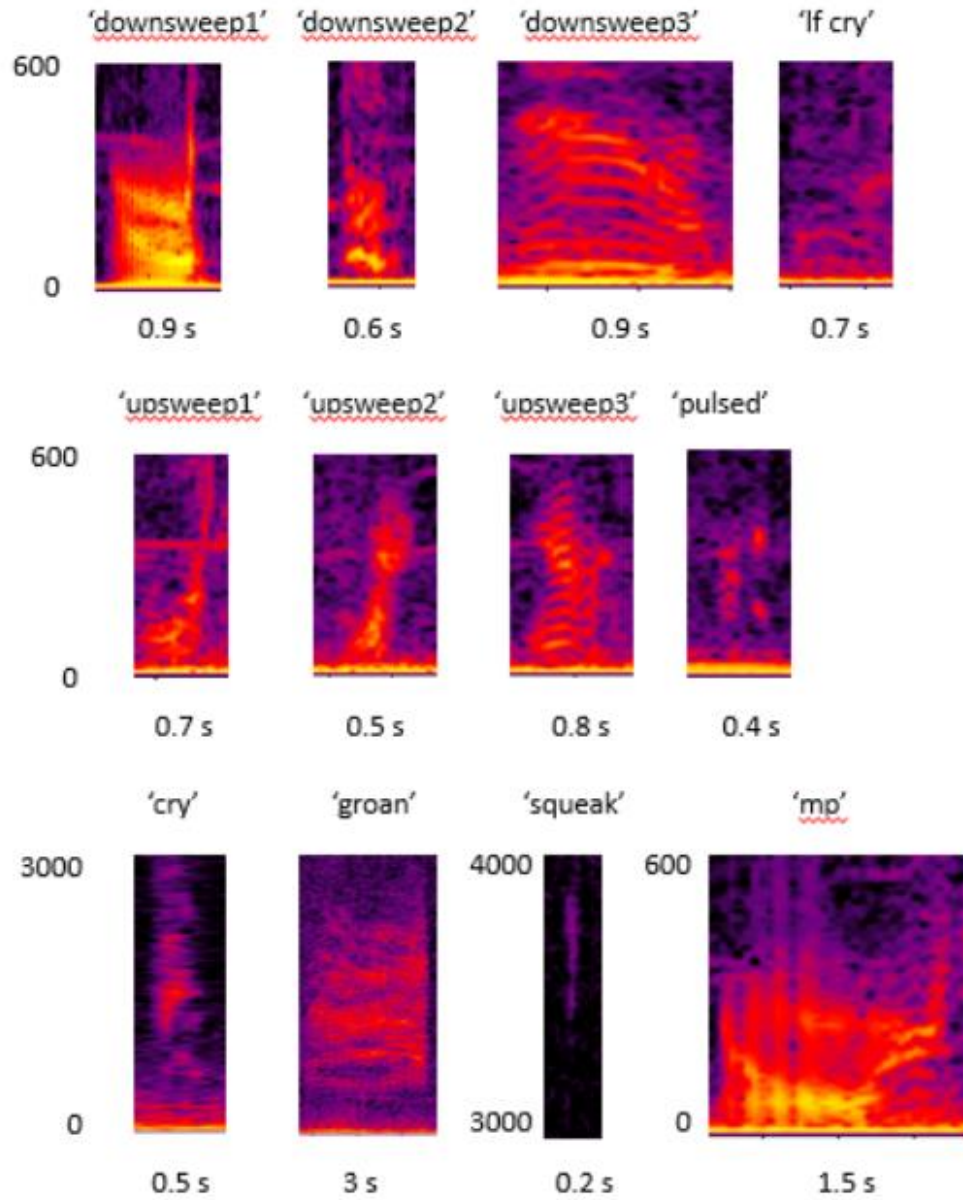


Figure 5.2: Representative spectrograms of the 12 call types. Duration of representative call is noted on the x-axis. Note the different frequency ranges for 'cry,' 'groan,' and 'squeak.'

Table 5.2: Mean (standard deviation) for spectrogram parameters duration, minimum frequency, maximum frequency, bandwidth, and number of pulses (if applicable) for each call type. All frequency measurements are in Hz.

