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Ambient acoustic environments and cetacean signals: baseline studies from humpback whale and gray whale breeding grounds

Author
Seger, Kerri Dawn

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Ambient acoustic environments and cetacean signals: baseline studies from humpback whale and gray whale breeding grounds

A dissertation submitted in partial satisfaction of the
requirements for the degree
Doctor of Philosophy

in

Oceanography

by

Kerri D. Seger

Committee in charge:

Aaron M. Thode, Chair
David Checkley, Co-Chair
Lisa T. Ballance
Sarah Mesnick
Peter Narins
Joel Watson

2016

The dissertation of Kerri D. Seger is approved, and it is acceptable in quality and form for publication on microfilm and electronically:

Co-Chair

Chair

University of California, San Diego

2016

DEDICATION

To Nora Rose Seger and future generations of not only human families, but of all Linnean families on this planet. May scientific information's use as a conservation tool be fully realized sooner rather than later.

EPIGRAPH

They like you very much, but they are not the hell "your" whales.

–Spock

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VITA

2007	B. S. in Muzoocology (Personalized Study Program), The Ohio State University, Columbus, OH
2011	M. S. in Marine Biology, Scripps Institution of Oceanography, La Jolla, CA
2016	Ph. D. in Biological Oceanography, Scripps Institution of Oceanography, La Jolla, CA

PUBLICATIONS

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ABSTRACT OF THE DISSERTATION

Ambient acoustic environments and cetacean signals: baseline studies from humpback whale and gray whale breeding grounds

by

Kerri D. Seger

Doctor of Philosophy in Oceanography

University of California, San Diego, 2016

Aaron M. Thode, Chair
David Checkley, Co-Chair

The past two centuries have seen an increased exploitation of marine habitats by humans, so a growing appreciation of the role ambient noise plays in cetacean studies has resulted. To achieve a broad acoustical view of understudied areas (namely Mexican waters), this dissertation tackles three overarching principles: (1) parameterizing current baseline ambient acoustic environments for subsequent comparisons, (2) determining whether the sounds that animals introduce into their environments can provide employable information for population estimation purposes, and (3) cataloguing and characterizing the sounds whales use to communicate so they can later be compared across time, geography, and

ambient noise levels. Only when we have a handle on the relative contributions of anthropogenic, physical / geological, and biological sounds in a whales habitat can we begin to understand how each source may elicit and / or change their calling behaviors.

Chapter 2 uses an 8-year acoustic dataset from Laguna San Ignacio (LSI), México, to investigate a complex acoustic environment, and to quantify the extent that human-generated noise contributes to this environment relative to natural sound sources. This lagoon has been deemed to be a critical habitat for breeding whales and calving mothers, so vessel traffic is minimized and regulated. I found that humans contribute some noise to the lagoon, but crepuscular snapping shrimp and dusk-centric croaker fish are more intense and pervasive. Therefore, my research validates current management policies for the lagoon and provides a baseline account of a stable acoustic environment that can be compared to future years, should tourist traffic increase.

Chapter 3 develops a model to estimate humpback whale density using ambient noise arising from the songs of many individual animals. What initially began as an analytical model for wind-generated ambient noise, using a collection of randomly distributed sources near the surface, was adapted for randomly-distributed calling whales. The model was tested using data collected in the Los Cabos region of México, which is a breeding ground and part of the migration route for the North Pacific substock. A Generalized Linear Model was used to link humpback-generated ambient noise intensity to concurrent visual surveys. I found that the analytical model provided good predictions of how the intensity of humpback-generated noise varies as a function of acoustic frequency, singer population size, and singer spatial density. In particular, the ambient noise model accurately predicted that singing humpback whales maintain the same separation distance from each other, regardless of singer population size.

Chapter 4 assembles a catalogue of social calls used by humpback whales in the same Los Cabos region and compares them to known social calls from Alaska, Hawaii, and

Australia. By using acoustic tags to collect twenty-one samples from three different social group types over two years, I was able to determine the geographical uniqueness, call rate, repertoire diversity, and repertoire entropy of the whales in that breeding ground. I then determined the variability of these behaviors between differently composed social groups. This work provides a starting point for subsequent studies of social calling behavior of Mexican whales, such as temporal changes in social call repertoire, behavioral context of calls between different social groups, and geographical comparisons between the acoustic composition of other humpback whale habitats.

By tackling all three of these acoustic principles, this dissertation aims to set the stage for understanding ambient noise as part of cetacean habitats by laying out how to measure it, how to use it to our advantage, and how to characterize and compare calls within it. With the new novel tools to quantify sound sources in ambient acoustic environments and to monitor population levels that this dissertation provides, my future research can delve into exploring any geographic and temporal commonalities and disparities.

Chapter 1

An introduction to gray and humpback whales and their acoustic habitats

1.1 Natural history of humpback whales and gray whales

Humpback whales (*Megaptera novaeangliae*) and gray whales (*Eschrichtius robustus*) are both in the Mysticeti parvorder, meaning they do not possess teeth, but rather garner nourishment with strips of baleen that they use to sieve fish and krill out of the sea water. Such behavior occurs on high latitude “feeding ground during boreal (and austral) summer months. Since this dissertation focuses on the North Pacific Humpback whale substock, and gray whales only exist in the northern hemisphere, the migratory schedules we are concerned with follow the boreal seasons. The International Union for Conservation of Nature (IUCN) lists both species as “least concern”.

After maximizing their blubber reserves, both species migrate to subtropical waters to breed and give birth during the boreal winter months. In their breeding grounds, little to no feeding activity occurs, but other behaviors come into play: vying for mates, mating, giving birth, and preparing offspring for the imminent northward migration. Acoustic communication is vital to all of these behaviors since either murky water, or even the general

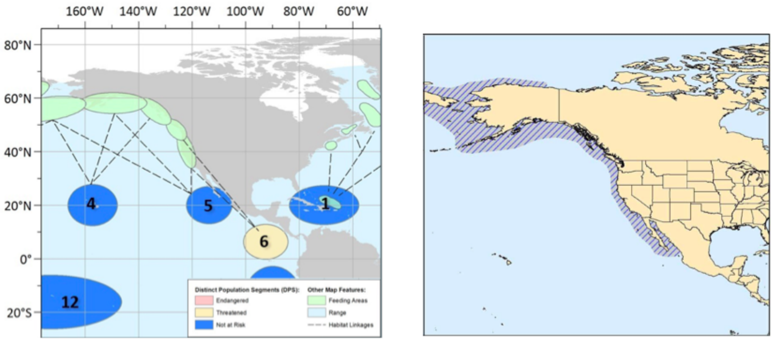

Figure 1.1: Range distribution of humpback and gray whales studied in this dissertation. (l) Adapted from the NOAA Fisheries proposal to delist the humpback whale to "not at risk", this map illustrates summer feeding grounds (green) and winter breeding grounds (blue circle 5) of the North Pacific distinct population segment (or substock) in question. It is of note that individuals from the yellow circle 6 transit through the research area investigated in this dissertation, so may have also been sampled. (r) From The NOAA Division of Protected Resources, the purple areas denote most of the gray whale feeding habitat at high latitudes, and show that its breeding lagoons range along the coast of the Baja California peninsula.

inability to see very far in clear water, limits sight as a viable communication method.

Humpback whale sounds have been heavily studied, with two broad types of their communication identified: songs and calls. Songs are rhythmic, continuous vocalizations, usually organized into phrases and themes (Payne & McVay, 1971; Winn, Perkins & Poulter, 1971). Social calls, which are formally defined in the fourth chapter, are vocalizations made once or in small repetitious bouts, but without the inherent structure of song (Payne, 1978; Tyack, 1982; Silber, 1986).

Male humpback whales may sing to facilitate their reproductive success by establishing territories in what Clapham (1996) calls "floating leks", or by attracting females (Tyack, 1981; Medrano et al., 1994). Social calls, however, are produced by more than just the males (Zoidis et al., 2008), and likely facilitate other behaviors such as protecting calves from predators, maintaining cohesion between mothers and their calves, or vying for position between individuals within competitive groups (Tyack & Whitehead, 1983; Silber, 1986; Clapham et al., 1992; Zoidis, 2008; Cartwright, 2005, Dunlop et al., 2008; Dunlop et al. 2007). Historically, songs have received most academic attention, but over the past two decades, research in social calls has garnered increasing focus.

Gray whales do not sing, but they do use a variety of vocalizations that are hypothesized to fulfill behavioral functions similar to the social calls of humpback whales (Wisdom, 2000). These include maintaining contact between individuals (Fish et al., 1974; Norris et al., 1977), and recognizing each other as conspecifics (Dahlheim et al., 1984).

In order for these songs and calls to reach the senders intended receiver(s), though, other sound sources in the whales habitats cannot impede transmission by masking the calls (i.e. covering them up). There are many natural, physical, and anthropogenic sources that exist in the humpback and gray whale breeding grounds, though, that could mask the signals. The combination of all these sound sources comprises a habitats “ambient acoustic environment”. Each habitat’s ambient acoustic environment is different, and the ones in question for this dissertation will be discussed in greater detail in the next section.

1.2 Geographic areas

1.2.1 Los Cabos, México

A collection of capes at the Southern-most tip of the Baja California Peninsula comprises the Los Cabos region. Here, the Pacific Ocean meets the Sea of Cortez. Cabo Pulmo is the closest marine sanctuary (about 90 km East), and maritime regulations on vessel traffic are relatively relaxed. Waters are typically warm (in the 20C range), currents can be strong, but tides are relatively inconspicuous (they vary about one meter between high and low tide), and the continental shelf drops off quite abruptly along most of the coastline. Humpback whales are joined by other cetacea such as dolphins, the occasional blue whale, and, on rare occurrences, a dwarf sperm whale. Sea lions, sea birds, and many fish species are prolific in Los Cabos, thus supporting large sport-fishing, commercial fishing, and whale-watching operations. Such operations bring the overwhelming presence of humans to the Los Cabos habitat, whereby trawlers, sport fishing vessels, yachts, jet skis, pangas of all types, glass-bottom boats, zodiacs, and more, speed in and out of two harbors in Cabo San Lucas and San Jose del Cabo. As evidenced from the recent Hurricane Odile, tropical storms, high winds, and rain are naturally occurring phenomena in the Los Cabos region. All of these biological, anthropomorphic, and physical entities introduce unique sounds to the Los Cabos ambient acoustic environment on their own schedules. These sounds are further shaped by the continental shelf, relatively deep waters, granite bottom, and single-sided coastline.

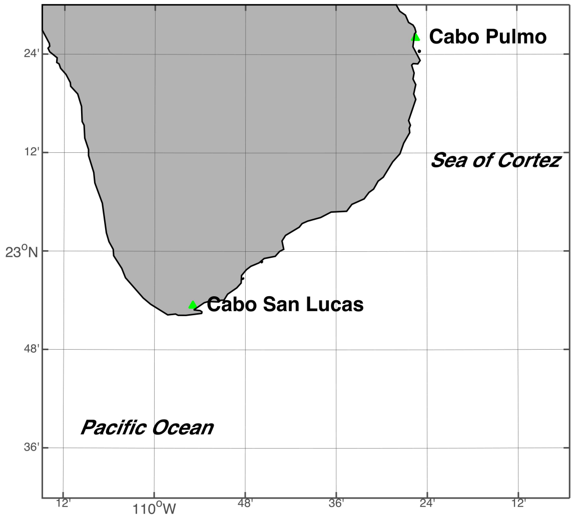

Figure 1.2: A zoomed in map of the tip of the Baja California peninsula that illustrates the productive waters where the Pacific Ocean and Sea of Cortez meet and where humpback whales migrate through and breed and calve in.

1.2.2 Laguna San Ignacio, Mexico

As one of several lagoons halfway down the Pacific Ocean side of the Baja California Peninsula, Laguna San Ignacio is a relatively contained environment. It is part of the Vizcaino Desert Biosphere Reserve, and regulations on boating traffic, fishing, and whale-watching are tightly adhered to. Water temperatures are similar to that of Los Cabos (averaging 20-25C in the winter months) and currents are very strong, especially during mid-tide as water rushes in and out of the mouth at the southern end. Tides cause the water height to vary a great deal (up to 2.4m) (pers. comm. Steven Swartz), with an area the size of a football field full of floating pangas one hour, and grounded pangas in wet silt the next. Being a lagoon, there is rarely a deep section, but rather “bajos” (underwater “mesas”) that can be less than a meter below the surface and thus navigational hazards. The lagoon is surrounded on three sides by coastline, so access to the open ocean is minimal and only at the mouth. Gray whales are joined by dolphins, lobsters, bivalves, many fish species, and snapping shrimp. The local fishing villages are small, and many fisherman become tour guides for the whale-watching seasons, thus limiting the number of vessels present. The occasional yacht enters the lagoon, but large fishing ships are unheard of and vessel activity is anything but superfluous. Laguna San Ignacio felt the effects of Hurricane Odile, also, but high winds and sand storms are commonplace in this desert-locked body of water. While some biological, anthropogenic, and physical sound sources overlap with those in Los Cabos, Laguna San Ignacio’s collection of contributors to its ambient acoustic environment is unique in and of itself. Perhaps the largest difference between Laguna San Ignacio and Los Cabos is that the former is relatively very shallow, silty, and surrounded on nearly all sides by land, thus creating a very different set of features to shape the sound waves traveling through it.

1.3 Data Collection and Analysis Overview

Acoustics can be studied actively or passively. Active acoustics involves producing a controlled sound, then receiving it from some distance away in the water column, or after it has reflected back from another surface (such as the ocean bottom, an ice shelf, or a vertical natural feature). Passive acoustics, on the other hand, requires no sound generation: a receiver placed strategically in the water column will capture the desired signals a

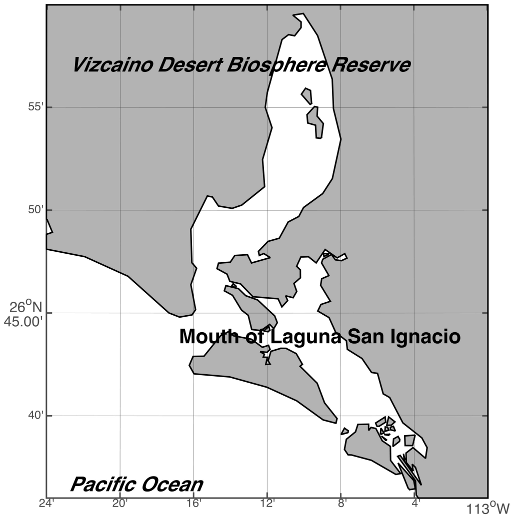

Figure 1.3: A zoomed in map of Laguna San Ignacio showing how unexposed it is to the open ocean as compared to Los Cabos.

researcher wishes to record. In the case of acoustics, a signal is the sound or set of sounds a researcher is interested in. For example, if one is investigating an ambient acoustic environment, every sound present in the environment is a signal. However, if one is investigating the call rate of a single species, only vocalizations produced by that species are the signal. Everything else is considered “noise”.

1.3.1 Hardware

The recorders used by acousticians vary greatly. Only a few commercial recorders exist, but the industry has grown over the past decade and continues to do so. Many acousticians build their own recorders. The main components of all recorders are: (1) a hydrophone that is calibrated to the desired sensitivity level for detecting sound as pressure waves and the frequency range (pitches) of interest, (2) a computer that converts these voltage readings from the hydrophone to bits that are stored on a hard drive, (3) a power source to provide energy to the system, and (4) a water-tight pressure case to house everything.

By design, then, data are stored internally until the recorder is recovered.

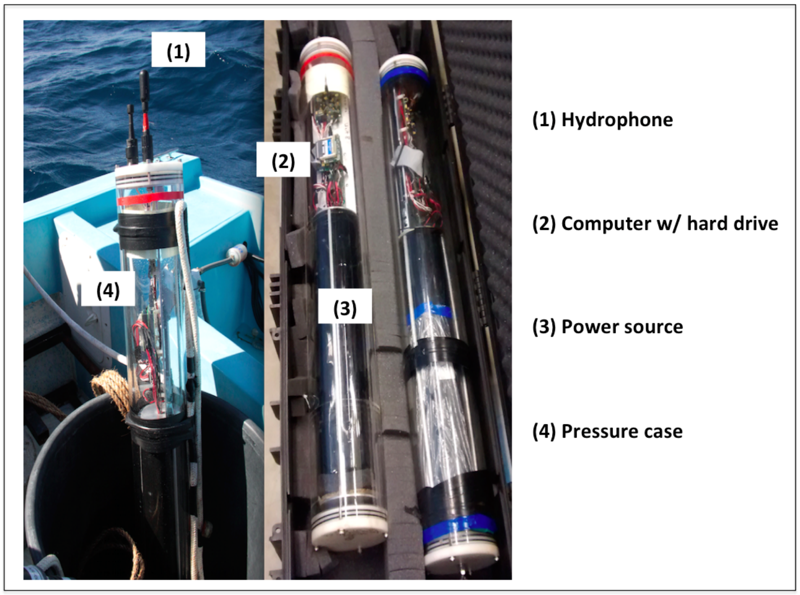

Figure 1.4: The components of most recorders are, broadly, a hydrophone, a computer, a power source, and a pressure case. The recorders used in this dissertation are pictured here both in the lab (r) and activated for deployment in a panga (l).

1.3.2 Field techniques

Many ways to deploy and recover recorders exist, and the method of choice is usually dictated by water depth. In shallow water, the recorders can be anchored to the ocean floor by a weight and installed by a diver, or placed on a line between two anchors and lowered over the side of a boat in a straight line. To recover recorders with these methods, divers do so by hand, or the recorder is reeled back in by catching the line between the anchors with a grappling line (a rope with a hook) as it is towed behind a boat. The line and grappling hook method was used for chapter 2's data collection.

In deep water (>50 m), however, the recorder is usually strung on a line between a weight, acoustic release, and buoys. The weights hold it on the ocean floor while the buoys at the top keep the entire assembly vertical in the water column. For deployment, the assembly is lowered by hand or by winch over the side of a boat so that it sinks to (hopefully) a flat and stable location. For recovery, a high frequency code is sent to the acoustic release, signaling it to either burn free or mechanically separate from the weight. The weights remain on the ocean floor, and the buoys carry the recorder and the acoustic release back to the surface where researchers watch for it to haul it back on board. Data for chapter 3 were collected using this method.

1.3.3 Post-processing for passive acoustic recorders

If data are successfully written to a recorders hard drive, they can be downloaded in many formats and processed for subsequent analysis. For this dissertation, the data were saved to the recorders on hard drives in .DAT files: a series of amplitudes sampled every so many milliseconds that can be converted into power spectral densities (PSDs) for any desired amount of averaging time per Hertz across the sampled spectrum (usually 0-6250 Hz in this dissertation). A power spectral density quantifies the acoustic power present per unit time per unit frequency (or pitch). With PSDs, other information can be gleaned, like statistical analyses of the distribution of sound intensity over hour-long segments, a topic that will be covered in the second chapter of this dissertation.

1.3.4 Complementary types of data collection

When narrowing a research focus to a single, animalian sound source within an ambient acoustic environment, other types of data can prove helpful. Visual surveys, for example, are a natural complement to acoustic data insomuch that researchers can monitor the distribution and categorize the behaviors and movements of the whales at the same time their songs and calls are being recorded. Visual and acoustic surveys have long been used separately for population estimation studies but are recently being co-employed (Clark & Fristrup, 1997; Raftery & Zeh, 1998; Mellinger & Barlow, 2003; and Barlow & Taylor, 2005). For chapter 3 of this dissertation, the line transect method was combined with passive acoustics and utilized to compare humpback whale song intensity to the number of whales present within the audible radius of a recorder.

1.3.5 Alternative recorder types

When narrowing a research focus to a single species or small subset of individuals within that species, compact recorders can aid in targeted signal collection. Recording vocalizations from just a few select animals has been done in the past by either localization algorithms with acoustic arrays (determining where an animal is by the angle at which its sounds arrive at a line of hydrophones) (Watkins & Schevill, 1972; Watkins, 1976), video recording while diving or snorkeling (Zoidis et al., 2008), or placing acoustic and/or video camera "tags" to their bodies (Stimpert et al., 2007; Goldbogen et al., 2014). National Geographics critter cam is a familiar example of such a tag.

The first acoustics tags were attached to elephant seals (Burgess et al., 1998), but their use has quickly spread to free-swimming cetaceans. Todays most popular professional tags are the DTAG built by Johnson and Tyack (2003), and the B-probes and Acousondes from Greeneridge Sciences, Inc. (Burgess, 2009). In addition to acoustic data, these tags also collect information about the depth, 3-D movement of the animal, vibrations along its body surface that coincide with its sound production, and geographic position (as a result of a new GPS addition made by myself and colleagues at Cetos Research). It is still impossible to tell whether the recorded calls are from the tagged whale or from one swimming nearby, though, unless the tag samples fast enough to detect bodily vibrations at all frequencies in the tagged whales vocalizations. This is analogous to placing a microphone on a persons shirt collar: his or her voice will get picked up, but so will everyone else's who is in a conversation with that person. Caution must be taken in processing tag data for this and several other reasons that will be discussed in chapter 4.

Figure 1.5: Three views of the Acousonde by Greeneridge Sciences, Inc. used in this dissertation: top right is the tag itself to the scale of a human hand, top left depicts the attachment method of the tag encased in a buoy with suction cups, and the bottom shows the scale of the tag to the size of a humpback whales body.

1.3.6 Post-processing for acoustic tags

Once data from an acoustic tag are collected, they are processed in the same way as the other recorders into power spectral densities. Another name for a power spectral density plot is a spectrogram: a "heat map" of the relative sound intensities across time and frequency. Analysts can manually scroll through these spectrograms to visually locate, describe, and classify song phrases, call types, boat engines, and other sound sources. After sufficient descriptions of each call type or song unit are made, automated algorithms can be written to detect and classify them using just the raw data. This dissertation goes as far as manual classification in chapter four since it is establishing a baseline catalogue of calls with too little information available for algorithm development.