Call Type	n	Duration (s)	Min Freq (Hz)	Max Freq (Hz)	Bandwidth (Hz)	# pulses
cry	4	0.561 (0.156)	771.5 (385.2)	1778.2 (420.5)	1006.7 (572.7)	NA
downsweep1	4	0.853 (0.146)	44.4 (21.5)	280.6 (41.2)	236.2 (60.2)	NA
downsweep2	17	0.457 (0.159)	50.3 (48.6)	164.1 (83.0)	113.8 (47.8)	NA
downsweep3	12	0.812 (0.350)	44.8 (14.9)	136.2 (63.5)	91.4 (56.9)	NA
groan	1	2.953 NA	390.8 NA	2469.4 NA	2078.6 NA	NA
lf cry	10	0.696 (0.194)	77.9 (30.3)	202.1 (75.0)	124.2 (51.1)	NA
mp	3	1.098 (0.454)	35.5 (24.4)	275.5 (28.5)	240.0 (8.1)	NA
pulsed	64	0.873 (0.686)	85.8 (120.9)	380.3 (229.3)	294.6 (178.1)	3.58 (3.93)
squeak	2	0.144 (0.027)	3309.0 (144.8)	3676.3 (264.7)	367.3 (119.9)	NA
upsweep1	79	0.681 (0.206)	54.5 (22.2)	224.3 (115.4)	169.8 (111.7)	NA
upsweep2	92	0.457 (0.130)	109.8 (146.6)	323.6 (230.5)	213.7 (157.0)	NA
upsweep3	10	0.728 (0.308)	88.8 (47.4)	218.3 (80.8)	129.5 (70.0)	NA

Calls occurred primarily during travel and surface active periods. However, behavioral state was not determined for calls that occurred when behavioral observations were not recorded because observations ceased due to late hour of day and the boat left, or because the group was lost.

Maximum dive depths of the tagged animals ranged from 19 to 109 m. The maximum depth in the areas that tracked groups visited was approximately 180 m. Stationary and presumably resting groups were located in shallower and inshore areas, with a maximum depth of approximately 100 m. Traveling groups traversed deeper and further offshore areas where the depth reached up to 180 m. It is likely that stationary resting animals were diving to the bottom. Mothers appeared to rest either at the surface or on the bottom, and the calf stayed in close proximity. There was no significant difference between the maximum dive depths of tagged mothers and calves.

Some sounds on the recordings were noted as resembling a surface impact. There were also sounds that might be expected from the tag's suction cups slipping along the animal's side, or from another animal rubbing against the tag or tagged animal (sounds like rubbing a balloon). The source of these sounds is currently unverified and require further investigation.

5.5 Discussion and Conclusions

Social call vocalization rates from 10 tags deployed on mothers and calves were determined to occur between 0 and 16 calls per hour with a mean of 8.5 calls. Large amounts of variation were seen from both mother and calf tags. Vocalization rates were not significantly different between tags deployed on mother vs. calf, nor were they significantly different between group types. However, the results may be confounded/influenced by the small and uneven sample size. A larger sample size (more than 20) may show a trend, since it appeared that tags on calves and in MCE groups recorded more calls. Ideally, equal numbers of tags on mothers and calves, and on MC and MCE groups would be tested. In addition, calls were often produced singly or in bouts, with long periods of quiet in between. Calls were primarily recorded during surface active and traveling periods, so the number of calls recorded was likely affected by the behavioral state of the group. On some of the tags where concurrent behavioral observations were not available, vocalizations were noted to occur in close temporal proximity to sounds that

appeared to be from surface activity. Efforts have begun to attempt to match specific call types with behavioral state and depth to determine if a correlation exists between call production and behavior. If call production is related to certain behaviors, specific call types may be functioning as contact, recall, or organizational calls. Other factors such as age of calf, nearby presence of a boat, other whales, or other disturbances may also influence call rates and types.

Some sounds on the recordings resembled sounds expected from a surface impact. There were also sounds that may be from the tag's suction cups slipping along the animal's side, or from another animal rubbing against the tag or tagged animal. Verification of the cause of these sounds may come from comparison to underwater video and comparison to behavioral records. Of particular interest would be a description of the sounds produced by surface impacts, since these have been hypothesized to be methods for long-distance communication. However, there have been challenges matching recorded impact-like sounds with behavioral observations, precluding further study at this time. Surface activity has an impact on the tag deployment duration. Two mothers appeared to knock off their tags during a breach.