1.4 Motivation and main dissertation questions

As stated at the beginning, IUCNs Red List considers both the humpback whale and gray whale “least concern”, but population sizes of humpback whales are becoming large enough to possibly remove them (Reilly et al., 2008). The gray whale population needs to increase more to be a candidate for delisting. It can be deduced then, that consistent measurements on population size and rate of growth are critical to ascertaining the level of endangerment for both species. Furthermore, understanding what constitutes “healthy” acoustic habitats for humpback and gray whales is vital to fostering continues population growth.

This dissertation was motivated by these two conservation concerns. It aims to provide baseline information about the ambient acoustic environments of cetacean habitats, to present a new method for monitoring their population size, and to offer the first details concerning social calls used specifically by humpback whales on one of their understudied breeding grounds.

This dissertation poses three objectives, one for each chapter:

1. How does one quantify the presence of human (anthropogenic) noise in an overall acoustic environment for management purposes? What other factors besides intensity, or “loudness”, should be taken into consideration?

2. If animal vocalizations are the dominant sound source in a particular environment (vs. physical or anthropogenic sources), can researchers use that sound to measure its population size?

3. How stereotyped is the calling behavior of the humpback whale on its breeding ground, and do different social groups use varying call types at different rates, suggesting a behavioral-dependent context for their calls?

In summary, research in bioacoustics can focus on sounds produced by (1) the entire ambient acoustic environment, (2) a single mechanism in that environment (e.g. wind, boats, or animals), or (3) produced by a particular species. This dissertation covers all three aspects: Chapter 2 analyzes entire Laguna San Ignacio acoustic environment, Chapter 3 analyzes the contribution humpback whales make to the overall acoustic environment off Los Cabos, and Chapter 4 examines some specific characteristics of social calls used by the Los Cabos humpback whale substock. Chapter 5 (the conclusion) interprets results from chapters 2 through 4 in terms of future applications for sanctuary and conservation management.

Chapter 2

The ambient acoustic environment in Laguna San Ignacio, Baja California Sur, México

2.1 Abstract

Each winter gray whales (*Eschrichtius robustus*) breed and calve in Laguna San Ignacio, México, where a robust, yet regulated, whale-watching industry exists. Baseline acoustic environments in LSI‘s three zones were monitored between 2008 and 2013, in anticipation of a new road being paved that will potentially increase tourist activity to this relatively isolated location. These zones differ in levels of both gray whale usage and tourist activity. Ambient sound level distributions were computed in terms of percentiles of power spectral densities. While these distributions are consistent across years within each zone, inter-zone differences are substantial. The acoustic environment in the Upper Zone is dominated by snapping shrimp that display a crepuscular cycle. Snapping shrimp also affect the Middle Zone, but tourist boat transits contribute to noise distributions during

daylight hours. The Lower Zone has three source contributors to its acoustic environment: snapping shrimp, boats, and croaker fish. As suggested from earlier studies, a 300 Hz noise minimum exists in both the Middle and Lower Zones of the lagoon, but not in the Upper Zone.

2.2 Introduction

2.2.1 Overview

The gray whale (*Eschrichtius robustus*) is a coastal baleen whale species whose modern range spans the North Pacific Ocean. The dominant Eastern North Pacific population breeds and calves during the winter months in lagoons along Baja California, México, where it migrates from summer feeding grounds in the Bering, Beaufort, and Chukchi Seas (Poole, 1984; Swartz, 1986). Laguna San Ignacio (LSI) is one such lagoon where wintering whales aggregate.

The lagoon is located halfway down the Pacific side of the Baja California peninsula. It is surrounded by flat desert and experiences strong sea breezes averaging 12 m/s with 15 m/s gusts (Guerra et al., 2010). The depth of the entrance is usually 281 m, but is known via traditional local knowledge to experience strong tidal flows that fluctuate up to 6-8 m during spring tides (Jones, 1981). As a result, large silt movements are capable of burying 0.5 m-tall lobster pots in a single day (pers. comm., local fishermen). Moving northward, away from the mouth, the lagoon becomes shallow and rocky, interspersed with silty patches. Long, sandy ridges, called “bajos”, are as shallow as 7 m and occur halfway between the mouth and northern-most boundary of LSI (Swartz and Urban, 2014).

Following conventions set forth by Jones and Swartz (1984), this project divided the lagoon into Upper, Middle, and Lower geographic “zones” (Fig. 1). The Upper Zone encompasses the northernmost 18 km of the lagoon; moving south from here, the Middle

Zone ends at Punta Piedra (a local landmark at the narrowest point of the lagoon), about 7.5 km further down from the Upper Zones boundary. The Lower Zone begins at Punta Piedra and extends about 7 km southward to where the lagoon meets the Pacific.

As documented by commercial whaling operations since the 19th century, gray whales begin to occupy the Baja lagoons at the end of each years boreal autumn. Pregnant females with quickly approaching due dates, or calves born en route, arrive in the lagoon firstgenerally in December and January (Rice and Wolman, 1971). They are followed sequentially by females in estrus, adult males, immature females, and finally by immature males (Herzing and Mate, 1984). Their peak density in LSI is usually reached by mid-February. Visual surveys suggest that adults ("singles") engaging in breeding activities and mothers with older calves occupy the Lower and Middle Zones. Females giving birth and nursing new calves predominantly reside in the Upper Zone, where the water is warmer and shallower. This distribution has become more pronounced in recent years (González et al., 2006; Swartz et al., 2012).

LSI is a UNESCO site within México's Vizcaino Biosphere Reserve, and is also one of México's federally designated marine protected areas and whale refuges. Local residents have fished the lagoon for over a century, and fishing remains the dominant human activity during whale-watching's off-season, but whale-watching tourism during the breeding season has become increasingly important to the local economy. Eco-tourism charter boats from San Diego began entering LSI in the 1970s to whale-watch during the winter, and in 1984 ecotourism groups began setting up temporary winter camps along its southern shore (Swartz, 2014). Today the Middle Zone contains five eco-tourism spots: Camp Kuyima, Kuyimita, Campo Cortez, Baja Expeditions, and Baja Discovery. The Upper Zone contains only Pachico Whalewatching.

Pangas, which are rigid-hull outboard motor boats with a 12-passenger capacity, are used for transporting tourists from these camps in the Middle Zone to whale-watch in the

Lower Zone whenever winds are calm enough. Once in the Lower Zone, the tourist pangas are permitted to approach and observe whales. Also, small (100 ton) cruise ships from San Diego, California, anchor in the Lower Zone, and local pangas take their passengers whale-watching in the Lower Zone. Tourism activity is regulated in terms of the number of pangas allowed in the Lower Zone at a given time; however, the expected completion of a paved road to the lagoon over the next couple of years is expected to lead to a boost in visitors and an incentive to increase the number of panga trips into the lagoon. Before this study, no information existed on the current ambient acoustic environment of the lagoon. It is difficult to anticipate how potential increases in tourist traffic might affect the ambient acoustic environment without knowing the degree to which it currently contributes.

This paper presents a multi-year analysis of the ambient acoustic environment of all three zones in LSI. The results tackled the following goals: (1) identifying sound sources in the lagoon, (2) determining whether any of these sources are inherently cyclical, (3) identifying the dominant source in each zone, and (4) determining the contribution of anthropogenic noise to the overall ambient noise environment. The rest of the Introduction reviews previous acoustic research in LSI, while Section II describes the acoustic instruments used for this study and outlines the methods for deploying and recovering them. Section III explains the analysis methods for comparing ambient acoustic environments on daily, seasonal, and annual bases, using power spectral density percentiles. This analysis approach has been applied in other waterways (Erbe et al., 2013; Merchant et al., 2013), but to our knowledge not to lagoon environments. Section IV presents comparisons of these diel, seasonal, and annual cycles in all three zones, but specifically focuses on data from 2009 and 2011 (when at least two zones were monitored simultaneously). Finally, Section V uses the observed patterns to discuss the degree to which panga noise contributes to the overall environment (relative to biological and physical processes). As the amount of tourist activity in LSI has remained relatively stable since 2008 in all three zones, the results of this paper can provide a baseline for comparing any modifications that future increases in tourism activity may create.

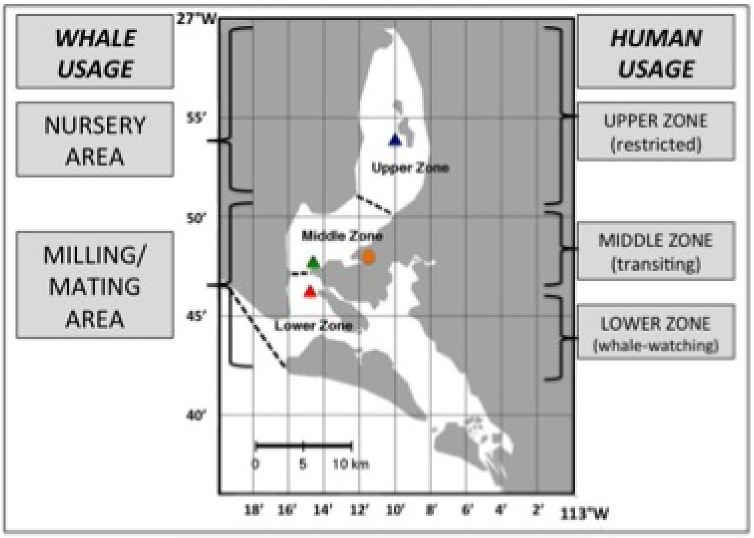

Figure 2.1: A map of Laguna San Ignacio with dotted lines delineating the three man-made "zones" that divide the lagoon into a relatively heavily-trafficked whale-watching zone (Lower), a moderately-trafficked transit zone (Middle) and a restricted nursery (Upper). The Middle Zone has been the only one monitored consistently since 2008. Triangles denote acoustic recorder deployments, while the circle denotes the weather station deployment location.

2.2.2 Previous acoustic research

As part of larger field studies by Mary Lou Jones and Steven Swartz, Marilyn Dahlheim conducted the first acoustic research in LSI at Punta Piedra (Middle Zone) during the 1980s (Dahlheim et al., 1984; Dahlheim, 1987). In addition to over-the-side audio tape recordings and playback studies starting in 1981, Dahlheim deployed a cabled hydrophone 8 m deep to measure the overall acoustic environment between 1982 and 1984. Dahlheim (1987) also compared gray whale calling rates throughout their migration routes and concluded that the most active calling occurs in their mating/calving grounds (such as LSI). She also conducted measurements of the ambient noise background and found a noise minimum near 300 Hz. She speculated that gray whales use vocalizations near 300 Hz to take advantage of this acoustic bandwidth "window" below the broadband snapping shrimp cacophony and above croaker and other pulsive biologic sounds at lower frequencies (e.g. near 100 Hz).

Later, Sheyna Wisdom conducted boat-based measurements in 1999 and 2000 (Wisdom, 2000) to study the developmental process of sound production in gray whales. She identified a new call type (type 1a) that tends to precede calves breaching, and associated higher calling rates with increased physical activity (rubbing and swimming compared to resting). Ponce et al. (2012) calculated calling rates of the three most common call typesrates that we will use later to consider how much gray whale vocalizations contribute to LSI's ambient acoustic environment.

These researchers have collectively established that gray whales in LSI use at least 6 call types, ranging from rapid, rhythmic pulses to FM sweeps between 100 and 1600 Hz (Ponce et al., 2013), which are consistent with recordings of gray whales from habitats beyond Laguna San Ignacio (Fish, 1974; Moore and Ljungblad, 1984; Crane and Lashkari, 1996; Ollervides et al., 2007; Stafford et al., 2007). Call functions are believed to include behavioral-state broadcasts, (Crane and Lashkari, 1996), contact calling (Fish et al., 1974; Norris et al., 1977) and/or species recognition (Dahlheim et al., 1984). Since these calls lie within the same bandwidth as sounds produced by pangas and tourist fishing vessels, there are conservation and management interests in understanding the relative contributions of vessel noise and gray whales to the acoustic environments.

Other resident sound-producing species include snapping shrimpeither Crangon dentipes or Synalpheus lockingtoni (Everest et al., 1948; Dahlheim et al., 1984) and croaker fish (DSpain and Batchelor, 2006; Aalbers and Drawbridge, 2008; Luczkovich et al., 2008). Snapping shrimp sounds fall within a 500 to ¿3000 kHz bandwidth and they exhibit crepuscular cycles in other tropical waters (Lammers, et al., 2008). Winds and tides also play a role in creating background noise levels, but generally at higher frequencies (e.g. above a kilohertz) (Urick, 1983).

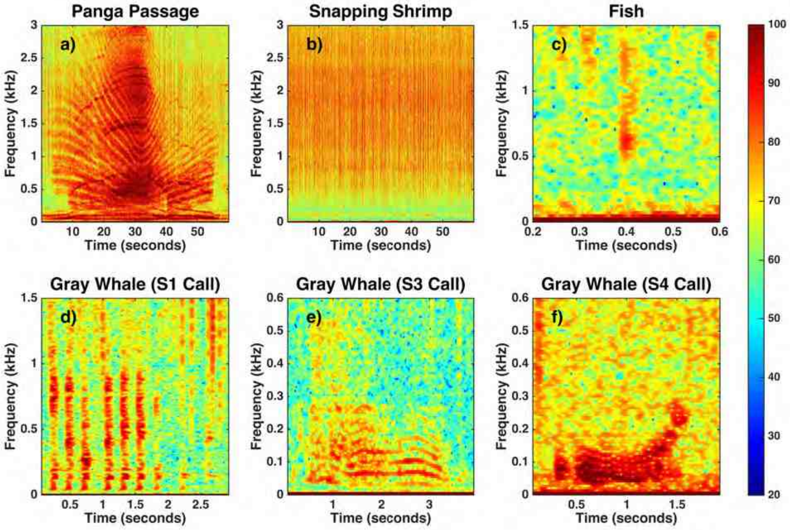

Figure 2.2: Sound sources in Laguna San Ignacio are physical, biological, and man-made. Non-cetacean examples from 2010 and 2011 are a) panga engines; b) snapping shrimp; and c) fish (most likely croaker). Gray whale calls include pulsive sounds like d) ‘S1’, and frequency modulated sounds like e) ‘S3’ and f) ‘S4’. The sampling rate for all examples was 12.5 kHz. Spectrograms were generated with a Hanning window and used sampling windows ranging from 512 to 2048 points, all with 90% overlap.

2.3 Methods

2.3.1 Acoustic Recording Equipment

Since 2008 researchers from the Scripps Institution of Oceanography have collected acoustic data in all three zones (Fig. 1), though rarely from multiple zones in the same season. The same bottom-mounted recorders described in Ponce et al., 2013, collected data. Sampling rates were either 6.125 kHz or 12.5 kHz, depending upon the year, and the data were sampled continuously, except for a few hours every two days, when data were written to a hard disk. HTI-96-MIN (High Tech Inc.) hydrophones with -171 dB re 1 V/ sensitivity were used for all six years.

2.3.2 Field procedures

Acoustic recorders were deployed each season in early February and recovered in mid-March. They were attached to a 100 m polypropylene line connected on each end to an anchor. Depending upon the year, one, two, or three recorders were attached to each line, and these sets of recorders will be referred to as “assemblies”. Each assembly was hand-lowered from the side of a slow-moving panga so it could be laid out horizontally along the lagoon’s bottom. Because polypropylene is buoyant, it could potentially entangle whales, so small lead fishing weights were attached every 5 m to hold the line close to the bottom. While this configuration reduced entanglement risk, it increased the potential that an assembly would be buried. To recover an assembly, a grappling hook was towed from the stern of a slow-moving panga to snag the polypropylene line and manually reel it in.

Specific deployment locations of acoustic assemblies within a zone will henceforth be referred to as “sites”, Instruments were deployed at specific sites within each of the three zones. The site in the Middle Zone (near Punta Piedra) is the same location as in Dahlheim’s 1980s research. Single, double, or six-recorder assemblies have occupied this site continuously since 2008. Single- or double-recorder assemblies have been deployed between 2009 and 2012 at a site in the Lower Zone. A single-recorder assembly was deployed near Isla Pelicanos in the Upper Zone during 2009 and 2011. Table 1 summarizes recording dates, bottom depths, and GPS coordinates of all deployments.

A weather station was set up all years except 2013 to supplement acoustic recordings with wind (30-second sampling rate), temperature, and rainfall data. The “HOBOware” autonomous weather station was mounted on a 5 m wooden pole, near the Baja Discovery ecotourism camp on Punta Piedra.

Table 2.1: A listing of the time frames, depths, and locations of all autonomous acoustic recorders (units) analyzed in this report.

Year	Lower Zone 26°47.136’ -113°15.134’ *No. of recorders* (date) [depth]	Middle Zone 26°47.658’ -113°14.645’ *No. of recorders* (date) [depth]	Upper Zone 26°53.664’ -113°10.948’ *No. of recorders* (date) [depth]
2008	*0 recorders*	*1 recorder* (Feb 9 - Mar 8) [13 m]	*0 recorders*
2009	*0 recorders*	*2 recorders* (Feb 23 - Mar 22) [11 m]	*1 recorder* (Feb 15 - Mar 12) [5 m]
2010	*1 recorder* (Feb 6 - Mar 4) [5 m]	*6 recorders* (Feb 6 - Mar 4) [10 m]	*0 recorders*
2011	*2 recorders* (Feb 5 - Mar 10) [not recorded]	*2 recorders* (Feb 5 - Mar 7) [12 m]	*1 recorder* (Feb 6 - Mar 9)
2012	*1 recorder* (Feb 11 - Mar 10) [20 m]	*2 recorders* (Feb 11 - Mar 10) [11 m]	*0 recorders*
2013	*0 recorders*	*1 recorder* (Feb 18 - Mar 6) [12 m]	*0 recorders*

2.4 Data Analysis

2.4.1 Acoustic data processing

Acoustic analyses for every site over all years began by downloading the raw binary acoustic data, converting them into pressure units, and correcting the frequency spectrum for frequency-dependent hydrophone sensitivities. Then power spectral densities (PSDs) were computed in dB re 1 μ Pa^2/Hz and estimated to 3-Hz resolution each minute, by averaging FFT snapshots (overlapped 50%) over one minute intervals. Data below 200 Hz were excluded because this frequency band lies outside the range of most gray whale calls and was often contaminated by flow noise and noise from the recorders rolling along the bottom.

These PSD time samples were then processed in three different ways. The first approach defined two bandwidths of biological relevance: 500-3120 Hz (the snapping shrimp band) and 200-500 Hz (the non-snapping shrimp band). The time-averaged PSD was integrated over each of these two bandwidths to produce an average sound pressure level (SPL) in terms of dB re 1 μ Pa for every minute. The 1st, 10th-90th (in tenths) and 99th percentile distributions of these SPL estimates were then generated every hour. As a result, a given percentile could be plotted against time with hourly resolution for all instruments in all zones for all years. This allowed both cyclical (fluctuating on a regular basis) and secular (long-term, non-cyclical) changes to be spotted. The 10th, 90th, and 99th percentiles were found to be particularly useful in that they were found to represent diffuse background noise levels (10th) and relatively extreme (intense) transient events (90th and 99th).

The second approach to analyzing the ambient noise background involved searching for diel cycles. A given SPL percentile would be averaged across all days at a specific time of day. For example, all SPL values from the 99th percentile computed between 0100 and 0200 from each day of a given deployment would be averaged together, with identical analysis repeated for each subsequent hour of the day. Plots of these averaged percentiles as a function of the hour-of-day were examined for potential diel cycles.

Finally, the estimated PSD percentiles were also computed for every frequency bin across timean approach that permitted an entire deployment record to be displayed as a set of frequency-dependent PSD percentile curves. Whenever multiple recorders were deployed together as an assembly, their seasonal PSD percentiles were compared, but data are presented here for select years and zones from a single recorder in each assembly.

2.4.2 Identifying potential source mechanisms

Cyclical patterns in the acoustic data were reflected in the diel plots and used to infer likely mechanisms behind the ambient noise field. Whenever pangas, snapping shrimp, or fish were postulated to be likely contributors, 2-minute long spectrograms were manually reviewed during times of high and low noise intensity to flag the presence of these distinctive signals. Ten of the hours in the data when SPL levels were lowest and when they were highest were selected, and these twenty hour-long spectrograms were reviewed. For the specific case of pangas, the number of transits was counted, and the SPL of each transit was noted. These levels were compared to various SPL percentiles to ensure that pangas were truly the driving source mechanism behind these cycles. Simultaneous measurements from the weather station also aided in identifying possible driving mechanisms. For example, Pearson's correlation coefficients were computed between wind speed time series collected at Punta Piedra and sound intensities recorded from the Middle Zone.

2.5 Results

Data from one recorder at each site for 2008 through 2013 are presented here, including results from 2009 and 2011 in the Upper Zone, all six years in the Middle Zone, and 2011 in the Lower Zone. There was considerable variation in spectral levels below 200 Hz from recorders spaced only a few meters apart. This was likely due to varying levels of silt burial and plants and gravel colliding with the recorder during heavy tidal flows, so analysis was restricted to frequencies above 200 Hz. The results are arranged by increasingly longer timescales: (a) short-term diel patterns, (b) seasonal patterns within and between zones, and (c) multi-year characteristics. 2011 will be used as a "reference" year, as it was the one season where all three zones were monitored simultaneously. Figure 2 shows sample spectrograms of the various source mechanisms in LSI.

2.5.1 General observations

Figure 3 displays examples of four-day time series (February 25^{th}-29^{th}, 2011) of SPL between 200-500 Hz and 500-3120 Hz in all three zones. Over the 500-3120 Hz band, the Upper Zone's median levels (118 dB re 1 μ Pa) were more intense than both the Middle (110 dB re 1 μ Pa) and Lower Zone's (103 dB re 1 μ Pa) median levels. By contrast, in the 200-500 Hz band, the Upper Zone's median levels (99 dB re 1 μ Pa) were only slightly higher than both the Middle (95 dB re 1 μ Pa) and the Lower Zone's (96 dB re 1 μ Pa) median levels. As will be shown later, these differences arise from higher snapping shrimp activity in the Upper Zone.