Thirteen different call types were described in this chapter. Some resembled single song units or social sounds reported from previous studies. The 'cry' and 'lf cry' were somewhat similar to the 'squeak' described by Dunlop et al. (2007) and the 'trumpet' described by Fournet et al. (2015), though at different frequencies. 'Downsweep1' was similar to the 'growl' and 'downsweep3' similar to the 'variable moan' from Fournet et al. (2015). The 'groan' was a broadband call that may be similar to the 'trill' from Dunlop et al. (2007). The 'lf mod' call with multiple inflection points appears similar to the 'groan' from Dunlop et al. (2007). 'Upsweep1' appears similar to the 'whup' from Fournet et al. (2015), the 'grunt' from Stimpert et al. (2011), and the 'wop' from Dunlop et al. (2007). 'Upsweep2' appears similar to the 'bark' from Dunlop et al. (2007) or may be similar to the 'short grunts/upsweeps' from Stimpert et al. (2011). 'Upsweep3' is similar to the 'modulated moan' from Dunlop et al. (2007) and Fournet et al. (2015). The 'downsweep2', 'mp', and 'squeak' calls did not appear to be represented in existing literature. The 'pulsed' calls also appeared to be different from the pulsed and repetitive calls that have been published.

Some calls were produced more frequently than others. The most common call types were 'upsweep2' (n=92), 'upsweep1' (n=79), and 'pulsed' (n=64). Several call types were

uncommon, occurring less than five times during the 44 hours of recordings. All calls were recorded from tags on both mothers and calves except for the ‘groan’ (n=1) recorded from a mother. Since the majority of call types were recorded from tags placed on both mothers and calves, and from both MC and MCE groups, they are likely used to communicate between mother and calf. These calls are relatively simple and short, compared to song units that are often longer and sometimes include multiple parts. This may allow the calf to quickly master these vocalizations. Most calls utilize the frequencies below 400 Hz similar to the social calls described by Dunlop et al. (2007) and Fournet et al. (2015), but were different to the higher frequency calf calls described Zoidis et al. (2008).

In a few cases, such as the upsweeps and the pulsed calls, more categories may be necessary. For example, the pulsed call category some that included 2 to 3 pulses, and a number of 10 to 20-pulse calls. The 2 to 3-pulse calls usually contained a lower frequency first pulse and higher frequency second and third pulses while the 10 to 20-pulse calls were more consistent in frequency content. However, a number of pulsed calls fell in between the two possible categories, so the pulsed calls were not subdivided into separate types. An automated clustering method may be useful to objectively classify calls. A quantitative comparison of the call types described here to those previously described could determine if some call types are present world-wide.

One of the difficulties of using tag recordings is that the vocalizing individual cannot be identified definitively. In some low-frequency baleen whales, the vibration from the vocalization can be picked up by the accelerometers (Goldbogen et al. 2014). However, the vocalizations from these humpback whales were not recorded by the Acousonde’s accelerometers, possibly because the sample rate of the accelerometers is not high enough. Though it was not possible to confirm that the tagged animal was calling, comparisons in vocalization rates were made based on the tagged individual since the calls are quiet and more likely to be recorded from the tagged individual. In examining call parameters, all calls were grouped together. This way, if some quieter calls were from a non-tagged animal in the group rather than the tagged animal, it would still be analyzed as a social call from the group. In the future, multiple tags deployed simultaneously on more than one individual within a group may be able to identify the vocalizing individual.

A major driving factor behind this project was to create a catalog of social sounds produced by mother-calf groups in the Hawaiian breeding grounds. The results presented here document a variety of sounds produced by mother-calf groups, though it is likely not a comprehensive list. Another motivating factor was to report the parameters of the social sounds so that estimates could be made of the impact of anthropogenic noise. Although no measurements of sound pressure level were presented here because the social calls were at times at the same sound level and overlapped with background chorusing, frequencies utilized in the calls are reported. Sometimes a social call was visible in the spectrogram only because it was a lower frequency than a song unit in the background. This makes analysis of frequency content possible but not analysis of sound pressure levels. Future analysis may be possible in order to determine sound levels of social sounds received at the tag. Frequency content can still inform researchers about possible effects of other sounds on the acoustic communications of mother-calf groups. Low frequency sounds between 30 and 400 Hz are most likely to mask the commonly used call types of mothers and calves. In Hawaii, boat engines are most likely to mask the vocalizations of humpback whale mothers and calves.