Over the 500-3120 Hz band, the maximum spread between the 99^{th} and 1^{st} percentiles (dash-dotted lines) in the Upper Zone was 9 dB, versus a 13 dB spread in the Middle Zone and a 17 dB spread in the Lower Zone. Over the 200-500 Hz band, the Upper Zone's spread was 12 dB, versus a 28 dB spread in the Middle Zone and a 34 dB spread in the Lower Zone. The relatively smaller spreads in the Upper Zone indicate that it is the most stationary acoustic environment, even though it is the most acoustically intense ("noisy") zone above 500 Hz.

One feature in the Lower and Middle Zones, but not in the Upper Zone, is a daily

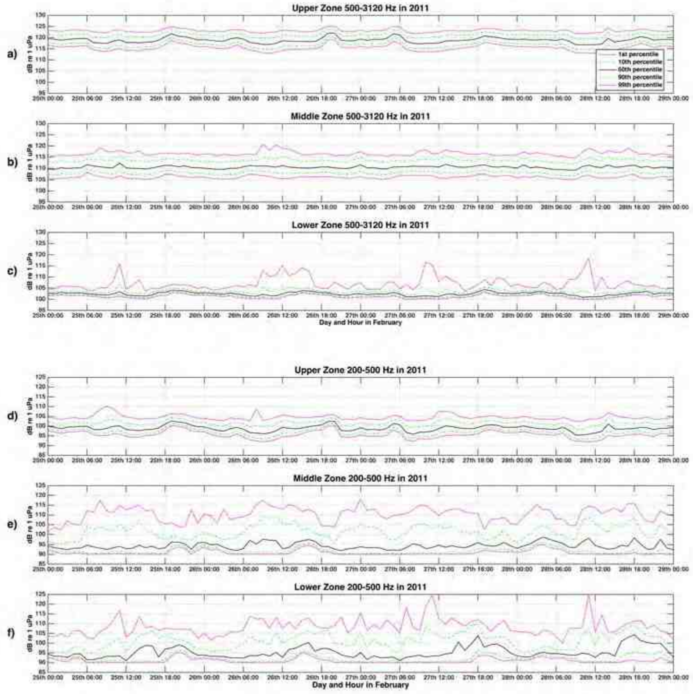

Figure 2.3: First (dash-dotted), tenth (dashed), median (solid), ninetieth (dashed), and ninety-ninth (dash-dotted) percentiles of intensity (dB re 1 μ Pa) calculated hourly across four days for the 500-3120 Hz (a - c) and 200-500 Hz (d - f) bandwidths at the Upper (a & c), Middle (b & e), and Lower (c & f) Zones.

waxing and waning of the 1^{st} to 99^{th} percentile spreads. The Middle Zone's percentile spread is greatest in the higher frequency band (500-3120 Hz) during daytime hours: usually between 08:00 and 15:00. The Lower Zone's 1^{st} to 99^{th} percentile spread peaks rapidly during evening hours (Figs. 3c and 3f). The next section examines these potential cyclical patterns more rigorously.

2.5.2 Diel cycles in all three zones

The initial impressions of cyclical activity in Fig. 3b and 3c are confirmed by Fig. 4, which displays the percentiles of averaged SPLs across both frequency bands for all three zones in 2011. Three distinct cycles can be seen. The first is a slight crepuscular (dawn/dusk activity) cycle visible in all zones across most bandwidths. For example,

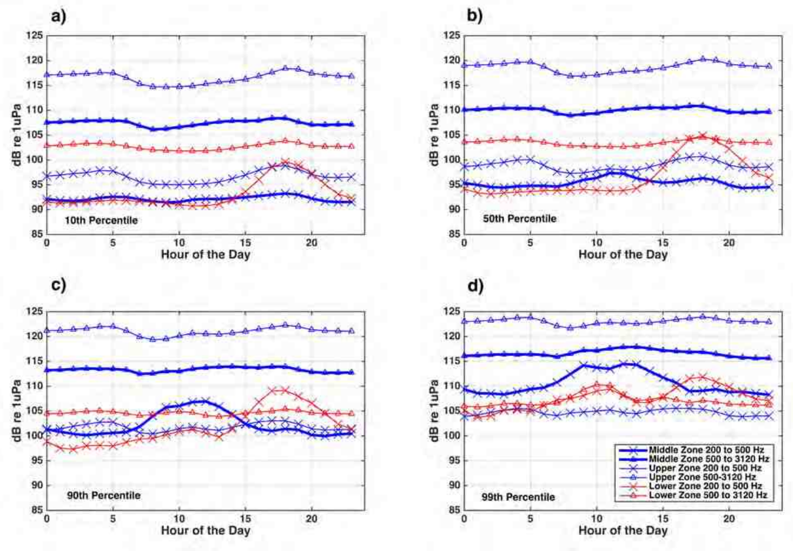

Figure 2.4: The average percentile intensity across each hour of the day during 2011 is presented for four percentiles across 200-500 Hz (x marker) and 500-3120 Hz (triangle marker), for the Middle, Upper, and Lower Zones of Laguna San Ignacio. The 10^{th} (a), 50^{th} (b), 90^{th} (c) and 99^{th} (d) percentiles of hourly samples are shown.

subplot (4a) shows these crepuscular peaks occur over the 500-3120 Hz bandwidth in the 10^{th} percentilea pattern consistent with crepuscular cycles exhibited by snapping shrimp in Hawaiian waters (Lammers et al., 2008).

This crepuscular cycle is superseded by other cycles in the Middle and Lower Zones. In the Middle Zone, a distinct daily cycle of extreme events (the 90^{th} and 99^{th} percentiles; subplots c and d) peaks at midday in the lower frequency band. Midday is when pangas return to the land-based camps for lunch break, and review of the raw acoustic data confirmed that numerous panga signatures exist at similar SPLs to those shown in Figs. 4c and 4d.

Of particular note in the Lower Zone is the 99^{th} percentile (subplot 4d), when the lower frequency band has bimodal peaks near 10:00 and 18:00, and a local minimum at 13:00. These times coincide with typical daily panga activity in the lagoon. For example, the 10:00 hour experiences high whale-watching traffic in the Lower Zone, whereas around 13:00 pangas return to the camps for lunch. Randomly selected samples of the raw acoustic data around 10:00 again confirmed panga activity.

The Lower Zone's peak in the 99^{th} percentile between 200-500 Hz in Fig. 4d, which occurs at 18:00, must arise from a different source mechanism than pangas, since most vessels are moored by dusk. Across nearly all percentiles, the background noise SPL increases by 10 dB in just a few hours. Inspection of raw data confirmed that these peaks arise from fish (croaker spp.). As all percentiles are affected, this suggests that the drumming fish dominate the acoustic environment at least 90% of the time (e.g. 54 minutes per hour) during the early evening hours. While the maximum is centered at 18:00, shifting sunset times across the season has diffused the diel peaks in Fig. 4.

Figure 5 provides three-minute snapshots of spectrograms from a single day that confirm many of the observations of Figure 4. One sees how the Upper Zone noise levels are the most intense and the least variable of the zones, and that the noon and midnight hours in the Upper Zone are indeed "quieter" than sunrise and sunset hours. The Upper Zone also displays higher SPLs across the snapping shrimp bandwidth than the Middle Zone, giving credence that these small crustaceans are the driving source mechanism shaping the Upper Zone's acoustic environment. Finally, Figure 5(g) illustrates a panga transit in the Lower Zone during the first 40 seconds.

2.5.3 "Seasonality" across all three zones

A "season" is defined here as the two months each year when acoustic data was collected. Therefore, "seasonality" in the zones will explore trends in the acoustic environment that existed over the couple months when gray whales occupy Laguna San Ignacio. Figure 6, which is a time expansion of Fig. 3, shows that the Upper Zone still displays the most intense yet least variable noise levels. The strong croaker chorusing peaks in the Lower Zone and the midday peaks in the Middle Zone that were rather obvious in Fig. 3 can still be spotted upon close inspection in Fig 6. From this larger "bird's eye view", how-

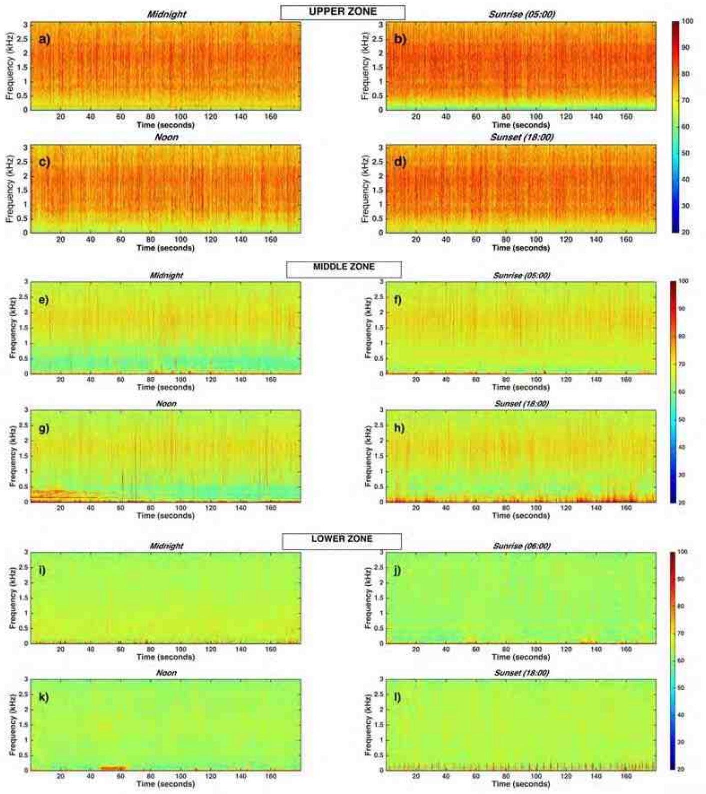

Figure 2.5: Typical snapshots of the ambient noise environment in the Upper Zone (top four plots) as compared to the Middle Zone (middle four plots) and Lower Zone (bottom four plots). The four snapshots in time are midnight (a, e and i), sunrise (b, f and j), noon (c, g and k), and sunset (d, h and l). All spectrograms were generated using a 1024 FFT size with 90% overlap.

ever, the croaker chorusing seems modulated by a 2-week cycle that is most pronounced in the median levels of the Lower Zone. While their activity could be related to the lunar phase, the restricted deployment time of 45 days prevents verification of this idea.

In addition to lunar phase, wind speed is a natural phenomenon that could be related to noise levels. The median values of measured wind speed (raw data sample rate = 30 sec. from the HOBOware weather station at Punta Piedra; medians calculated every hour) were compared against hourly 50^{th} percentile sound levels between both the 200-500 Hz and 500-3120 Hz bandwidths from the Middle Zone. Comparisons were time-lagged by shifting sound level response to wind speed from zero- to twenty-four hours. The maximum Pearson's correlation coefficient with any significant statistical comparison (p-value=0.05) was -0.12. We thus conclude that wind was not a driving source mechanism for the 50^{th} percentile of sound level in the Middle Zone's acoustic environment below 3 kHz.

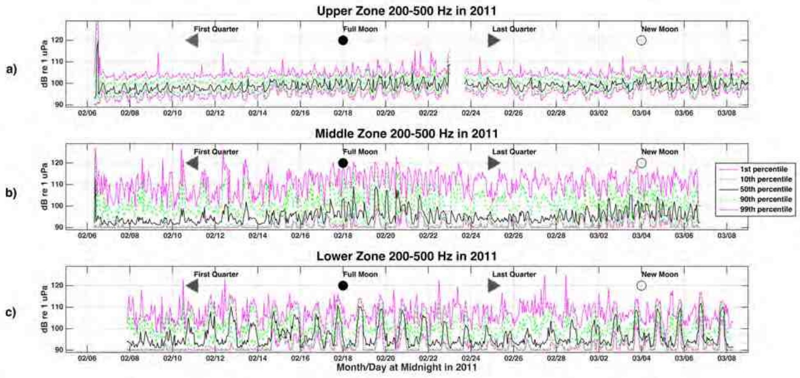

Figure 2.6: This is an expansion of Fig. 3 to the entire 2011 deployment, but only for the lower frequency band (200-500 Hz). SPL averaged across one-hour bins is shown for the Upper Zone (a), Middle Zone (b) and the Lower Zone (c). Black (new), gray (quarter), and white (full) circles denote lunar phases.

Figures 7 and 8 plot the percentile distributions of the PSD for all three zones during 2011. An example interpretation of these figures is that the PSD at 2 kHz in the Middle Zone (black lines) is at or below 85 dB re 1 μ Pa^2/Hz during 99% (thickest line) of the season. Similarly, the PSD at 2 kHz in the Upper Zone is at or below 92 dB re 1 μ Pa^2/Hz for 99% of the season.

Above 700 Hz, the Upper Zone has sound levels 8-12 dB higher than the Middle Zone for all percentiles. Below 700 Hz, however, the Middle Zone begins to have higher sound levels (Fig 7 grey arrow). The largest difference (15 dB) lies in the 99^{th} percentile across the 200-300 Hz bandwidth (Fig 7 dashed arrow). The Lower Zone displays similar PSD values in Fig. 8, and its PSD spectrum is more closely related to the Middle Zone than to the Upper Zone. The largest swings in PSD (a 20-40 dB separation between 10^{th} and 90^{th} percentiles denoted by the gray arrow in Fig 8) occur below 500 Hz in the Lower Zone, and will be discussed further in the next section.

Figure 8 also shows that the Lower Zone has a 300 Hz sound minimum in the 10^{th} and 50^{th} percentiles, but it shifts to a 1000 Hz sound minimum in the 90^{th} and 99^{th}

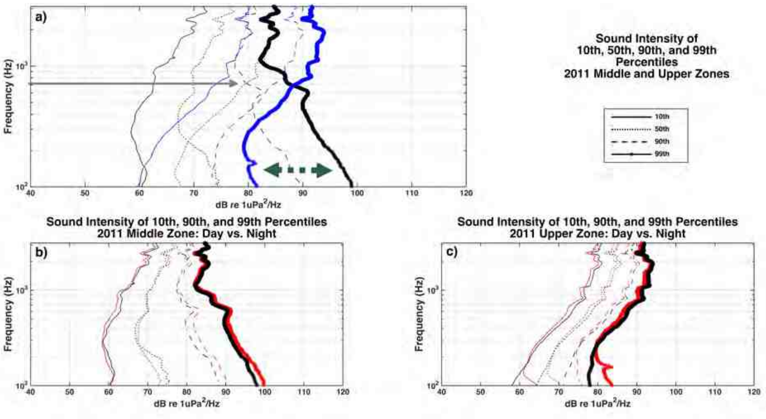

Figure 2.7: Contour lines for the 10$^{[}th$ $(solid)$, 50^{th} (dotted), 90^{th} (dashed), and 99^{th} (thick) percentiles compare these four power spectral densities on a logarithmic scale between 100 and 3125 Hz in the Middle (dark shaded) and Upper (light shaded) Zones in the lagoon for 2011. Subplot (a) shows sound intensity across 24 hours. Subplots (b) and (c) divide sound intensity between night (1800-0600) in a dark shade and day (0600-1800) in a gray shade for the Middle (left) and Upper (right) Zones.

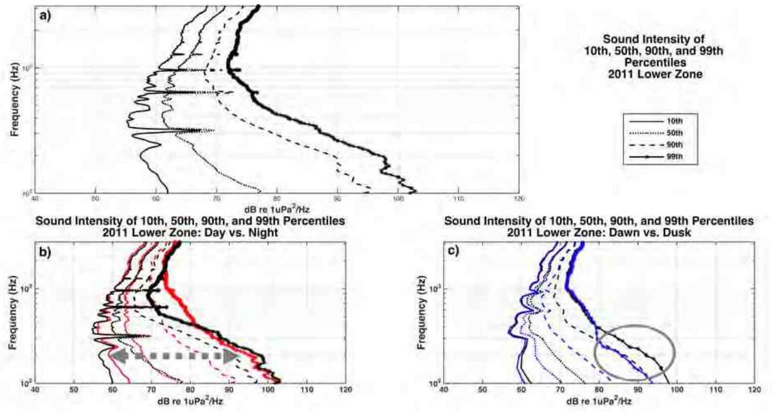

Figure 2.8: Same as Fig. 7, but data for the Lower Zone are plotted. A dawn vs. dusk comparison has been added, however, to show the impact of the croaker chorusing. Dusk covers noon to midnight and is shown in the dark shade; dawn covers midnight to noon and is shown in the gray shade.

percentiles. Thus, loud transient sound sources tend to have lower-frequency components than the diffuse noisea characteristic of panga transits. The Upper Zone seems to have no sound minimum with respect to frequencythe apparent minimum in the 99th percentile falls too closely to 200 Hz to rule out flow noise contamination.

When comparing daytime versus nighttime PSDs (subplots b and c of Fig. 7), the

Middle and Upper Zones in 2011 have a negligible difference in daytime and nighttime sound levels. However, the Lower Zone, at the 90^{th} (dashed line) and 99^{th} (thick line) percentiles, has a nighttime with higher sound levels below 500 Hz, but a daytime with higher sound levels between 500-1000 Hz (Fig. 8b). Daytime vs. nighttime comparisons were split at 6 pm and 6 am-times of rapid changes in ambient noise levels in the Lower Zone. Thus Fig. 8c displays dusk-centered and dawn-centered PSDs to avoid splitting sound level measurements during times of high fluctuation. As a result, sound levels from noon to midnight (dusk) were higher than from midnight to noon (dawn) for extreme events across nearly all frequencies, consistent with the timing of croaker activity (Fig 8c grey circle).

2.5.4 A 2-year comparison in the Middle and Upper Zones

2009 was the only other year that data was simultaneously recorded in both the Upper and Middle Zones. Figures 9 and 10 present the 2009 results in the same manner as Figs. 4 and 7 did for 2011.

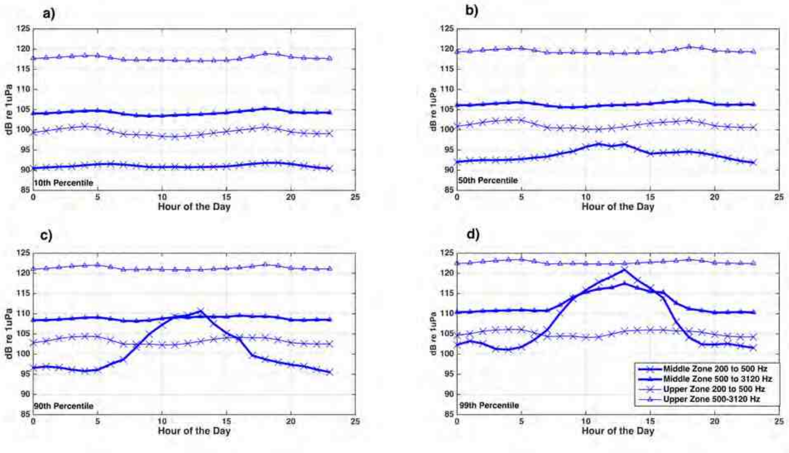

Figure 2.9: Same as Fig. 4, but with data plotted for 2009.

The Upper Zone's diel patterns in 2009 are similar to those of 2011. One very minor difference is that, in 2011, a very small peak in the 90^{th} and 99^{th} percentiles at the

10:00 hour (Fig. 4c and 4d) did not exist at all in 2009 (Fig. 9c and 9d). A very small amount of panga traffic exists in the Upper Zone, and may have been less in 2009 than in 2011, but no records are available to verify this. The Middle Zone percentiles in 2009 were consistently 5 dB higher than 2011 for both frequency bands throughout the day. Also, Figures 9c and 9d show that the panga-related peaks at the 90^{th} and 99^{th} percentiles were more pronounced in 2009 than in 2011below 1000 Hz; daytime hours are as much as 10 dB higher than during the night. (Recall that 2011 had daytime sound levels only 1-2 dB higher than nighttime sound levels.) This contrast exits not because the daytime hours in 2009 were so much "louder", but because the nighttime hours in 2009 were so much "quieter" (compare thick Xed lines in figure 4 c & d to those in figure 9 c & d). According to Figure 10a the 300 Hz minimum was more obvious in 2009 than in 2011. However, below 800 Hz, the 99^{th} percentile PSD in 2009 is nearly 14 dB lower than in 2011.

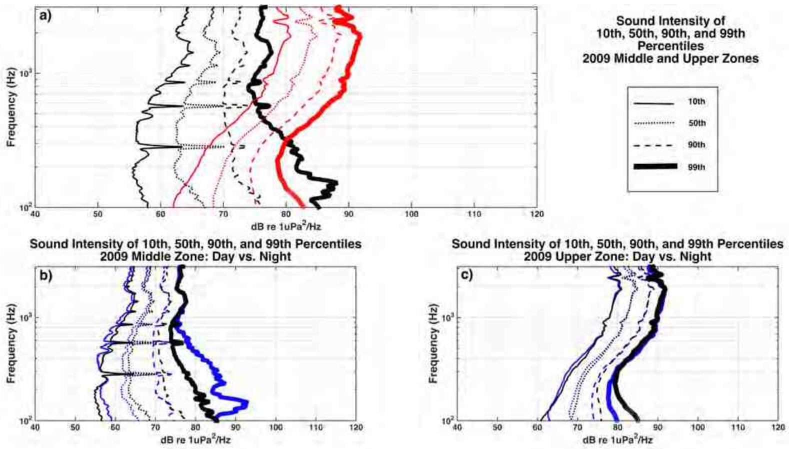

Figure 2.10: Same as Fig. 7, but with data plotted for 2009.

The statistical results presented here are consistent with spot-checks of the acoustic data. For example, ten random perusals of raw data at 18:00 in the Lower Zone (i.e. the center of the hourly averaged peak from Figs. 4a-c) showed that panga activity never existed, but the drumming of croaker fish was consistently high. At the same times in the Middle and Upper Zone data, relatively moderate and low croaker activity existed. These results are consistent with current understandings of croaker activity whereby the fish tend to inhabit shallow waters in silty areas very close to the entrances of Baja coastal lagoons (Fish, 1964; Fish and Mawbray, 1970; Johnson 1948, H. Batchelor, pers. comm.).