This is the first study to describe vocalizations from mother-calf groups in the Hawaiian breeding grounds. Previous studies of social sounds have been limited to migration routes, feeding grounds, or calls attributed only to calves in Hawaii. Analysis is underway to determine if the behaviors of the animals are correlated with sound production. The hope is to continue working to expand the social sound catalog for the Hawaii region. The catalog could be a useful tool in describing part of the acoustic environment of Hawaii during the winter and for acoustically identifying non-singer groups.

CHAPTER 6

Conclusion and future directions

The goal of this dissertation was to develop a holistic understanding of the acoustic behavior of Hawaiian humpback whales. This involved examining the sounds produced and received by individuals and groups of individuals at various spatial scales. Both the songs produced by male humpback whales and the non-song vocalizations produced by mother-calf groups were investigated to examine the population structure, habitat use, soundscape, and vocalization repertoire of humpback whales in Hawaii.

6.1 Summary of conclusions

1. Humpback whales wintering in the Northwestern and Main Hawaiian Islands appeared to be part of a continuous population with differences in song unit use occurring as the location changed from one end of the island chain to the other.
2. Humpback whale chorusing around the island of Kauai added approximately 6 dB to the soundscape during humpback whale season compared to non-humpback season.
3. Sound pressure levels (SPL) during the humpback whale season at most locations off Kauai exhibited a diel pattern where sound levels increased by approximately 1 dB during the day compared to night, while no pattern existed during the non-humpback season.
4. SPL at northern locations were generally higher than southern locations around Kauai during humpback season.
5. A humpback whale calf traveling with a singing escort was exposed to the full SPL of song at 126 to 158 dB re 1 μ Pa depending on its distance from the singer.
6. Non-song vocalizations produced by mothers and calves were quieter and less frequent than the songs prevalent on breeding grounds, generally occurring in calling bouts at rates of up to 16 vocalizations per hour.
7. Thirteen non-song vocalization call types were identified.

8. Non-song vocalizations primarily used low frequencies in the 30 to 200 Hz range although some calls were up to 2.5 kHz.

6.2 Challenges and limitations

Two primary methods of data collection were utilized: autonomous acoustic recorders and suction cup acoustic recording tags. In addition to the challenges in working with free-ranging and underwater wildlife, each method has unique limitations. Autonomous recorders were easier to deploy and recover, and could gather data from wide spatial and time scales, but also resulted in enormous amounts of acoustic data. The large volume of data made manual analysis too time-consuming, necessitating the use of automated algorithms. It was also limited in ability to identify or verify the source of recorded sounds and would not detect animals that were not vocalizing or otherwise producing sounds. Tagging humpback whale mothers and calves was also challenging. It required a lot of patience, tolerant groups of whales, and good weather, which prevented large sample sizes. However it provided more detailed information at an individual scale and could be paired with other behavioral observations to provide context to sound production. Even if the individual was not vocalizing, the tag provided movement data and recorded the sounds of the environment around the individual.

6.3 Future Directions

The production method of vocalizations of baleen whales are still largely unknown. Mysticetes are hypothesized to produce sounds using vocal folds in the airway (Reidenberg & Laitman 2007), but this has not been confirmed. In addition, the directionality or “beam pattern” of vocalizations is poorly characterized. Mysticetes vocalize at lower frequencies than odontocetes, so their calls are expected to be less directional. However, it is still important to elucidate the directionality of calls. This would provide context for passive acoustic monitoring efforts and may be important in tracking whale movements. The source levels of non-song vocalizations have also been minimally studied. Previous studies have suggested that the source levels of most non-song vocalizations are relatively low compared to song. Many significant questions still remain regarding humpback whales: Are feeding calls at similar levels to song and louder than other non-song vocalizations? Are calls from mother-calf groups quieter than

competitive and migrating groups? Is source level of calls related to activity, group type, or individual? Or are certain calls produced at approximately the same SPL no matter the context? Also, what about other populations? Are the mother-calf vocalizations from Hawaii the same as those in Mexico, the South Pacific, or the Atlantic? These are important areas requiring study for a better understanding of vocalizations of humpback whales and their context.