2.5.5 Multi-year comparisons for the Middle Zone

Between 2008 and 2013, the same recorder (Unit 2) was deployed in the Middle Zone every year except 2010. In 2010 Unit 2 was more deeply buried than the other recorders, but a different unit (same design and calibration) recorded a less contaminated dataset. Thus, a multi-year comparison of this acoustic environment is feasible.

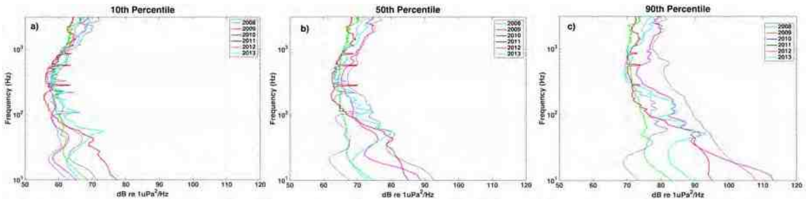

Figure 2.11: The 10^{th} (a), 50^{th} (b), and 90^{th} (c) percentiles for all six years between 2008-2013 in the Middle Zone are plotted against each other.

Figure 11 shows that the overall ambient noise environment was stable across all six years, although the first three years (2008-2010) have less intense PSD levels than the next three years (2011-2013). The greatest difference in PSD levels between 2008 and 2013 was 12 dB, which occurred at 450 Hz at the 90^{th} percentile between 2011 and 2013. A review of the acoustic data confirmed that recorder motion on the ocean floor does tend to contaminate frequencies below 200 Hz, explaining the wide variations observed over this frequency range. The noise minimum at 300 Hz found in 2009 and 2011 persists across all six years in the Middle Zone, supporting Dahlheim's (1987) observations that gray whales (whose vocalizations center around 300 Hz) tend to call where noise from snapping shrimp and boat engines is least prevalent. Thus, the 300 Hz acoustic minimum in the Middle Zone.

2.6 Discussion

The main motivations of this paper were to investigate the underwater ambient noise environment of a World Heritage site where the last acoustic research is from over 20 years ago, and to determine the extent of noise contributions from panga traffic. Other research in whale-watching waters, particularly in Puget Sound, identifies noise from vessels as a key threat in the recovery and survival of southwest resident killer whales (Holt, 2008). Currently, LSI is a low trafficked area and not comparable to many other highly trafficked whale-watching locations, but that may change if tourism grows in the future. Therefore, it is important to identify baseline sound sources and their relative contributions to the acoustic environments now. Both power spectral densities and SPL percentiles were analyzed. This is a relatively recent approach that has been applied to a strait, a continental shelf, and a firth (Erbe et al., 2013; Merchant et al., 2013), but not to a subtropical lagoon.

Sound sources in LSI that could be identified using diel cycle analysis included snapping shrimp, panga transits, and croaker vocalizations. Common physical source mechanisms were also examined, but wind speed did not associate as closely with sound levels as did biological and anthropogenic sources; for example, croaker and snapping shrimp activity generated the largest diel patterns in the data.

To confirm that pangas were a source of background noise at the 99^{th} percentiles of the Middle and Lower Zones, panga passes were tabulated in the raw acoustic data from all three zones in 2011. The results suggest that pangas, indeed, make a measurable contribution to ambient noise levels, but only for short and sporadic periods throughout the dataset. In the Upper Zone, the most intense 99^{th} percentile values were usually concurrent with a single close panga transit or the occasional amount of heavy flow noise. In the Middle Zone, the most intense 99^{th} percentile values were concurrent with multiple panga transits. In the Lower Zone, the most intense 99^{th} percentile values concurred sometimes with multiple panga transits, but mostly with high levels of croaker activity.

Interestingly, gray whale calls make a smaller contribution to the bulk ambient acoustic environment than pangas. Their relatively low intensity, as well as their low production rate as established by Ponce et al. (2012), provides an explanation for why. Received levels of gray whale calls tend to be less than 145 dB re 1 μ Pa in our data and from past research (Moore & Ljungblad, 1984; Dahlheim, 1987). Even though these levels are clearly higher than the ambient SPL percentiles shown in Fig. 3, the calls occur relatively infrequently. According to Ponce et al., (2012), the call rates of their three most common detected vocalizations were 198 calls/hour (S1), 29 calls/hour (S4), and 21 calls/hour (S3). Considering typical call durations of a second or less, these vocalizations would theoretically be detected only at the 99.5^{th}, 99.993^{rd}, and 99.985^{th} SPL percentiles, respectively. In addition, as the calls are much shorter than the 1-minute averaging window used to estimate the SPL percentiles, their contribution to a one-minute SPL average is relatively miniscule.

Panga transits also leave a relatively minor temporal acoustic footprint in the noise statisticsonly the 90^{th} and 99^{th} percentiles exhibit a "lunch-time" effect when pangas are shuttling tourists back to their land-based eco-tourism camps for a meal. Once in awhile, this effect creeps into the 50^{th} percentile. In other words, the acoustic presence of pangas is usually only "felt" for 1 to 6 minutes each hour (1-10% of the time) during mid-morning to early afternoon, and rarely "felt" for half of an hour (50% of the time) during other times of the day. Direct comparisons to other whale-watching areas are difficult to make since daily cycles of percentile data are not available. However, vessel activity in Haro Strait, where the Southern resident killer whales inhabit, is comprised of more (and "louder") vessel types that increase SPL during summer days by 5 dB re 1 μ Pa above summer nights and winter-time. Furthermore, this location already contains nearly constant non-whale-watching vessel noise year round (Holt, 2008).

Often studies of anthropogenic contributions to acoustic environments implicitly assume that undisturbed environments have low noise levels. A contrary situation exists in the Upper Zone, otherwise known as the “nursery”, where the most intense and sustained ambient noise levels are generated by snapping shrimp. The fact that a whale nursery exists in a “loud” environment seems counterintuitive at first. Upon further consideration, however, a constant din might provide protective cover. To protect a calf from predators and a mother from male harassment, disguising the calf’s (and mother’s) whereabouts is desirable. The Upper Zone may provide such protection because it is turbid, which provides visual camouflage. It is also shallow, meaning that a mother who keeps her calf along the shore only has three of the six directions to monitor (i.e. the top, bottom, and coastal side of the calf are protected while the front, back, and open lagoon side of the calf is exposed). Along with providing visual camouflage, the Upper Zone may provide an analogous “aural camouflage” by impeding a predator’s ability to hear a calf, or an aggressive male whale’s ability to harass a mother. In this relatively loud acoustic environment, snapping shrimp maintain a received level above a 115 dB re 1 μ Pa level 90% or more of the time, and the lower limits of their bandwidth do overlap with the upper frequencies of gray whale calls. A mother and calf right beside each other would be able to communicate sporadically at low source levels, albeit above the surrounding din, thereby partially masking their calls from predators or aggressive males. While there are no natural predators in the Upper Zone of LSI, other researchers have proposed that during their migration north, it would be critical for calves and mothers to detect each other’s calls over a noisy din, and the Upper Zone’s snapping shrimp cacophony could provide a training area to develop this skill (pers. comm. W. Perryman and D. Weller). Aside from predators, the Upper Zone could also be an escape from particularly active and / or aggressive conspecifics. Other explanations exist for why mothers and newborn calves tolerate high noise levels in the Upper Zone. For example, mother whales may simply prefer the warmer and saltier waters of the Upper Zone, or may reside there to avoid the aggressive mating behaviors of single animals in the Lower and Middle Zones.

2.7 Conclusion

The main features in the ambient noise structure across all of LSI's zones can be summarized in a few main points. First, all recorders at a single site collected very similar data above 200 Hz. Below 200 Hz, self-movements of the recorders contaminated the datasets from each recorder differently, so analyses were only performed for bandwidths above 200 Hz.

Second, broadband sound pressure levels are greatest in the Upper Zone, as compared to relatively moderate levels in the Middle Zone and Lower Zones. The least variation (smallest spread between 1^{st} and 99^{th} percentiles) in SPL also exists in the Upper Zone. We speculate that this consistently "louder" acoustic environment in the Upper Zone may conveniently provide aural camouflaging for both mothers and young calves.

Third, although snapping shrimp, pangas, croaker fish, gray whales, and wind are all potential sound sources in Laguna San Ignacio, only the first three contribute substantially to at least one portion of the lagoon. Gray whale calls are so intermittent that they are difficult to detect with the percentile methods used in this study, and wind speed did not correlate significantly with SPL at any percentile. Diel cycles are strongly present in panga and croaker activity, and partially so in snapping shrimp activity. Each zone has its own set of distinctive sound-source mechanisms with their own diel cycles. In the Upper Zone, snapping shrimp dominate higher frequencies and their SPL levels peak crepuscularly. In the Middle Zone crepuscular snapping shrimp still dominated the higher frequencies, but lunch-time panga transits also generated a diel cycle this is apparent at the 90^{th} percentile level (i.e. present around 6 minutes per hour at midday). Wind speed does not correlate significantly with median sound levels in the Middle Zone. In the Lower Zone the same snapping shrimp contributions are evident, but panga transits that coincide with the morning and afternoon whale-watching time periods contribute to the 99^{th} percentiles. Croaker activity is the dominant source of noise in the Lower Zone at frequencies below 1500 Hz during a sunset-centered cycle.

Fourth, noise from panga transits, although relatively rare, contributes more to the ambient noise environment than gray whale calls. The noise contribution from pangas is most prominent in the Middle Zone above the 90^{th} percentile during the day. Based on the day/night PSD comparisons from Fig. 9, pangas impact the frequency band between 300-1000 Hz. This noise impact is much more noticeable in 2009 (when tourism activity may have been higher) as compared to 2011. Although gray whale calls can be 20-30 dB above background noise levels, their relatively low detection rates and short duration means that they occur less often than panga transits during the "busy" whale-watching hours. For example, whale calls theoretically occur 0.7% of the time in the Middle Zone at any given hour, while panga transits can empirically be detected up to 10% of the time during pre and post lunch-time transits. The relative contribution of panga-generated sound to the lagoon's overall noise levels seems small compared to other whale-watching regions. Panga noise is most intense in regions where they are transiting with passengersnot where actual whale-watching is taking place, and not in the nursery environment. Even in the transit areas, pangas are usually only detected 10% of the time, and their SPL levels are still lower than those generated by snapping shrimp in the Upper Zone nurseries, and their occurrence is less common than the noise spikes generated by croakers each evening.

Finally, the various physical and biological contributions to the acoustic environment have remained stable in the Middle Zone over six years of observations, and in the Upper Zone over two years of observations. Indeed, the ambient environment for the Middle Zone is similar to the environment measured nearly 30 years ago, down to the existence of a noise minimum at around 300 Hz.

Expanding this dataset into the future is desirable. The zonation is satisfactory as is, although more years of data from the Upper Zone would be beneficial, and a deployment spot in the Lower Zone where recorders do not run the risk of getting lost would be ideal.

An interesting future application of this work would be to estimate relative levels of tourist activity across years by flagging noise events at the percentile level indicative of the panga traffic's footprint. Anecdotal evidence suggests that tourism activity in 2009 was higher than in 2011, consistent with the relative levels of panga activity reported here, but a more formal comparison should be possible as more panga and acoustic information become available. If tourism increases in the future as the access road is paved, will the pangas' acoustic footprint increase? Continued work on these topics could permit passive acoustic monitoring to become a useful monitoring and oversight tool for managers and regulators of this unique and enchanting lagoon, and could provide a controlled environment for testing the ability of passive acoustics to detect small vessel activity in other marine protected areas.

2.8 Acknowledgements

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Chapter 3

Humpback whale-generated ambient noise levels provide insight into singers' spatial densities

3.1 Abstract

Baleen whale vocal activity can be the dominant underwater ambient noise source for certain locations and seasons. Previous wind-driven ambient-noise formulations have been adjusted to model ambient noise levels generated by random distributions of singing humpback whales in ocean waveguides and have been combined to a single model. This theoretical model predicts that changes in ambient noise levels with respect to fractional changes in singer population (defined as the noise "sensitivity") are relatively unaffected by the source level distributions and song spectra of individual humpback whales (*Megaptera novaeangliae*). However, the noise "sensitivity" does depend on frequency and on how the singers' spatial density changes with population size. The theoretical model was tested by comparing visual line transect surveys with bottom-mounted passive acoustic data collected

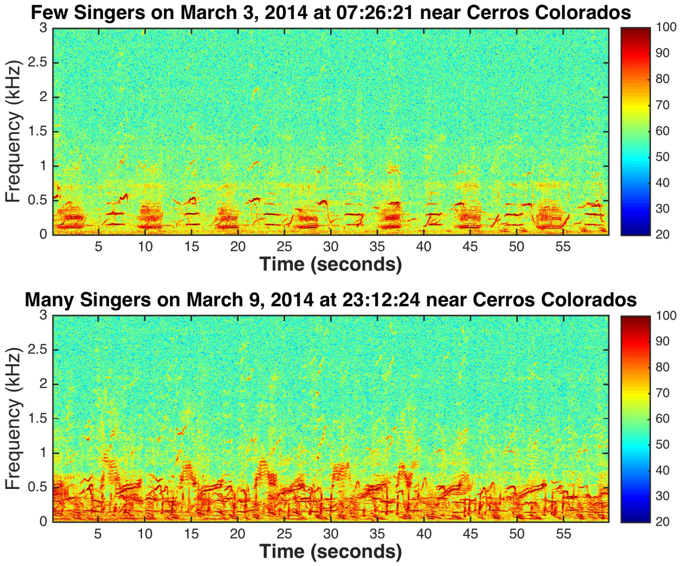
during the 2013 and 2014 humpback whale breeding seasons off Los Cabos, México. A generalized linear model (GLM) estimated the noise "sensitivity" across multiple frequency bands. Comparing the GLM estimates with the theoretical predictions suggests that humpback whales tend to maintain relatively distant spacing with one another while singing, but that individual singers either slightly increase their source levels or song duration, or cluster more tightly as the singing population increases.

3.2 Introduction

To estimate the relative abundance and/or density of cetaceans, passive acoustic surveys complement visual surveys because they can be performed overnight or in inclement weather (Clark & Fristrup, 1997; Raftery & Zeh, 1998; Mellinger & Barlow, 2003; and Barlow & Taylor, 2005). However, acoustics alone (after verification using visuals) could be used to estimate the overall abundance and/or growth rates of marine animal populations within protected regions (Raftery & Zeh, 1998).

The use of passive acoustic monitoring to estimate population densities of animals began by using cue rates in the terrestrial realm with mammals, amphibians, songbirds, bats, and insects (Dawson & Efford, 2009; Buckland, 2006; and Blumstein et al., 2011). Such techniques have also been applied to the marine realm for fish (Lucskovich et al., 2008) and cetaceans, such as Blainville's beaked whale (Marques et al. 2009), the right whale (Marques et al. 2011), the fin whale (McDonald & Fox, 1999), and the minke whale (Martin et al. 2013). Marques et al. (2013) summarize recent literature on passive acoustic density estimation for cetaceans.

All the research cited above used individual call detections (cue rates) as a basis for marine mammal population estimates. However, during breeding seasons at certain locations, several baleen whale speciesincluding the fin whale, blue whales (McCauley et al., 2001), and the humpback whale (Au et al., 2000)vocalize so often that individual cue rates cannot be measured; instead, individual sounds blend together to create a diffuse and continuous din across species-specific frequency bands in the acoustic environment. In the case of humpback whales, proliferous singing activity from multiple animals overlaps to create this din and makes it impossible to tease apart separate song units (Figure 1). Therefore, for the remainder this paper, the din created by humpback whale song will be referred to as "noise", even though it contains potential information about the population size.


Few Singers on March 3, 2014 at 07:26:21 near Cerros Colorados

Many Singers on March 9, 2014 at 23:12:24 near Cerros Colorados

Figure 3.1: Ambient "noise" generated from humpback whale song varies throughout the day. Two 60-s spectrograms illustrate times of relatively low (top) and high (bottom) singing activity at Cerros Colorados in 2014 as recorded on an autonomous bottom-mounted hydrophone.

Humpback whales use song and social calls on both feeding and breeding grounds, as well as along migration routes, to facilitate their behaviors (Sharpe, 2001; Dunlop et al., 2008; Zoidis et al., 2008; Stimpert et al., 2011). Song is a male communication strategy that does occur on migration routes (Clapham & Mattila, 1990; Norris et al., 1999; Charif et al., 2001) and feeding grounds (Mattila et al., 1987; Clark & Clapham, 2004; Stimpert et al., 2012; Vu et al., 2012), but is especially prevalent on breeding grounds. It was originally thought to serve as a means of attracting females (Payne & McVay, 1971; Winn

& Winn, 1978; Tyack, 1981). Other theories reviewed by Darling & Brub (2001) include how song may serve as a mechanism for males to space themselves evenly from other singers (Tyack, 1981; Frankel et al., 1995; Au et al., 2000). If song contains information about spacing, then measuring its intensity would contain information about the number of singers producing a certain singing level.

Au et al. (2000) was one of the first to propose that the diffuse ambient "humpback-generated noise" levels from many males singing together might be used to estimate their abundance. As part of the "DECAF" project sponsored by the Oil and Gas Producers' Association, Mellinger et al. (2009) developed a numerical model for estimating ambient noise levels generated by random distributions of fin whales.

In this paper we adapt existing analytic wind-driven ambient noise models to estimate the diffuse ambient noise levels that would be generated from random distributions of singing animals. Section 2 derives this theory, and defines a quantity dubbed the "sensitivity" of ambient noise measurements, in terms of how noise levels change with changes in relative population size. While this sensitivity is shown to be relatively independent of an individual humpback whale's source level or duty cycle, it does depend on acoustic frequency and on how the animals adjust their spatial density as their population increases. Section 3 describes the study area, equipment, procedures, and analyses used to test the analytic model, using combined acoustic and visual survey data collected in 2013 and 2014 from humpback whale breeding grounds off Los Cabos, México. Section 4 compares the analytic model predictions of noise sensitivity with empirical estimates of sensitivity using a Generalized Linear Model (GLM). Finally, we discuss how the results provide a connection between humpback whale behavioral adjustments with an increasing number of singers, and speculate about other species and environments where these methods might be useful.

3.3 Theory and simulations

This section presents a theoretical model for the ambient noise field generated by a random distribution of singing whales (or any distribution of continuously vocalizing animals). It is a reinterpretation of previously derived analytic models of ambient noise levels generated by randomly distributed wind-driven breaking waves near the ocean surface. Given an acoustic propagation environment, and assuming various parameters about humpback whale singing behavior, the model predicts (1) ambient noise levels as a function of frequency and singer population size and (2) the "sensitivity" of ambient noise levels to changes in the singers' relative population size. As will be shown below, this sensitivity is relatively independent from the source levels and fraction of singing time (which will be referred to as duty cycles) assumed for a "typical" singing whale, but it depends strongly on how the spatial density of singers (or how they "pack" themselves) may change with fluctuations in population size.

3.3.1 Key features of the "KIP" model

Analytic models exist for ambient noise intensity in an ocean waveguide, given a distribution of random, uncorrelated noise sources throughout a finite ocean area (Kuperman & Ingenito, 1980; Perkins et al., 1993; Jensen et al., 1994). In the original Kuperman-Ingenito-Perkins ("KIP") model (Appendix A), the acoustic sources were assumed to be wind-driven and just beneath the ocean surface. In this paper, however, we interpret the uncorrelated noise sources to be generated by a set of randomly distributed singing whales over a certain bandwidth. (Therefore, a fundamental assumption of the model is that the songs of all animals are temporally uncorrelated over the time width of the window used to compute a power spectral density estimate.) The KIP model is general enough that the singers can be at any depth. However, to simplify the following discussion, it will be assumed that all singers are (1) singing at the same depth, (2) using a song that has equal and constant proportions of vocalizing and non-vocalizing times (i.e. the same "duty cycle"), (3) emitting the same and constant source levels, and (4) maintaining a constant spatial density within the effective radius. Appendix B shows that relaxing these assumptions (including introducing a linear gradient in spatial density) does not alter the fundamental points that are about to be discussed.

In essence, the KIP model has the following form:

$$I = Sf/(A(N)/N) * P(z_w, z_r, R) \tag{3.1}$$

where I is the ambient noise intensity in terms of *linear* units of power spectral density (μPa^2/Hz, not dB). S is the source spectral density (in μPa^2/Hz @ 1 m) of a typical singing whale and is weighted by f: the fraction of singing time, or "duty cycle" (i.e., to account for times when a singer is not producing sound, such as the intervals between units and song cycles). N is the number of animals present in a region A that surrounds the recording hydrophone. (Eq. (1) explicitly shows how this region A can depend on N.) The term $S/[A(N)/N]$ thus represents the average source intensity spectral density per unit area within the region A. Finally, the term $P(z_w,z_r,R)$ represents an acoustic propagation term that can be interpreted as a spatial average of the propagation losses between all possible singer positions at depth z_w within distance R of a receiver at depth z_r. R is the radius of the circular region A, centered over the bottom-mounted recorder. Appendix A also discusses situations where the receiver is in an arbitrary non-centered location with respect to the circular area.

P strongly depends on the acoustic propagation environment, including the water depth, ocean bottom composition, sound speed profile, and receiver depth. As a result the marine mammal-generated ambient noise intensity produced by Eq. (1) is highly dependent on the ocean environment in which the animals are singing. For the purposes of this paper, a flat bathymetry for region A is assumed, but Perkins et al. (1993) discuss how the KIP model can be adapted to range-dependent bathymetries. Any water depth can be modeled, provided that the environment can be described in terms of a set of propagating normal modes. Appendix A presents the complete KIP model and discusses the collection of terms that comprise P in greater detail.

Equation (1) shows that ambient noise levels are directly proportional to the source intensity of a typical whale. If all whales in a region double their singing intensity, then ambient noise levels will double as well. Equation (1) also shows a direct proportionality between the ambient noise intensity and the spatial density of singers. For example, if the mean distance between singers halves, then both the spatial density and ambient noise spectral density will quadruple.

As Appendix A demonstrates, the P term in Eq. (1) asymptotically approaches a fixed value as R gets large (the area covered by singers increases to infinity). This means that ambient noise levels depend not only on the spatial density of singers, but also the physical size of region A. In terms of dB units ($10*\log_{10}$), Eq. (1) can be expressed as

$$I_{dB} = S_{dB} + 10log_{10}f + 10log_{10}N - 10log_{10}A + 10log_{10}P \tag{3.2}$$

where I_{dB} is the noise power spectral density level (dB re 1 μPa^2/Hz) and S_{dB} is the source level power spectral density (dB re 1 μPa^2/Hz @ 1m) of a typical individual.

In principle, Eq. (2) could be used to estimate population density (N/A) from ambient noise level measurements, provided a random distribution is assumed, and one has sufficient knowledge about (1) the acoustic behavior of singers, including S, f, and z_w; (2) the propagation environment in terms of water depth, sound speed profile, and bottom composition; and (3) the actual geographic region of A (with effective radius R) that is occupied by singing animals.

Unfortunately, both S and f have large variations and uncertainties associated with them, which means that a large range of possible ambient noise levels exists for a given population density. Therefore, the next section explores a more robust means of testing the KIP model that does not require assumptions about S and f.

3.3.2 The sensitivity of the ambient noise field to changes in singer population size

Equation (2) permits an estimate of the "sensitivity" of the ambient noise field to changes in population size. After converting to natural logs and canceling factors of $\log_{10}e$, one takes the derivative of Eq. (2) with respect to the base-10 logarithm of population size N:

$$\delta = (\partial(I_{dB}))/(\partial(10log_{10}(N))) = Q_{indiv} + 1 - (N/A) * (\partial A/\partial N) + (N/P) * (\partial P/\partial N) \quad (3.3)$$

Here δ is defined as the "noise sensitivity". The choice of $10\log_{10}N$ (i.e. dB "whales re 1 whale") as a measure of population change is convenient since we are using dB units to describe ambient noise levels. The term $Q_{indiv} = (\partial(S_{dB}))/(\partial(10log_{10}N)) + (N/f) * (\partial f/\partial N)$ measures the change in the acoustic behavior of an individual singer in response to a small fractional increase in the population size around it. For example, whales may increase their source levels slightly with increases in ambient noise level. This "Lombard effect" is incorporated into the Q_{indiv} term.

An interesting consequence of Eq. (3) is that δ (the sensitivity) is relatively independent of S and f, provided that an individual animal's singing behavior does not change much with a small fractional increase in singer population size [i.e. if the term Q_{indiv} is small compared to the other terms in Eq. (3)]. Stated another way, details about individual whales' acoustic behaviors do not need to be assumed: what is assumed is that the behaviors (whatever they are) change negligibly with a small change in relative population size. The sensitivity term, δ, in Eq. (3) thus becomes dominated by spatial density terms (the dependence of area A on population N) and acoustic propagation factors (the propagation P term). Since propagation parameters can be estimated with knowledge about the ocean floor's geology and the sound speed profile measurements, the only remaining unknown parameters in Eq. (3) include those describing how the species in question is spatially distributed.

Equation (3) can be simplified further by introducing a population density "packing" model. This packing model relates increases in region A with changes in population N. To do this, note that many scenarios of interest in the open ocean can be modeled as a power law, where A is proportional to N_υ, (i.e. $dA/A=\upsilon dN/N$) and υ is a fixed constant. Using this expression, Eq. (3) becomes

$$\delta = 1 + Q_{indiv} + \upsilon[(A/P) * \partial P/\partial A - 1] \tag{3.4}$$

An exploration of Eq. (4) yields two extreme scenarios of how animals may "pack" together: a "constant-area" (CA) scenario (υ=0) and a "constant density" (CD) scenario (υ=1). Figure 2 illustrates these two extremes.

3.3.3 Constant area (CA) scenario (υ=0)

Under the CA scenario, it is assumed that the region occupied by singers is independent of population size, so that doubling the population would double the singers' spatial density. The "density estimation" approach of line and point transect theories implicitly assumes a constant area scenario, where population density is expected to be proportional to population (Marques et al., 2009; Marques et al., 2013). To simulate this, υ can be set to zero in Eq. (4) to yield

$$\delta_{CA} = 1 + Q_{indiv} \tag{3.5}$$

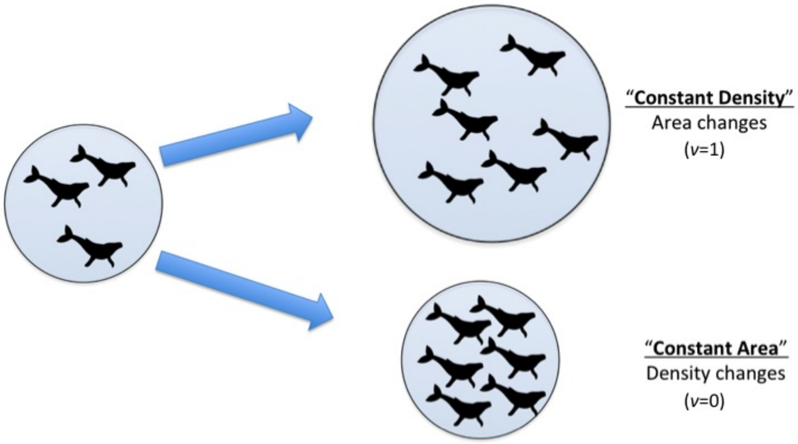


Figure 3.2: In a constant density (CD) scenario (top), the area over which whales are singing expands in order to maintain a constant spatial density. In a constant area (CA) scenario (bottom), the spatial density within that area increases in order to maintain the same the regional size over which the whales are singing.

Thus, δ, as defined in Eq. (3), should be close to or greater than 1 as long as Q_{indiv} is negligibly small. Eq. (3.5) is of particular interest to our study because it predicts that δ, the "sensitivity", is independent of not only the propagation environment, but also of the acoustic frequency being measured (that is, unless Q_{indiv} is frequency-dependent).

3.3.4 Constant density (CD) scenario (υ=1)

At the other extreme of Eq. (4), singers may space themselves apart evenly. The regional area A becomes proportional to N, and $\upsilon=1$. That is, the spatial density of the singers does not change, but the region occupied by singers expands and contracts with respective increases and decreases in the number of singers present. In this case, Eq. (4) becomes

$$\delta_{CD} = Q_{indiv} + \upsilon(R/2P) * (\partial P/\partial R) = Q_{indiv} + 1/2 * ((\partial log_{10}P)/(\partial log_{10}R)) \qquad (3.6)$$

where we have assumed a circular sector for A, so that $dA/A = 2dR/R$. Eq. (A6) gives an explicit expression for the second term of 3.5 as sums of normal modes.

For high seabed attenuation and large values of R, noise levels become insensitive to population size, so δ_{CD}=Q_{indiv}. The sensitivity becomes higher when both the regional radius R and the seabed attenuation become small. The upper limit of this sensitivity is Q_{indiv} + 0.5, which can be seen by taking the Taylor expansion of terms like (1 - $e^{-2\alpha R}$) $\sim$ $2\alpha\, R$ in Eq. (A6). In other words, ambient humpback-generated noise levels increase with the square root of the number of animals (ignoring Q_{indiv}) in the limit of no attenuation. An intuitive explanation for this relationship is that, for a perfectly transparent ocean, the intensity of a single whale will fall off like $1/R$ (cylindrical spreading). The contribution to ambient noise produced by a set of either evenly spaced or randomly-spaced whales inside a small annular ring, dR wide, will then be proportional to $(2\pi R)(1/R)dR$, or $2\pi dR$. The total intensity thus becomes proportional to the regional radius R: the square root of the area A, and the square root of the number of evenly spaced animals *(N)* within that A.

In summary, the KIP model predicts that the ambient noise sensitivities of a CD scenario ($Q_{indiv} < \delta_{CD} < Q_{indiv}$+0.5) lie below the sensitivities of a CA scenario (1+ $Q_{indiv} < \delta_{CA}$). The reason this sensitivity is lower for the CD scenario is that whenever additional animals arrive, they effectively sing at greater ranges from the sensor, which would not be the case under a CA scenario where all animals would be singing from a predetermined maximum distance. The larger distances in the CD scenario decrease the contribution of an individual singer to the overall ambient noise level being detected at the recorder.

Furthermore, Eq. (3.5) shows that, if Q_{indiv} can be neglected, δ_{CD} is a strong function of the propagation environment in terms of both frequency and range R, while δ_{CA}

is independent of frequency and details of the propagation environment. Furthermore, if Q_{indiv} can be neglected, δ must lie between 0 and 1, and υ (the packing model parameter) can be inferred from δ. If δ can be empirically measured as a function of frequency, then this theoretical model can be stringently tested. In the next section, we discuss how δ can be empirically measured.

3.3.5 Measuring sensitivity (δ) using visual transect surveys

The sensitivity, δ, defined in Eq. (3) can be measured if information about relative population size over time can be determined using separate visual surveys from the acoustic recordings. Since only relative population changes need to be measured [as $d(\log N)=dN/N$], a small line transect survey can be used to estimate δ as long as the following criteria are met:

(a) The area covered by a visual survey is equal to or smaller than the total area A monitored by the hydrophone (assuming that the number of animals present in the visual survey area is proportional to the total population monitored in region A).

(b) The number of animals visually sighted is proportional to the number of singing whales in the larger region; that is, assuming singing whales are a constant fraction of the total demographic population.

(c) The visual survey conditions remain the same throughout the survey (e.g., visibility and effort per unit area), so that raw counts can be used to measure relative changes in population. Thus typical line transect correction factors such as g(0)the number of animals likely to be right on the transect lineare not required.

Note that assumption (b) allows for an estimate of δ even under a constant density (CD) scenario. One might think that under a CD scenario, repeated visual surveys over the same small area should yield the same number of animals (since the spatial density of singers remains constant). However, a constant spatial density only exists for the particular subset of the population that is singing during a particular moment in time. As behavioral states change over time, we assume humpback whales (including non-singing whales) rotate through different spatial density patterns (alone, in pairs, or in multiple animal competition pods).

If these three conditions are met, then measuring δ becomes straightforward. Changes in raw animal counts made during small visual surveys can be used to estimate the relative fractional changes of the singing population between days, hours, weeks, etc., because then $d(\log N_{survey}) = d(\log N_{singers})$. The advantage of a combined visual and acoustic dataset is that the resulting estimates of δ provide a more stringent test of the KIP model.

As seen above, the magnitude of δ provides insight into how the animals distribute themselves with respect to each other. Neglecting the term Q_{indiv}, if singing animals do not space themselves apart (CA model), then $\delta \sim 1$, independent of the acoustic frequency measured. If animals do space themselves apart (CD model), the noise field becomes less sensitive to changes in population size so that $0 < \delta < 0.5$, and δ will vary with acoustic frequency.

3.3.6 Simulations of ambient noise levels (I_{dB}) and sensitivity (δ) from singing males)

Here we estimate various model parameters to illustrate some values of the noise intensity (I) and sensitivity (δ) that might be expected from singing humpback whales off Cabo San Lucas, México, assuming a CD scenario. For these simulations, all whales are assumed to have source levels of 155 dB re 1 μPa @ 1m, with 4 km spacing between the singers. A duty cycle of 65% is used, based on typical time intervals between units as known from song recorded in this region over the past few years as well as previous findings of typical lengths of units and inter-unit intervals (Payne & Payne, 1985; Mednis, 1991). The most egregious assumption is that the spectral density of the entire song is assumed to be constant between 100 Hz and 1 kHz. Additionally, the whales are modeled to sing 20 m deep, even though they have been observed to sing both shallower and deeper.

Beyond behavioral assumptions, this model uses a 90-m deep waveguide with a 1500 m/s isovelocity profile, and a receiver placed at 80 m. The ocean lies on top of a 25 m layer of sand that in turn lies on granite bedrock. Sand has a compressional speed of 1650 m/sec, density of 1.9 g/cc, and p-wave attenuation of 1.3 dB/wavelength (Hamilton, 1980). Bedrock has respective values of 2700 m/sec, 2.3 g/cc, and 0.16 dB/wavelength. As discussed in Appendix A, a sediment layer needs to be included in the model so that the resulting normal modes can approximate the near-field continuous contribution to the ambient noise field. The most unrealistic physical assumption in the model is that the surrounding bathymetry is flat, whereas a sloping bathymetry with finger canyons would be more appropriate off Cabo San Lucas.

Figure 3(a) shows the resulting received ambient noise power spectral density in dB re 1 $\mu\text{Pa}^2/\text{Hz}$ for the recorder (Eq. A3), as a function of both frequency and regional radius R. One sees that for small regions, the noise levels change quite rapidly with regional radius, but the low-frequency components of the noise spectrum (about 200 Hz and below), become relatively fixed as R increases past 15 km. Higher frequency components are still approaching their asymptotic limit as R reaches 50 km. Even though the original source spectrum was flat, we see that the propagation environment favors the lower frequencies: 50 Hz displays a 25 dB higher spectral density than 1 kHz.

Figure 3(b) shows δ_{CD} as a function of frequency and regional radius R, using the analytic formulas in Eq. (5b) and (A6), and setting $Q_{indiv} = 0$. As predicted for small regions, the value of δ_{CD} approaches 0.5, while for large regions and lower frequencies, the value of δ_{CD} approaches 0: noise levels become unaffected by changes in singing population. Due to the effects of acoustic propagation and receiver depth, the sensitivity in our model is greatest at 600 Hz, and least near 350 and 850 Hz. Although not shown here, these bands of minimum and maximum sensitivity shift frequency with receiver depth. The constant-area δ_{CA} scenario is not plotted, as it would simply be 1 for all regions and for all frequencies.

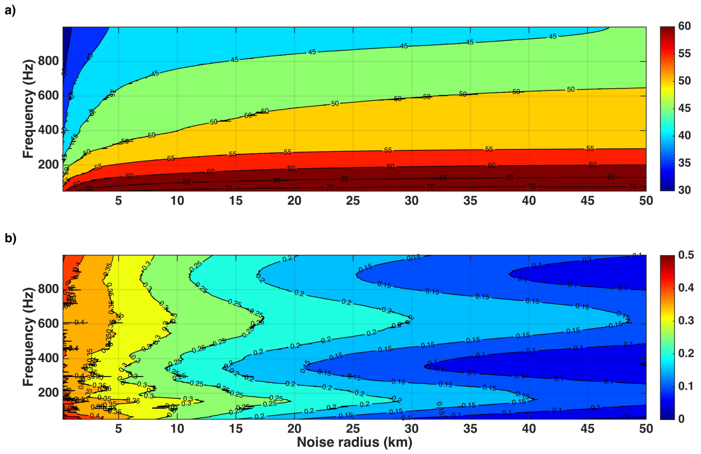


Figure 3.3: (a) Modeled ambient noise power spectral density generated from singing humpback whales in an ocean environment representative of Los Cabos, México, as detected by a recorder deployed 80 m deep in a 90 m deep waveguide. The noise is displayed as a function of frequency and the radius R of the singing region. The power spectral density of the whale song was assumed to be a constant value of 125 dB re 1 μPa^2/Hz between 100 and 1000 Hz (total source intensity of 155 dB re 1 μPa). (b) Modeled noise sensitivity δ as a function of frequency and regional radius R for a constant density (CD) case, computed from Eq. (5b) and (A6), and neglecting Q_{indiv}.

Figure 4 displays the ambient noise intensity modeled by integrating the power spectral density in Fig. 3(a) over a set of 50 Hz bandwidths, with five center frequencies between 125 and 925 Hz. A 50 Hz bandwidth was selected because the humpback source level power spectral density (constructed across an entire 20-30 minute song duration) is (1) relatively constant over any given 50 Hz bandwidth, and (2) most song units span at least 50 Hz. Appendix B shows that sensitivities estimated from narrowband-integrated ambient noise intensities are still independent of source level and duty cycle. Figure 4(f) differs from the other subplots in that it shows the broadband ambient noise intensity integrated between 100 and 1000 Hz, to give some sense of what the model predictions would be for broadband measurements. For each bandwidth, a linear fit to the ambient noise level vs. regional radius yields estimates of δ_{CD} that can be compared to empirical data later, as the

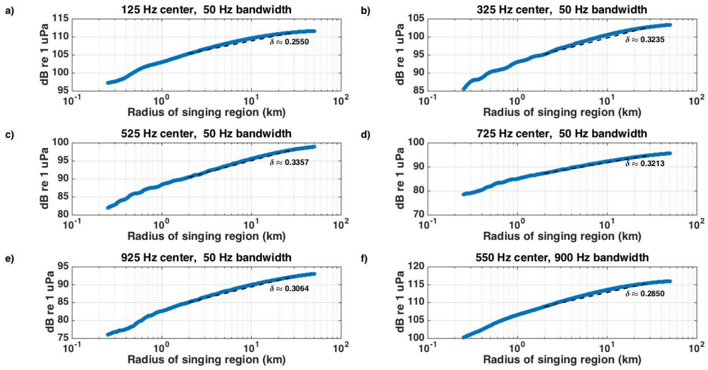


Figure 3.4: Model of humpback whale ambient noise intensity generated over 50 Hz bandwidths, as a function of singing region radius R, using parameters identical to Fig. 3. Values of an "empirical" δ_{CD} are shown, estimated by a linear fit (dashed line) between 2 and 20 km, and then using Eq. 5(b). Center frequencies of the bandwidth samples are (a) 125 Hz; (b) 325 Hz; (c) 525 Hz; (d) 725 Hz; and (e) 925 Hz. Subplot (f) shows a noise estimate integrated between 100 and 1000 Hz and assumes a flat song spectrum.

linear fit mimics the fit of a generalized linear model to the data. The values displayed in Fig. 4 show that the Los Cabos propagation environment causes the largest sensitivity values to fall between 500 and 700 Hz, consistent with Fig. 3(b). The rest of this paper discusses how empirical estimates of δ were produced from field data, for comparison with the values shown in Fig. 4.

3.4 Methods

3.4.1 Study location

Geographically speaking, "Los Cabos" (Fig. 5) denotes a collection of capes around the tip of México's Baja peninsula. Cabo San Lucas lies on the southwestern-most tip of the Los Cabos region and boasts a large marina primarily used by whale-watching and sport-fishing companies. Boat traffic tends to decrease eastward (from Punta Ballena to Punta Gorda to Cerros Colorados) with distance from this marina.

A subset of the Central North Pacific humpback whale stock breeds off Los Cabos over the boreal winter months, typically from late January to early April (Calambokidis et al., 2008; Jiménez-López, 2006). From past visual survey research, it is known that humpback whale density tends to increase further eastward from Punta Gorda to Cabo Pulmo (Jiménez-López, 2006). This is the opposite trend of boat traffic. In the future, a sanctuary at Cabo Pulmo may extend into the Los Cabos region (pers. comm. Serge Dedina).

There are several reasons why this region provides an opportune location to test the KIP model. First, the local bathymetry allows acoustic recorders to be placed at nearly the same depth, in the same expected propagation environment, and the same distance from shore at several sites throughout the area. Second, visual surveys of the local humpback population have been extensively conducted by Laboratorio Marinos Mamíferos at the Universidad Autónoma de Baja California Sur (UABCS) in La Paz throughout the past couple of decades. UABCS has found that humpback whales stay close enough to shore to feasibly perform boat-based visual line transect surveys at multiple sites between Punta Ballena and Cerros Colorados over the course of a single day (Jiménez-López, 2006). Third, the spatial population gradient mentioned above means the number of whales between locations differs substantially, even though these locations are close enough to be surveyed in a single day.

3.4.2 Passive acoustic locations

Acoustic recorders were deployed along the Los Cabos coast for approximately two months during both 2013 and 2014. For the remainder of this paper, specific deployment locations will be called “sites”. Sites were chosen based on past knowledge of both relative boat activity and gradients in humpback whale density. An attempt was made to place recorders equidistant from shore, as long as bathymetry allowed them to sit at nearly the same targeted depth of 90 m. Acoustic recorders were also placed close enough so all sites could be easily traversed by the same whale, increasing the likelihood that all three sites would monitor the same whale population. Conversely, there was sufficient spacing between recorders to prevent their effective recording radii from overlapping, preventing a singing whale from being recorded concurrently at more than one site.

In 2013 the sites included Punta Ballena (high boat activity, low whale concentration), Punta Gorda (moderate boat activity, medium whale concentration), and Cerros Colorados (low boat activity, high whale concentration). In 2014 it was determined that Punta Gorda was too close to Cerros Colorados for a true representation of an area with moderate boat traffic, so a site farther West at Punta Palmilla replaced it. Punta Ballena and Cerros Colorados, however, were still monitored in 2014. Figure 5 maps locations for both years.