There is still much to explore specifically about the vocalizations of humpback whales. The understanding of the behavioral context of mother-calf vocalizations is still limited. Much more data, including determining which individual is vocalizing, is needed to determine the functions of specific non-song vocalizations. If two or more individuals in a group can be tagged for simultaneous deployments, the received levels at each tag can be used to determine which individual is vocalizing. With the continuous improvements in technology it may soon be possible to create and deploy a relatively small and inexpensive tag with low-light video in addition to the calibrated audio and existing sensors. Such a tag could provide a “whale’s eye” view to correlate underwater behavior to vocalizations without the impact of a videographer in the water. With the rapid changes in technology passive acoustic monitoring hardware, software, and analysis techniques are continuously improved. Perhaps in the future, analysis techniques will allow for detection and analysis of single calls in high noise or multiple overlapping call contexts. This could provide better calculations of source levels and better characterizations of non-song vocalizations in the midst of background song chorusing.

The effects of anthropogenic noise on humpback whales are an ongoing area of research. One particular area of interest is the effect of whale-watching boat noise on the non-song vocalizations of mother-calf groups in Hawaii, due to the thriving whale-watching industry. Many significant questions relevant to conservation of this species have yet to be answered: How many boats and/or how far away do they need to be before the boat motors mask the calls between mothers and calves? If a boat is close enough to mask mother-calf calls, does the behavioral state of the group change the possible effect of masking? In addition, in order to determine the effects of anthropogenic noise, it is necessary to gain a better understanding of whale hearing. No empirical mysticete audiograms exist; all estimates are based on models utilizing anatomical predictions and vocalization frequencies. They are too large to keep in captivity to train for behavioral audiograms and the auditory brainstem response method does not

appear to work due to the distance between skin and auditory nerves. Hopefully in the near future, new developments in technology, methodology, and opportunity will arise to test the hearing abilities of mysticetes.

Results of the studies reported here provide novel information regarding movements and habitat use of humpback whales in Hawaii. Some follow-on studies are immediately evident to continue and better determine patterns of vocalizations. Further study with more fine-scale resolution of on and off-shore daily movements of singing humpback whales could be conducted with more passive acoustic monitors deployed in a pattern perpendicular to shore. Passive acoustic monitors recording at higher duty cycles to record full songs and deployed at locations optimal for humpback whales in the NWHI could be utilized in conjunction with additional methods such as genetic, photo identification, and satellite tagging to determine if humpbacks in the NWHI are part of the same population in the MHI. Satellite tagging could be used to determine if humpbacks in the NWHI are using the area as a migration corridor or as breeding grounds.

Humpback whales are a particularly interesting species in the current environment, due to their apparent recovery from whaling throughout much of the world, which prompted NOAA to delist 9 of 14 distinct population segments. This is great progress, but threats to humpback whales and other cetaceans still exist. The continually increasing amounts of sound in the ocean from anthropogenic sources is likely one of the most important direct threats to whales given their reliance on sound for socializing, finding mates, and finding food. Understanding the vocalizations and hearing abilities of odontocetes has progressed rapidly through studies of wild, stranded, and captive individuals. Each group provides unique insights into the abilities of each species. For the largest species of odontocetes as well as mysticetes, however, studies are limited to wild and stranded individuals. Thus it has been impossible to conduct controlled experiments on any members of these taxa. Humpback whales are one of the most studied species of mysticete, and therefore provide insight into the capabilities of other less-studied baleen whales. Identification of the many sounds produced by humpback whales allows them to be identified on passive acoustic monitoring systems. Determining the behavioral context of sounds allows scientists to match sounds recorded at passive acoustic monitoring (PAM) locations with activity. Movement patterns determined by vocalizations could be translated to

protective regulations in certain areas. For example, if humpback whales move close to shore at night and offshore during the day, ships could be asked to transit offshore at night and slow down during the day to minimize the risk of colliding with a whale. Though humpback whales appear to be thriving throughout much of their range, ongoing research is vital to improve protective measures, and ensure the continuation of this species into future generations.

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