3.4.3 Passive acoustic equipment and deployment procedures

The same bottom-mounted recorders described by Ponce et al. (2012) collected acoustic data. Although duty cycle differed by year, the sampling rate was 6.125 kHz for both years at all sites. In 2013, data were recorded for thirty minutes every hour (50% duty cycle), but in 2014 data were recorded continuously (except for a few hours every two days, when data were written to a hard disk). The hydrophones used for both years were HTI-96-MIN (High Tech Inc.) with a 171 dB re 1 μPa/V sensitivity. The recorders were combined with handmade anchors (four burlap bags filled with gravel in 2013; four 25 kg cement blocks in 2014), a Sub Sea Sonics A-60E acoustic release, and two 714 Trawlworks subsurface buoys, using both manila and nylon line to create an assembly. HOBOware Tidbits and inclinometers were also attached to the assemblies to collect temperature and tilt data. The final assembly placed the hydrophone 10 m above the ocean floor, consistent with the simulations in Section 2.2. Table 1 lists the dates, coordinates, and depths for all acoustic recorder sites. Note that depths are bottom depths, but the hydrophone actually sat

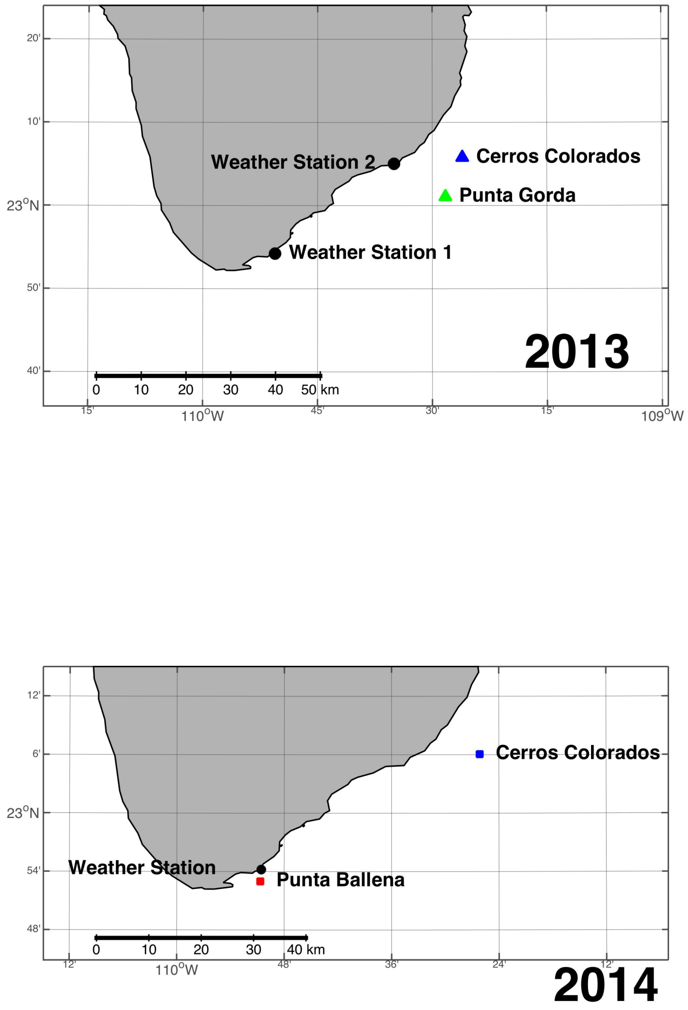


Figure 3.5: Positions of passive acoustic recorders and visual transects during two breeding seasons off Los Cabos. Visual transects were conducted at all sites for both years, but only transects associated with successful recording sites are shown here. Transect lines were always 10 km long and spaced 4 km apart (causing lines to be centered over Cerros Colorados, but not over Punta Gorda in 2013). In 2013 (top), two track lines were surveyed; in 2014 (bottom) only a single track line was surveyed.

10 m above the ocean bottom.

Table 3.1: A listing of the time frames, depths, and locations of all autonomous acoustic recorders analyzed in this report.

2013	**Punta Ballena**	**Punta Gorda**	**Cerros Colorados**
Lat/Long	*n/a*	*23.027 N, 109.472 W*	*23.094 N, 109.437 W*
Depth		105 m	105 m
Acoustic Survey		**Feb 8 - Apr 1**	**Feb 8 - Apr 1**
Visual Surveys		***Feb 18, 19, 24*** ***Mar 7, 18, 21, 27***	***Feb 18, 24*** ***Mar 6, 18, 31***
2014			
Lat/Long	*22.884 N, 109.843 W*	*n/a*	*23.102 N, 109.437 W*
Depth	92 m		95 m
Acoustic Survey	**Feb 7 - Mar 26**		**Feb 6 - Mar 26**
Visual Surveys	***Feb 13, 15, 22, 25*** ***Mar 1, 4, 13, 20***		***Feb 11, 15, 22*** ***Mar 1, 5, 12, 20***

3.4.4 Visual transect protocol and procedures

Visual transects using standard line transect protocols were performed both years using the panga *Yubarta*, but with slightly different track lines an important factor that was considered in subsequent statistical analysis. In 2013, two transect lines were traversed at 4-km spacing from each other, starting 2 km from the coast (since the visual range from the *Yubarta* was 2 km). This centered track lines above Cerros Colorados, but caused them to be off-center above Punta Gorda. For better efficiency in 2014, the track lines were reduced to a single line that passed over the top of each acoustic recorder (Figure 5).

All other protocols remained the same for both years: the *Yubarta* was driven at 5 knots along the 10 km-long transect lines that ran parallel to the coast. The visual observers scanned the forward quadrant on their respective sides of the panga and, upon sighting a whale, reported the group type, number of animals, and distance from the *Yubarta* to an onboard scribe. To decrease chances of resighting animals, whales were only counted when their sighted location was orthogonal (“off the beam”) to the transect line.

Environmental conditions were observed before each survey. These included water temperature, Beaufort level, cloud cover, wind direction, visibility, swell height, and glare.

Each transect line took roughly one hour to complete. Visual surveys were performed only in seas at Beaufort levels 0 and 1, so the visual detection range (and detection function) was consistent across the surveys, fulfilling one of the requirements listed in Section 2.3.

3.5 Statistical analysis

3.5.1 Visual data analysis

Several types of analyses of the visual surveys were used to tabulate sighted whales. Multiple possibilities existed for measuring the relative singing population: (1) counting only whales that were sighted alone, since singers tend not to sing in groups ("solo"); (2) counting all sighted whales, excluding mother/calf pairs ("no m/c"); and (3) counting all sighted whales, including mother/calf pairs ("all"). Ideally, only male whales should be counted, since only males sing, but since whales could not be sexed all three options could easily include females. We thus assume that males comprise a consistent fraction of the sighted population, as discussed in Section 2.3.

3.5.2 Acoustic data analysis

The acoustic noise data analysis required several steps. First, the raw binary acoustic data were downloaded from the recorders and converted into pressure units, and the frequency spectrum was corrected for the hydrophone sensitivities. Short-term power spectral densities (PSDs) in dB re 1 $\mu\text{Pa}^2/\text{Hz}$ up to 3.125 kHz were estimated to 24-Hz resolution by averaging the FFT snapshots (overlapped 50%) over one minute. Subsequent calculations were restricted to a 100-1000 Hz bandwidth because humpback whale song mainly resided between these frequencies (see figure 1). Nine 50-Hz bands within that bandwidth were also computed: 100-150 Hz, 200-250 Hz, 300-350 Hz, 400-450 Hz, 500-550 Hz, 600-650 Hz, 700-750 Hz, 800-850 Hz, and 900-950 Hz. Next, 1-min averaged PSDs were integrated over these bandwidth estimates to compute the average acoustic intensity each minute. Percentile distributions of these intensities were then generated over one-hour intervals, and the 1st, 10th-90th (in tenths) and 99th percentiles were extracted for further analysis. As a result, a given percentile could be plotted against time with hourly resolution for all sites over both years. Cyclical and secular fluctuations were easily spotted in these plots (see Fig. 7 for an example plot).

To determine whether a diel song cycle was occurring in Los Cabos, as is the case at Hawaii and other breeding grounds (Au et al., 2000; Cholewiak, 2008; and Sousa-Lima & Clark, 2008), the PSD percentile histograms were averaged and plotted as a function of the hour of day. For example, all the intensity values from the 50th percentile computed between 0100 and 0200 from each day at a given site were averaged, and then repeated for all twenty-three subsequent hours. A strong diel cycle did exist, whereby whales off Los Cabos tend to sing most actively near midnight and taper off at sunrise, and this phenomenon was accounted for when comparing visual transect data to the acoustic data.

Fig. 6 illustrates five acoustic metrics that were used in an attempt to remove this diel effect. All of the acoustic metrics were measured using the 50th percentile from the one-hour “noise” samples. The metrics included (A) the peak sound intensity from the night before a visual survey, (B) the peak sound intensity from the night after a visual survey, (C) the sound intensity from the hour concurrent with the visual survey, (D) the average of the peak intensities from the nights before and after a visual survey, and (E) the average of the peak-to-trough intensities from the nights on either side of a visual survey. This last metric (E) measures the extent (or strength) of the diel cycle and assumes that the daytime troughs are the contribution of non-whale noise sources to the environment. While metric (C) might seem to be an obvious choice, it is contaminated by boat engine noise from *Yubarta* during the visual survey effort.

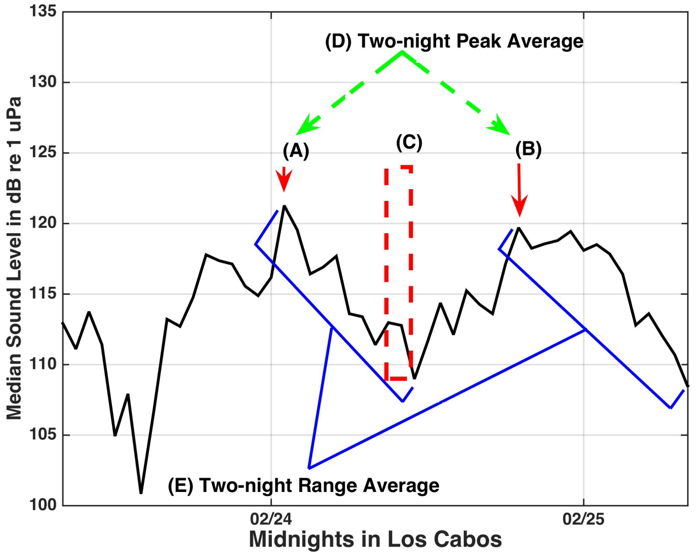


Figure 3.6: The five sound metrics used were the hourly average of the 50^{th} percentile of the sound level at (A) the peak hour the night before a survey, (B) the peak hour the night after a survey, (C) the hour concurrent with a visual survey, (D) the mean of the peaks from the nights before and after a survey, and (E) the mean of the maximum dB variation of the nights before and after a survey.

3.5.3 Estimating the sensitivty

The final step in data analysis was to combine the various visual counts and acoustic metrics for each frequency band via a generalized linear model (GLM) to determine which pairing had the most significant fit, and then measure the δ (sensitivity) of that combination.

To estimate δ (Eq. 3) from the data, the following GLM was used:

$$I_{dB} = +(10logN) + [Year] \tag{3.7}$$

where I_{dB} is one of the acoustic metrics described in Section 3.5.2, expressed in dB, and N represents one of the visual counts discussed in Section 3.5.1. β (dB) is the y-intercept of the fitted line, and γ is the coefficient of a categorical variable *Year* that accounts for differences in methodology between years. The specific methodological differences include (1) recording duty cycles (50% in 2013; 100% in 2014), (2) track lines (two in

2013; one in 2014), and (3) site locations (Punta Gorda and Cerros Colorados in 2013; Punta Ballena and Cerros Colorados in 2014), (4) song unit changes (humpback whales can change their song every two to three weeks (Norris et al., 2000), and (5) hydrophone depths (104 m and 105 m in 2013, 92 m and 95 m in 2014).

The predictor coefficient of the multiple regression (δ) can be interpreted as the slope of the line relating the base-10 logarithm of the visual count with the dB value of the acoustic metric after the visual counts were corrected for year. This coefficient is an empirical estimate of the sensitivity δ. The corresponding values from the model were obtained by computing the linear slopes from the subplots in Fig. 4, between regional radii that were expected to be the minimum and maximum encountered over the course of a season. These values were estimated to be 2 and 20 km respectively.

All combinations of the five acoustic metrics and three visual counts were run through generalized linear model scripts in the Matlab statistics toolbox. The R^2, test statistics, p-values, and all coefficients were tabulated for all combinations and compared to find the best R^2 value that was also significant to a p-value of 0.05. The visual count and acoustic metric pairing that yielded the highest R^2 values with the lowest p-values (as presented in Table A1) were then explored with multiple model specifications for the best AIC value.

3.6 Results

3.6.1 Visual surveys

The cumulative visual survey results are presented in Table 2 in terms of the three visual counts. These counts are used to provide an illustration of seasonal whale densities. For example, over the course of 2013 observers noted 22 “solo” whales, 47 “no-m/c” whales, and 51 “all” whales at Punta Gorda. These counts are consistent with the expectation from Jiménez-LÓpez's (2006) master's thesis that humpback whale density increases eastward from Cabo San Lucas. Also note that more whales were detected in the Los Cabos area in 2013 than in 2014.

Table 3.2: The total number of all whales counted, all whales excluding mother/calves, and solos counted at each site for each year.

Year	**Punta Ballena**	**Punta Gorda**	**Cerros Colorados**
	"all"/"no-m/c"/"solos"	*"all"/"no-m/c"/"solos"*	*"all"/"no-m/c"/"solos"*
2013	*n/a*	*51 / 47 / 22*	*142 / 136 / 58*
2014	*50 / 46 / 26*	*n/a*	*97 / 85 / 34*

3.6.2 Noise measurements

In 2013 an electronic malfunction in the recorder at Punta Ballena caused it to stop logging after only five days. The Punta Gorda and Cerros Colorados datasets lasted from February 8, 2013 to April 1, 2013. In 2014, recorders at Punta Ballena and Cerros Colorados successfully collected data from February 7 to March 28, but the recorder at Punta Palmilla broke free and drifted 13 km Southwest until it slipped into a finger canyon and was never recovered.

Figure 7 displays the 50^{th} percentile of the ambient noise level between 300-350 Hz, computed for each hour during the 2013 recording season at Cerros Colorados. Clearly, the noise intensity over this bandwidth can vary greatly (up to 15 dB or more) on a daily basis. From Eq. (2), a 15 dB daily noise shift corresponds to fluctuations in N numbers by a multiplicative factor of 30. When comparing sites from the same season, Punta Gorda (moderate boat traffic) and Cerros Colorados (low boat traffic) in 2013 are more similar than Punta Ballena (high boat traffic) and Cerros Colorados (low boat traffic) in 2014. In 2013, the average 50^{th} percentile values were 104 dB re 1 μPa at Cerros Colorados and 100 dB re 1 Pa at Punta Gorda. The average 50^{th} percentile values for 2014 were 101 dB re 1 μPa at Cerros Colorados and 96 dB re 1 uPa at Punta Ballena. Since Cerros Colorados was the only site recorded over both years, we find that the same midnight-peaking trend exists at both years, but the average 50^{th} percentile value for 2014 was 3 dB less than in 2013 (Fig. 7).

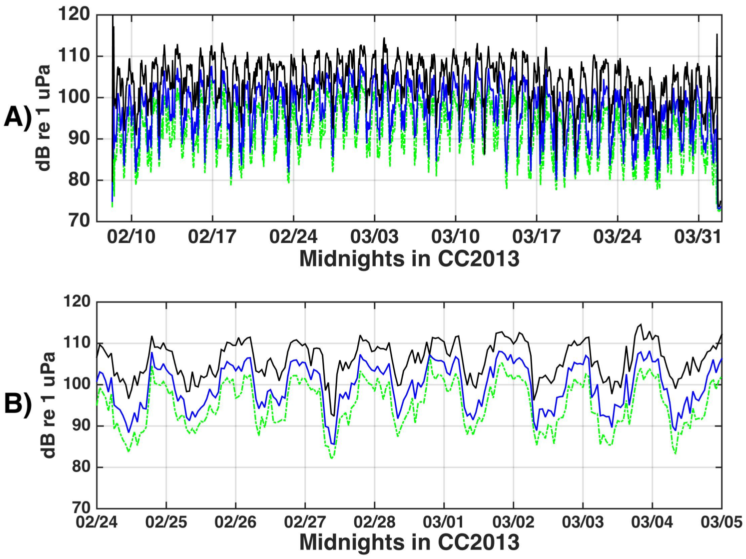


Figure 3.7: (A) Plots of the 10^{th}, median, and 90^{th} percentiles of the noise intensity computed between 300 and 350 Hz for every hour across the entire 2013 recording season at Cerros Colorados. (B) An expansion of time scale in (A) to show nine days in detail. A diel cycle is clearly visible, with a peak:trough dynamic range of 10-15 dB.

Figure 7 illustrates that nightly peaks in sound intensity at the 50^{th} percentile tend to fall between about 102-107 dB re 1 μPa in the 300-350 Hz bandwidth. (The peaks are more consistently about 120 dB re 1 μPa in the 100-1000 Hz bandwidth.) Recall that the simulations in Fig. 4(f), which assumed whale source levels of 155 dB re 1 μPa @ 1m and animal separations of 4 km, predicted a received level of 100 dB re 1 μPa for R = 10 km for the 300-350 Hz bandwidth. Some of the nightly 50^{th} percentile peaks, especially near the end of the season, do fall near 100 dB re 1 μPa.

3.6.3 GLM results

The GLM was applied to several bandwidths. After calculating δ for all visual counts and acoustic metric combinations for both combined and separated years, the R^2 values with significant p-values were compared. The model [sound $\sim$ 1 + year + count] using only linear terms in the two predictor variables performed better than (had lower AIC values than) using an interaction term between the two. AICs were also higher for using quadratic terms in the models ([sound $\sim$ 1 + year + count + count^2] and [sound $\sim$ 1 + year + count^2]). Therefore, the simplest linear model using acoustic metric D and visual count "all" best explained our empirical data.

Figure 8 shows dB noise vs. the logarithm of the transect counts (adjusted for the effect of year) along with the best-fit lines for each year. It also shows the predicted values, the slope (δ) of the combined years, and the slope's 95% confidence bounds. The estimated δ-value for the 300-350 Hz bandwidth was 0.436 ± 0.114 dB re 1 μPa (p-value = 6.12e^{-4}, *t*-test statistic = 3.81), a value that falls within the theoretical range (0 to 0.5) of the CD scenario, and is too low for the CA scenario.

The low p-value indicates that we can reject the null hypothesis that the acoustic metric did not differ statistically from a constant (i.e. the probability that the sensitivity coefficient is zero). Table 3 summarizes the results for all bandwidths using the acoustic metric D and the "all" whales visual count, since this pairing consistently yielded the best R^2 values. Note that not all bandwidths were affected equally by year, but did fall within reasonable (1-6 dB) differences considering the five methodological changes between 2013 and 2014.

As presented in Table 3, the best R^2 value was found between 300-350 Hz (0.60) using acoustic metric D (averaged peak intensity from night before and after the survey) and the "all whales" count. Table A1 is an expansion of Table 3 for all acoustic and visual metrics. The "no m/c" visual count yielded nearly equivalent results. For the remainder of

Table 3.3: Best-fit coefficients for GLM in Eq. (6), for different noise bandwidths, combining both years of data. The predictor variables with the highest R^2 were "all" whales and a categorical year with no interaction term. Acoustic metric D (Fig. 5) yielded the best-fit response variable. The year coefficient quantifies the difference in sound intensity between 2013 and 2014. The intercept projects the sound intensity of the ambient environment if no singing activity was occurring based on the best fit line through the year-adjusted data.

Bndwidth	**d slope (SD)**	**R^2**	**p-value**	**Year g (SD)**	**Intercept (SD)**
100-150 Hz	*0.365 (,0.090)*	*0.38*	*3.11 e-4*	1.63 (0.73) dB	104 (0.86) dB
300-350 Hz	*0.436 (0.114)*	*0.60*	*6.12 e-4*	5.80 (0.93) dB	105 (1.10) dB
500-550 Hz	*0.518 (0.140)*	*0.31*	*8.15 e-4*	1.09 (1.14) dB	92 (1.34) dB
700-750 Hz	0.524 (0.144)	0.43	9.70 e-4	4.43 (1.17) dB	89 (1.38) dB
900-950 Hz	0.445 (0.120)	0.36	8.19 e-4	2.38 (0.98) dB	85 (1.15) dB
100-1000 Hz	0.383 (0.087)	0.42	1.24 e-4	1.74 (0.71) dB	115 (0.84) dB

this section, we focus on the results of this 300-350 Hz bandwidth. β, or the y-intercept, was 105 $\pm$ 1.10 dB re 1 μPa. γ was 5.80 $\pm$ 0.93 dB re 1 μPa: that is, for a given value of $10\log N$, a roughly 5 to 7 dB difference in background noise levels existed between years (p-value = $6.73e^{-7}$, test statistic = 6.21). The 300-350 Hz bandwidth had the largest γ. Other bandwidths exhibited smaller differences between years (1.09 to 4.43 dB). The three methodological differences between acoustic and visual data collection between 2013 and 2014 are contributing factors to the non-zero value of γ; the possibility that changes in song structure between years may also affect γ will be discussed later.

Figure 9 shows histograms and normal probabilities of the residuals of the GLMs for the fit in Fig. 8. The residuals approximately have Gaussian distribution, except possibly at the tails, indicating that the choice of a Gaussian-based GLM is appropriate.

3.6.4 Comparing measured sensitivity with analytic model predictions vs. bandwidth

Figure 10 shows δ for the Section 2.5. constant-density scenario (Eq. (6)), a singing region 20 km radius, for nine 50-Hz bandwidths discussed in Section 3. In addition, the linear least-squares estimate of δ (average sensitivity between 2 and 20 km) is also plotted

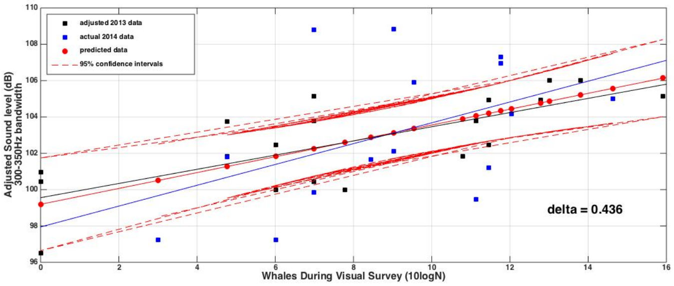


Figure 3.8: Plot of ambient background noise level (acoustic metric D) in the 300-350 Hz bandwidth vs. the base-10 logarithm of the number of all whales sighted during concurrent visual transects. Shown by squares in two hues are the adjusted data points and best-fit lines for both years (2013 darker and 2014 lighter). The slope of the GLM-fitted values (δ), which corresponds to the population sensitivity defined in Eq. (3), is designated by circles. Data have been weighted by year because 2013 tended to be 5-7 dB higher overall than 2014. 95% confidence bounds are shown in dotted lines. The slope of the combined-year data (δ = 0.436) is displayed as text.

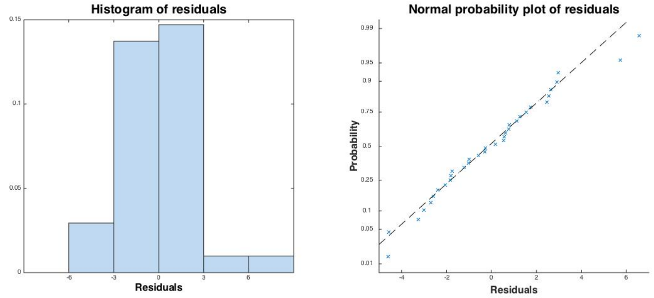


Figure 3.9: The distributions of residuals (left; observed minus fitted values) and cumulative distribution functions of residuals (right) from the GLM for the 300-350Hz bandwidth.

for each bandwidth (e.g., Fig. 4). Also shown are the GLM δ values from Table 3, and their standard errors. As illustrated, all of the actual δ values fall between 0 and 0.5. Even when accounting for standard errors, the CD scenario (where $0 < \delta < 0.5$) is a much better fit to the actual data than the CA scenario ($\delta \sim 1$). Stated another way, Fig. 10 suggests that singing humpback whales tend to maintain a relatively consistent distance between individuals as additional whales arrive.

The observed sensitivities also obtain their maximum and minimum values at the same bandwidths as the modeled values. For example, both observed and modeled sensitivities are minimal between 300-400 Hz and between 800-900 Hz. Even though the observed δ values fall between 0 and 0.5, they all lie above the analytically expected values for a strict CD (υ=1) case. The Discussion lists three possible interpretations for this mismatch between the measurement and the CD simulation.

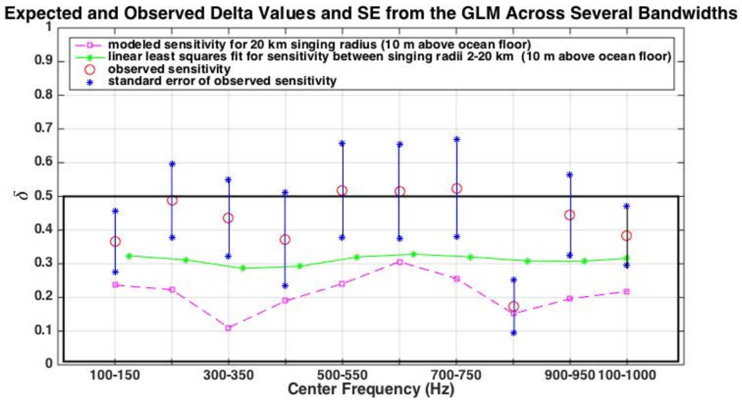


Figure 3.10: The observed values (open circles) of δ for nine different bandwidths and their standard errors (starred lines) compared with the analytically derived values (solid and dotted lines) for a constant-density scenario. The solid line reproduces the linear-fitted values of δ obtained from the simulations shown in Fig. 4. This line effectively estimates the average sensitivity to be expected from a singing population that expands from a region with radius 2 km to a region with radius 20 km. The dashed line represents the sensitivity expected from a population with a fixed singing radius of 20 km. Observed values are obtained directly from the GLM using all counted whales and acoustic metric D. The solid box represents theoretically permissible values of δ for a constant-density model, where $Q_{indiv} = 0$. A constant area scenario would yield values of 1 or larger.

3.7 Discussion

3.7.1 Interpretetation of the best acoustic metric and visual count

Considering several acoustic metrics and visual counts, the best ones for the generalized linear model (highest relative R^2 value with significant p-values at the 0.05 level) were, respectively, an average sound intensity of the peaks the night before and after a visual survey (metric D), and either “all whales” or “no m/c”. It makes sense that the average nightly peak in sound intensity is a representative metric if we assume that the same whales spotted during the visual survey were representative of the whales that sang in the vicinity of that recorder during the nights before and after they were counted.

An advantage to using nightly peaks (instead of daytime levels) is that it avoids contamination from boat engines since vessel activity is very low, and likely nonexistent, between dusk and dawn. A second advantage comes from measuring the sound intensity peaks each night instead of limiting measurements to the same hour each night, presumably compensating for any lunar effects that humpback whales may have responded to over the two fortnights that visual surveys took place (Sousa-Lima & Clark, 2008).

As for visual counts, “all” whales and “no m/c” in the model provided similar results. This supports the assumption in Section 2.3 that the numbers of singing males and mother/calf pairs are constant fractions of the total population. Even the best visual team cannot sex all whales spotted. Using “all” as the visual count considers all potential singers at each site in case; for example, if a pair of males was falsely classified as a mother and calf or a single male was in fact a female.

3.7.2 Explaining the difference between simulated and measured noise sensitivity

The simulated sound intensity values over a broad bandwidth (Fig 4(f) at large R) fall very close to the nightly peaks of sound intensity (Fig. 7). Actual data showed a fairly consistent 105 dB re 1 μPa sound level for the 300-350 Hz bandwidth at the 50^{th} percentile. Figure 10 shows that the measured δ values fell more within the permissible δ values for the CD scenario instead of the CA scenario. Furthermore, the measured sensitivities showed the same general dependence on frequency as the CD simulations. These results suggest that humpback whales generally space themselves equidistantly from each other while singing, and that the region covered by singing whales expands as more whales enter the area. However, the actual δ values were higher than what was expected from the modeled CD scenario. Some insights into why this discrepancy exists include:

1. Animals may pack a little tighter when the population grows by acquiescing to the higher numbers and tolerating a slightly closer spacing. If they behaviorally reduced their distances between each other slightly over the same area, then an intermediate scenario between the extreme CD and CA scenarios can explain our empirical results. In order for the simulated model to reproduce the empirical GLM model values, a packing coefficient value of υ=0.7 is assumed instead of 1, the observed sensitivity at 500 Hz would decrease from 0.5 to 0.35. A value of 0.7 translates into a reduction in spacing by about 20% as the singing population doubles.

2. Animals may alter their individual acoustic behavior (Q) in one or a mix of the following two ways: (A) by increasing their source level when other animals are present, or (B) by "speeding up" the "tempo" between their units, or by using units that have smaller inter-unit intervals. Either of these behavioral changes would make Q_{indiv} in Eqs. (3) and (4) nonzero. For example, the results suggest that if Q_{indiv} were 0.15 then the constant density simulation would match the observed results at 500 Hz. This value of Q_{indiv} could be generated if humpback whales increased their source level by 0.3 dB (increased their output intensity by 7%) if the population doubles.

3. The bathymetry of Los Cabos is not actually flat as assumed in the model.

4. The male/female mixture may change when more females are present. More whales counted during a survey may have included more females and, as a result, the nearby males may have been singing differently if it coincided with more females since the effect of ovulation on singing is not well-known (Nishiwaki, 1959; Tyack, 1981; Baker & Herman, 1984; Darling & Bérubé, 2001).

5. Animals may not be randomly distributed throughout area A, and therefore individual singers may not contribute equally to the overall noise levels recorded. However, Appendix B discusses how a simple linear spatial gradient in singer density would not

affect these conclusions.

The discrepancy between the observed and modeled CD values may arise from a mix of all of these factors. Regardless, our results (Fig. 10) are consistent with the hypothesis that humpback whales in Los Cabos space themselves according to a CD scenario moreso than to a CA scenario. This prediction is consistent with published observations of how singing humpback whales separate themselves while singing (Winn & Winn, 1978; Tyack, 1981; Frankel et al., 1995). In addition, consistency of the magnitude and frequency-dependence of the sensitivity between measured and modeled values (Fig. 10) supports the fundamental assumptions of the KIP model.

3.8 Conclusion

This paper presents an applied use for theoretical waveguide models. The main caveat is that the vocalizing species of interest produces nearly continuous sound in a specific bandwidth. In essence, the goals of this technique was to model an expected δ value for an area's bathymetry and sound speed profile, and then compare it to a GLM using empirical data so δ could be appropriately adjusted and interpreted. This theoretical model showed that changes in ambient noise levels with respect to fractional changes in singer population are relatively unaffected by the source level distributions and song spectra of individual humpback whales, but δ does depend on frequency and on how the singers' spatial density changes with population size. As a result of comparing the theoretical model with the GLM, it is suggested that humpback whales tend to maintain relatively distant spacing with one another while singing. The small discrepancies between the two models are likely due to individual whales singing slightly "louder" or longer when other singers are nearby, or that they cluster a bit more tightly as the singing population increases.

The techniques discussed here are not restricted to just humpback whales, but could be applied to other ambient noise situations that are dominated by bioacoustic signals. Depending upon the season, blue, pygmy blue, and fin whales may be good future candidates for testing and applying these models (McDonald & Fox, 1999; Gavrilov & McCauley, 2013) and would be valuable for reserve management personnel or scientists who are interested in quantifying a general increase or decrease in the relative abundance of animals.

3.9 Acknowledgements

Many thanks to my co-authors: Aaron Thode, Jorge Urbán-R, Pamela Martínez-Loustalot, Esther Jiménez-López, and Diana López-Arzate. This project would not have been possible without the extensive dedication of our visual team from UABCS in La Paz, México. First and foremost: a huge thanks to Juan Carlos Salinas as our panga-driving extraordinaire with his general masonry know-how. Next, thank you to photo ID and humpback whale experts (and co-authors) Pamela Martínez-Loustalot and Esther Jiménez-López. If not for their knowledge, passion, patience with certain native English-speakers, and a beloved dusty hatchback, fieldwork would have actually felt like work. Others from UABCS and SIO who have helped include Hiram Rosalez-Nanduca, Carlos López-Montalvo, Lorena Viloria, Jit Sarkar, Melania Guerra, Ludovic Tenorio-Hallé, Romina Carnero-Huaman, and Cedric Arissdakessian. Robert Glatts built the acoustic recorders and David Brem made certain that the acoustic releases were easy to operate. Thank you also to Garret Eaton, Art Taylor, and Celia Condit for their assistance in making sure that all gear arrived at its desired destinations. The Ocean Foundation funded this work.

Chapter 4

Preliminary analysis of social calls used by tagged humpback whales in the Los Cabos, México, breeding ground

4.1 Abstract

Bioacoustics research on the humpback whale (*Megaptera novaeangliae*) has focused more heavily on their song than on their social sounds. Social sound repertoires and their basic acoustic features have been documented along an Australian migration route, in an Alaskan feeding ground, and on a Hawaiian breeding ground. This project presents a repertoire of social calls recorded on the North Pacific humpback whale population's eastern breeding ground off of Los Cabos, México, over two years. Sounds from several demographic groups were recorded in 2014 and 2015 during February and March using Acousondes and Bioacoustics Probes built by Greeneridge Sciences, Inc. Reported here are (1) calls unique to the Los Cabos breeding ground as compared to other published works, (2) call rates, repertoire diversity, and repertoire entropy within and across group

types, and (3) a comparison of the call type distributions used within and between the groups. The variability with which humpback whales vocalize is not yet captured by a single dataset and deserves continued monitoring and collaboration with researchers working in other geographical areas.

4.2 Introduction

4.2.1 Natural history of humpback whales and a review of social sound studies and social call terminology

The humpback whale (*Megaptera novaeangliae*) is a global species that is split into separate populations, stocks, and sub stocks, which are defined both genetically and by the geographical regions each population uses for seasonal breeding and feeding (Calambokidis et al., 2008). On breeding grounds, humpback whales group themselves into three main assemblages: mothers with calves (MC pairs), mother and calves with one or multiple escorts of unknown gender (MCE groups), and competition pods (CPs) where multiple males pursue one female. Payne and McVay (1971) began studying their song several decades ago, and at that time the understanding was that song only occurred on breeding grounds. These authors defined song as a highly-structured and continuous set of small, repetitive units that are organized into specifically sequenced phrases and themes. Since then, research has shown that song changes slightly from one year to the next (Payne et al., 1983), even at the individual level (Guinee et al., 1983); that it changes substantially decadally (Payne and Payne, 1985); that it varies across subareas within the same breeding region, suggesting dialects (Winn and Winn, 1978); and that song changes similarly over time in the course of a season, as well as between seasons, when comparing two breeding regions, suggesting some level of cultural transmission (Cerchio et al., 2001). These findings show that, on the whole, song is plastic (variable) rather than static.

In bioacoustics studies of other species the term “vocalization” is defined as an emotional signal that may provide the listener with information about the caller’s dominance rank, age, and competitive ability, but does not assume the caller’s intention to provide it (Seyfarth & Cheney, 2003). This lack of known intention is what separates animal vocalizations from human language. Since insufficient direct observations exist to prove whether humpback whale vocalizations have biological meaning or may elicit either random or stereotyped responses from conspecifics, the term “social sound” may be more appropriate for these non-song sounds until more research, like the underwater ethograms by Zoidis et al. (in progress) have culminated. The next paragraphs will serve as a literature review of how social sound research has evolved in the last 30 years, and then establish the verbiage that will be used for the remainder of this chapter.

After many decades of studying song, marine mammal researchers began exploring the function and variability of social sounds in humpback whales about three decades ago. Silber (1986) published the first paper on social sounds in humpback whales on the Hawaiian breeding grounds. He did not find social sounds in humpback calves but did in adults. Zoidis et al., (2008) published the first indication of calves producing social sounds using underwater videography. Dunlop, in several papers, created a humpback whale social sound catalogue, named calls by onomatopoeia, and documented the acoustic features that might be later used for temporal and spatial comparison (Dunlop et al., 2007; Dunlop et al., 2008). Dunlop’s techniques differed from Silber’s and Zoidis’s studies in that she used bottom-mounted recorders, therefore her results cannot be tied to specific individual animals, age classes, or group compositions. Stimpert et al. (2011) examined social calls using DTAGs for the first time, on a North Atlantic feeding ground, and established that two social sounds are sufficiently common and robust to monitor with passive acoustics. Rekdahl and her colleagues, using Dunlop’s datasets, provided the first evidence of plasticity (variability) in social sounds and applied information theory to explore the context of social sounds in bouts (Rekdahl et al., 2013; Rekdahl et al. 2015). Fournet (2014) built on all of this research by creating a social sound catalogue for an Alaskan feeding ground using bottom-mounted recorders accompanied by visual observations, and verified that random forests provide the most robust classification method. Other unpublished but ongoing collections of social calls in Alaska include those documented by Fred Sharpe (1984) and those collected by Christine Gabriele.

Bodily-generated (percussive) sounds such as those typically made by humpback whales (e.g. slapping their pectoral fins or flukes) can be grouped as social sounds in that they are generally assumed to transmit an acoustic signal to a conspecific (Thompson et al., 1977; Tyack, 1983; Silber, 1986), however, they are considered different than calls made directly from the animal via their physiology (sound producing organs). As visual observations coupled with acoustic data becomes more prevalent, a few sounds can be classified as bodily-generated (for example “clacks” in Los Cabos occurred in the acoustic data at the same times that breaches were observed on the surface).

This chapter dichotomizes the anatomical mechanisms behind social sounds, and will henceforth use two separate terms. A “social sonance” will designate the non-phonated (bodily-generated) social sounds while a “social call” will designate the phonated (vocalized) ones, which are the sole focus of this chapter. Many social call types have been found in several breeding and feeding grounds, and continued analysis steadily increases the number of call types that are known to exist.

In 2015 Rekdahl et al. showed that whale calls are sometimes produced in “bouts,” a term commonly used in avian and primate research, but which has been previously called “trains” by Thompson et al. (1986) in the cetacean realm. Either term refers to the same situation; namely, the same call type is repeated at least twice and occurs less than 4 seconds after the previous call. In other words, the inter-call interval is 4 seconds or less between two of calls of the same type. As defined by Darling (2015), each time a call type is produced in a bout, it is a “pulse.” These pulses can be evenly spaced, as Rekdahl found, or unevenly spaced, and therefore in sub-series of “packets.”

Two final terms defined in this chapter are “simple calls” and “composite calls.” Simple calls are what researchers have historically named a social sound: a single call whereby the interval between it and the following call is distinguishable in a spectrogram. In other words, the intercall interval is at least the same duration as one of the calls themselves. A composite call is a set of two simple calls strung together without a distinguishable space of silence between the two. In other words, it has practically no inter-call interval: analogous to how a compound word in English is not written with a space between its parts.

There are many levels of call variability that can be measured. One type of variability would be found when an individual (single) animal can produce the same call type repeatedly, and each time the call will be slightly different. This would be “individual variability”. Another type would occur if we assume every whale has its own individual variability in its call production, but is in a group of whales. Then the variability in calls from a small group of whales (like mother/calf, mother/calf/escort(s), or competition pods) should be slightly higher, and this will be called “intra-group variability”. The next broader step (next example of a higher level of expected variation) is found when we compare call variability between these different group types (such as mother/calf vs. mother/calf/escort[s]): defined here as “inter-group variability”. Compiling all the group types from a single feeding or single breeding ground into one large dataset and measuring the variability within that area would then be called “intra-ground variability”. This brings us to the final comparative step: the variation between different feeding grounds to other feeding grounds, or different breeding grounds to other breeding grounds, which is defined as “inter-ground variability” and is more popularly referred to as biogeographical variability. (There is one final category that would consist of comparing feeding ground calls to breeding ground calls. This has not been previously defined, and has limited applicability since the behaviors are so widely different and ecologically dissimilar. Since the biological significance of this comparison is limited, it is eliminated from further discussion). A flowchart of the variability levels utilized in this paper is given below:

Individual→Intra-group→Inter-group→Intra-ground→Inter-ground/Biogeographical

All variability is relative to individual variability, and would be expected to increase from left to right (fewer individuals to more individuals) provided that humpback whales do not have stereotyped calling behavior. Any varying usage of social calls may be an indicator of age, sex, body size, behavioral state (Silber 1986; Zoidis et al. 2008, 2014), geographical region, and/or level of disturbance (Frankel & Clark, 2000). Therefore, to tackle any research questions about social call variability (or plasticity), there must be a baseline understanding of call repertoires and expected variation in social call behavior. Such variation should be as close as possible to the individual level. This chapter will quantify the intra- and inter-group variation.

4.2.2 Acoustic tags as the common recording platform

The same recording platforms should be used across all datasets in an attempt to remove as many propagation, attenuation, and hardware biases as possible. Tags have a distinct advantage over both bottom-mounted and over-the-side hydrophones because the tag stays on a fixed location of the whale's body. Some tags are even capable of detecting surface vibrations on a calling whale in order to assign vocalizations to the tagged individual (Johnson & Tyack, 2003; Goldbogen et al., 2014). If the accelerometer of a tag does not sample fast enough for the species of interest, though, calls cannot necessarily be assigned to the tagged individual. Furthermore, the most intense calls may not be from the tagged whale, but rather from a nearby conspecific. Since accelerometers at the pertinent sampling rate were not available for this study, we do not assume that a tag represents an individual whale, but that a tag is representative of a single small group: namely M/C pairs, M/C/E groups and CPs.

4.2.3 Los Cabos, México, as the study site choice

The waters off Los Cabos, México, serve as both a breeding ground and part of the migration corridor for whales continuing to more southern Mexican waters. This region is currently the least acoustically studied portion of the Central North Pacific humpback whale population range. Bottom-mounted recording studies from Hawaii were first conducted in 1998, but these studies focused on song and chorusing (Au et al., 2000). Over-the-side hydrophone recordings for social calls in Hawaii date back to 1986 (Silber), while underwater video and in-water dual hydrophone studies combined more recently with tagging data collection have been ongoing since 2001 (Zoidis et al., 2008 and 2014). Other more recent acoustic tagging humpback studies (Stimpert et al., 2012; Darling, 2015; Jessica Chen, pers. comm.) are ongoing. In Alaska, Fred Sharpe began researching feeding calls and calling behavior for his 1984 thesis and other researchers continue to build on his findings (Fournet, 2014). Some data from Los Cabos exist, but they are sporadic. For example, Thomas Norris and Ken Balcomb collected over-the-side hydrophone recordings almost 20 years ago, but the work was never published. The Marine Mammalogy Lab at Universidad Autónoma de Baja California Sur (UABCS) has over-the-side hydrophone recordings for projects such as Jiménez's master's thesis (2006), but the projects focused on song.

The Cabo region of México includes a series of capes that wrap around the tip of the Baja California Sur peninsula as the Sea of Cortez joins the Pacific Ocean. Humpback whales here inhabit a largely deep open ocean environment with minimal shelf space less than 200 m deep. The habitat can be seen in Figure 1.

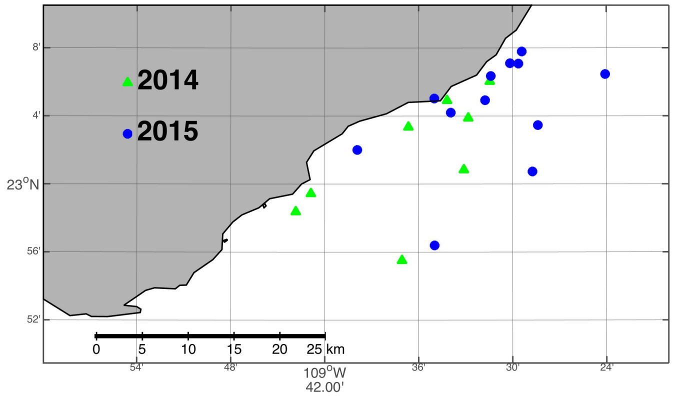


Figure 4.1: Tags deployed on all whales during 2014 (circles) and 2015 (triangles).

4.3 Methods

4.3.1 Behavioral quantification definitions

The behavioral quantifications for this chapter rely on comparing how three group types use social calls. Humpback whales group themselves on their breeding grounds as mother/calf pairs (MC), mother/calf pairs with one or more escorts of either gender (MCE), and competition pods of multiple males pursuing a female (CP). The calling behaviors of interest for this chapter are how rapidly the tagged group calls per unit time (calling rate), how diverse the repertoire of calls is for each group (also known as H_0, or zero-order Shannon information theory), the uniformity over which those calls are used in a repertoire (also known as entropy, H_1, or first-order Shannon information theory), and how each call type is used in proportion to other call types (call type distributions).

4.3.2 Fundamental hypotheses tests

To test the relative variability in social call behavior on the intra- and inter-group levels, the following null and alternative hypotheses are examined:

1. Call types used in the Los Cabos breeding ground are the same as those used in Alaska, Hawaii, and Australia. Alternatively, there are call types unique to the Los Cabos breeding ground.

2. All tags (A) within a group type ("intra-group") and (B) across group types ("inter-group") display the same calling rate. Alternatively, one group of tagged animals or one group type will call more often than another.

3. All tags (A) within a group type ("intra-group") and (B) across group types ("inter-group") have the same amount of diversity in their call repertoires (e.g. in information theory, $\mathrm{H}_{0(group1)} = \mathrm{H}+0(group2) = \mathrm{H}_{0(groupN)}$). Alternatively, one or more groups or group types will have a richer repertoire.

4. All tags across group types ("inter-group") share the same call entropy. Alternatively, different group types use repertoires of different entropies.

5. All tags (A) within a group type and (B) between group types use the same call types most commonly (e.g. have the same call-type distributions). Alternatively, different group types use different call types more commonly than others.

If hypotheses are not rejected, then "intra" and "inter" group variability will be considered insignificant or a result of under sampling. Rejected hypotheses do not indicate that variability in humpback social call behavior is not present on larger geographical scales. If hypotheses are rejected, then a behavioral context for social call usage can be assumed, and any larger-scale studies of variability can be related to the amount of variability found here.

4.3.3 Equipment and tagging procedure

Two types of acoustic tags were used in this study. Greeneridge Science, Inc., builds both the Bioacoustic probe (B-probe) and the Acousonde (the updated version of the B-probe) (Burgess, 2009). See Figure 2. Data were collected continuously. Gain was set to 0 dB (no amplification of signals before sampling). Acoustic data were sampled up to 8000 Hz. Temperature and pressure auxiliary channels were sampled at a 1-Hz rate. The Acousonde's additional 3-dimensional accelerometer auxiliary channel was sampled at 800 Hz: the fastest sampling rate possible. Even though Goldbogen et al. (2014) was able to use the accelerometer to identify calls made by individual blue and fin whales, the Acousonde's accelerometer did not have a high enough sampling rate to do the same for humpback whale calls, thus preventing individual variability from being addressed in this chapter.

Once the acoustic tag was suctioned to the whale, and if the tagging vessel (the *Yubarta*: a panga type vessel equipped with an open outboard motor) could safely follow the whale by at least 100m, surface behavior and nearby vessel activity were noted in data sheets. Once the tag detached from the whale, it was recovered using a VHF radio signal and all data were downloaded that evening on land.

4.3.4 Field procedures

The research team in Los Cabos began collecting acoustic tag data in January 2014 as a trial run for the larger tagging effort planned for the 2015 breeding season. Jiménez (2006) showed that, in Los Cabos, humpback whales tend to congregate over a $<$200m deep continental shelf and stay close to shore farther to the east. Therefore, most of the tagging effort focused east of Cabo San Lucas, away from highly trafficked whale-watching and fishing waters.

Figure 4.2: The Acousonde (top right) and B-probe look similar, and are both attached to the whale using a tagging pole (top left). Suction cups hold the tag on the whale's body for a few hours while an orange buoy and VHF antenna (bottom) keep it above water for recovery once it fell off the whale.

4.3.5 Data analysis

The following steps were taken to detect and classify social calls in a standardized fashion.

1. A comprehensive catalogue of social sounds was assembled.

Before analyzing the actual tag records, a comprehensive catalogue was compiled using call types that had already been named from an Australian migration route (Dunlop et al., 2007; Rekdahl et al., 2013; Rekdahl et al., 2015), an Alaskan feeding ground (including tag records, courtesy of a data agreement with Ari Friedlaender and Alison Stimpert, from Christine Gabriele's unpublished bottom-mounted recordings, and from the theses of Michelle Fournet in 2014 and Fred Sharpe in 1984), and a Hawaiian breeding ground (courtesy of acoustic tag data from collaboration with Ann Zoidis). While it has been previously stated that breeding and feeding behavioral contexts may elicit different call types, or call type functions, the lead author included each already-named type in this analysis to remain consistent with previous nomenclature and to prevent the renaming of any calls already identified by previous researchers. This catalogue is a living document. Therefore it was updated continually throughout the data analysis period for this chapter and continues to be refined as social sound researchers meet during conferences each year.

There were several occasions when seemingly new calls were found in the Los Cabos datasets. To be designated as a new call type in the catalogue two criteria had to be satisfied: the call type in question had to be present on more than one tag record and it had to occur more than once on at least one tag records. This greatly reduced the number of potentially new call contributions, but it did control against potentially arbitrary, non-vocalized sounds.

2. Datasets were manually annotated

Once data were downloaded from the acoustic tags in the ".mt" format used by the B-probe and Acousonde systems, the files were divided among several volunteer analysts and paid research assistants. Each file was loaded into a custom Matlab GUI written by Drs. Aaron Thode and Jit Sarkar. This GUI (Ulysses) displays a spectrogram, and FFT sizes and percent overlap can be controlled for viewing ease. Analysts were trained to use this GUI, to recognize social calls in the presence of song, and to identify the different call types in the aforementioned catalogue. The analysts searched through the spectrograms, "annotated" all sounds they thought to be social calls, and classified each one to call type. False positives, such as song units, masked calls, and those with low signal-to-noise ratio (SNR) were later eliminated. Since human error is highly likely, all annotations were quality controlled by the lead author.

3. Datasets were quality controlled by eliminating false positives

Once an analyst had annotated and classified as many social calls as they could find in a file, the annotations were checked in three steps. First, any calls that could have been part of a song were deleted. (If two calls occurred more than twice with another repeating call type, then this was assumed to be part of a song phrase and not a bout of social calls.) Second, the VHF transmitter in the tag's buoy contaminated many of the datasets, creating loud pings every 0.5 seconds. Any call masked by these VHF pings was deleted, along with any calls that masked each other (overlapped in the spectrogram). Third, any calls with low SNR (<6dB above background levels) were deleted.

4.3.6 Statistical analysis

This chapter focuses on statistical analysis of several quantitative features of social call usage: call rate and independence of call rate samples, repertoire diversity, repertoire entropy, and call type distribution. Call rate is defined as the number of calls per minute detected on a tag, measured over 60 minute intervals. Repertoire diversity and entropy calculations build on work conducted by Rekdahl et al. (2015), Suzuki et al., (2006), and Miksis-Olds et al. (2008). Call type distributions plotted the relative usage of each call type, normalized in units of calls produced per hour.

Autocorrelation

Tag record lengths varied greatly, so instead of using each tag as an independent sample, each dataset was separated into 10-minute segments where the call rate was measured and a distribution was created for each tag record. Auto-correlating each 10-minute segment to one another, it was found that a 60-minute delay between samples was sufficient for two samples to be uncorrelated and thus independent. Therefore, call rate distributions were re-calculated using 60-minute segments from each tag record. See Figure 3.

Call rate

Call rate (calls per minute) was calculated for each 60-minute segment for tags over one hour long, and their distributions were plotted. These distributions were then compared

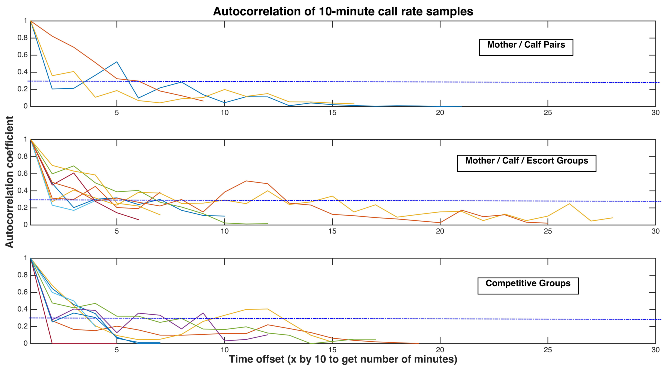


Figure 4.3: Autocorrelations of 10-min segments offset from the first 10-minute segment. The blue line denotes an autocorrelation coefficient of 0.3, which is considered a "weak association level." Most tag records drop below 0.3 when call rate samples are sampled by 60 minutes.

across tags from a single group type using ANOVA. The distributions from all tags within a group type were then combined to create call rate distributions for each group type. The group type distributions were compared using ANOVA, Kolmogorov-Smirnov (KS) tests, and Student's t-tests to determine whether any of the means of the distributions or the distributions themselves were significantly different from other group types (e.g. testing Hypothesis 2).

Repertoire Diversity

In information theory, zero-order Shannon entropy (H_0) measures relative diversity with the equation $\log_2$(no. of call types). For example, a value of 0 would indicate that only a single call type is used. The maximum value is determined by the overall possible repertoire of the population in question, and indicates that all call types are used at least once. For Los Cabos, the maximum value (5.5850 for 48 call types) was calculated by only including the 42 call types from the large catalogue that were detected in Los Cabos, plus the six that passed the "new" call type test. Therefore, the higher the H_0 value, the richer the repertoire. Like call rate, 60-min segment distributions were generated for H_0 and these distributions were compared within and across group type.

Repertoire Entropy

The relative usage across a set of call types can be calculated by the first-order Shannon informational theory, or "*b*-ary entropy." *B*-ary entropy is a quantitative measure of "information" in the call repertoire, and is a maximized when every call type is equally likely to be present in the tag. The same set of 48 call types that was used for H_0 calculations were used to compute H_1 using the formula

$$H_1 = -\Sigma_i^N P_i * log_2(P_i) \tag{4.1}$$

where N is the number of call types, i is each call type, and P is the probability of each call type occurring.

For example, with Los Cabos' 48 call types, the maximum possible value of H_1 is 5.5. H_1 was computed for an entire tag instead of being divided into 60-minute sections like call rate and H_0. Therefore, only distributions of H_1 values for each group *type* were calculated and compared with ANOVAs, KS tests, and t-tests.

Call Type Distributions

One drawback to H_1 is that it only shows how uniformly calls are used instead of how often one particular call type is used in comparison to others. For example, if group 1 uses call type A 10 times, then switches to call type B 10 times, and group 2 uses call type B 10 times, then switches to call type C 10 times, H_1 will be the same value for both groups, even though the specific types of calls used in each detailed call repertoire is different.

As a final analysis step, call type distributions from each tag were computed by calculating the proportional number of times each call type occurred per unit time. These individual tag distributions were combined by group type, and then compared using ANOVAs, KS tests, and t-tests both within and between group types.

4.4 Results

After two years of tagging humpback whales in the waters of Los Cabos, México, 30 tags (10 in 2014; 20 in 2015) were placed on whales, but only 21 (8 in 2014; 13 in 2015) successfully recorded acoustic data. These datasets contained at least six social calls unique to Cabo that have not yet appeared in the published literature from Hawaii, Alaska, and Australia (Table 1 & Figure 4). The rest of this section will step through calling rate and H0 by group type, then H_1 for all group types, and finally call type distributions by group type.

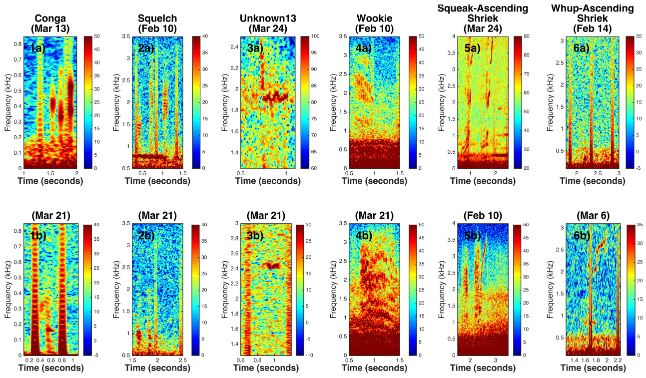


Figure 4.4: Two examples (rows) of the six call types (columns) unique to the Los Cabos breeding ground that occurred on at least two separate tags and more than once on one of those tags.

4.4.1 Calling Rate and Repertoire Diversity in Mother / Calf Pairs

For mother/calf pairs, 3 tags (404 minutes, 258 calls) were analyzed. Plotting histograms of call rate and H_0 in 60-minute segments of M/C tags indicated that they do not use a set calling rate or repertoire diversity within their own pair, nor between pairs (Fig. 5). ANOVA, however, indicates that there is no significant difference between the means of the distributions from M/C tags for both call rate and H_0. See Table 3 for a full summary of ANOVAs, KS tests, and Student's t-tests.

Table 4.1: *whup is the new spelling for what Dunlop et al 2008 called the “wop”
*If 0, call found, but did not pass quality control in any dataset

Social call type	No. of tags	As a bout? (Y/N)
Conga	2	Y
Squelch	11	Y
Unknown 7	0**	N
Unknown 8	0**	N
Unknown 9	1	N
Unknown 12	1	N
Unknown 13	2	N
Wookie	3	Y
Ascending moan-whup	1	N
Ascending shriek-squeak	1	N
Bellow-whup	1	N
Growl-creak	1	N
Growl-whup	1	N
Grumble-snort	2	N
Grumble-whup	1	N
Grunt-grumble	0**	N
Moan-whup	1	Y
Scream-bark	0**	N
Scream-hiccup	1	N
Snort-squeak	1	Y
Snort-whup	1	N
Squeak-ascending shriek	3	N
Squeak-squelch	1	N
Squelch-ascending shriek	1	Y
Squelch-squeak	1	N
Whup-ascending shriek	2	Y
Whup-squeak	1	Y

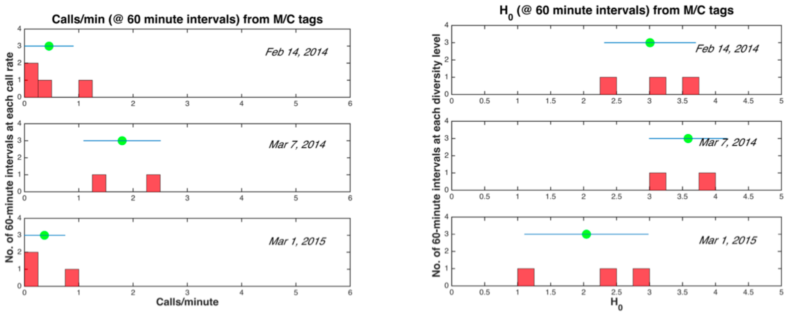
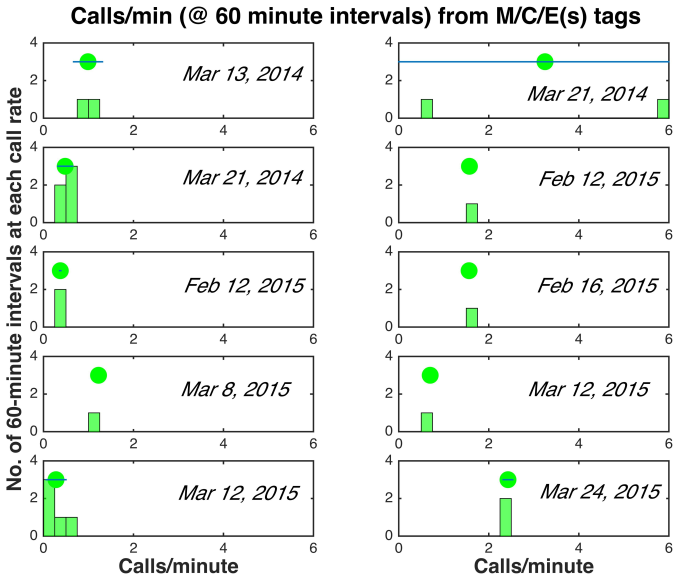


Figure 4.5: 60-min section distributions of call rate (left) and H_0 (right) for M/C tags with means (green dots) and SDs (blue lines).

4.4.2 Calling Rate and Repertoire Diversity in Mother / Calf / Escort(s) Groups

For mother/calf/escort(s) groups, 10 tags (985 minutes, 611 calls) were analyzed. After dividing the tag records into 60-minute segments (see Figure 6), ANOVA tests indicate that there is no significant difference between the means of the calling rate and H_0 distributions from these M/C/E tags.



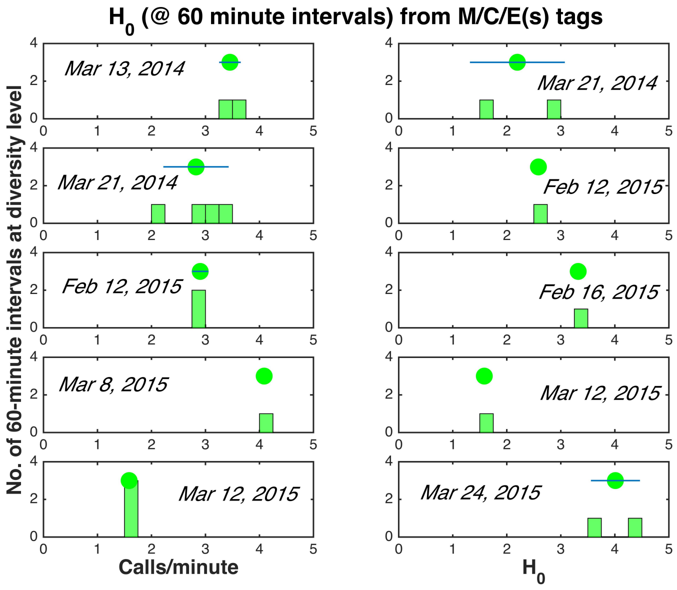


Figure 4.6: 6(a) The calling rates of all 10 M/C/E(s) groups and their respective H_0 values (b) with means (green dots) and SDs (blue lines).

4.4.3 Calling Rate and Repertoire Diversity in Competition Pod Tags

For competition pods, 8 tags (869 minutes, 718 calls) were analyzed. 60-minute segment calling rate and H_0 distributions are shown in Figure 7. An ANOVA test does indicate a significant difference between the calling rate distribution means (p-value = 0.005), but not the H_0 distribution means.

4.4.4 Calling Rate and Repertoire Diversity Across Group Types

The above plots (figures 5 through 7) indicate “intra-group” variation. To measure “inter-group” variation, the distributions of each group type were combined and plotted against each other as shown in Figure 8. In terms of call rate, distributions are non-Gaussian and skewed to lower calling rates. The M/C/E(s) group distribution extends to the fastest calling rate compared to other group types while the M/C pairs have the lowest average calling rate. In terms of repertoire diversity, all group types are fairly normally distributed around $H_0 = 3.0$, but M/C pairs tend to have a larger spread of repertoire diversity.

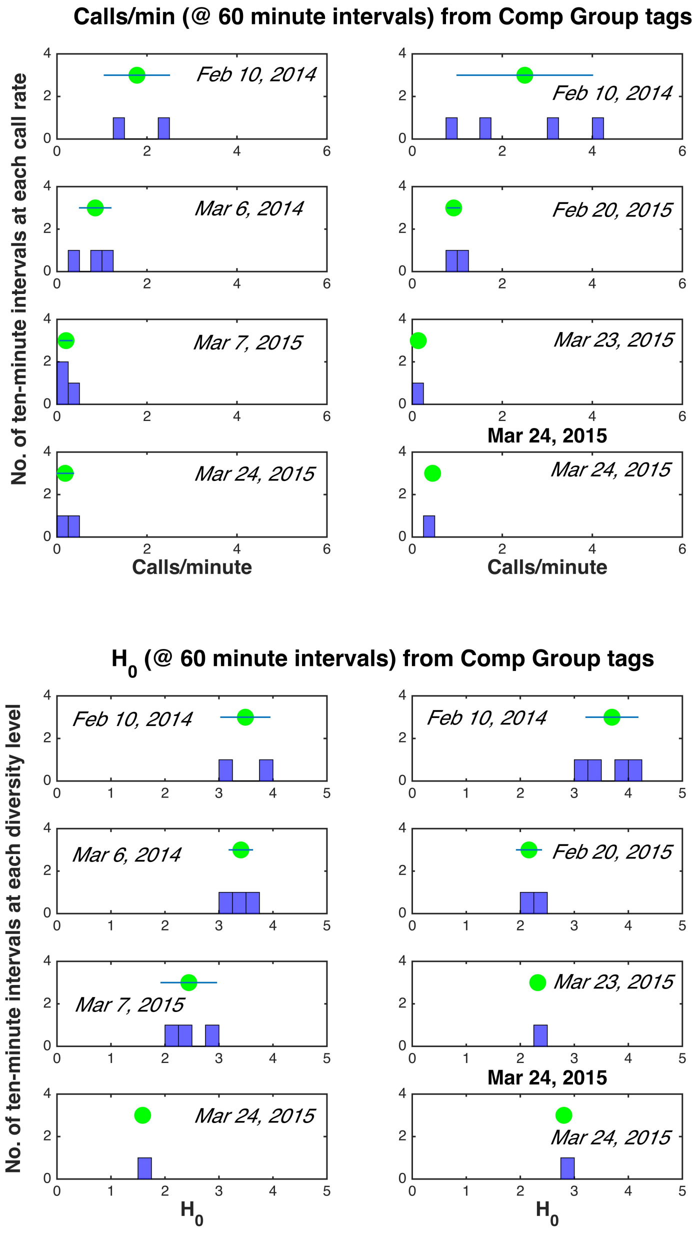


Figure 4.7: The call rates (a) and H_0 values (b) of competition pods with means (green dots) and SD (blue lines).

ANOVA indicates that a significant difference exists in the means from each group type for both calling rate (p-value = 0.049) and H_0 (p-value = 0.0002). KS tests performed for pairs of group types, however, indicate that the distributions are drawn from the same underlying continuous population and are therefore NOT significantly different. Pairwise

Student's t-tests indicate that the distributions of both calling rate and H_0 are significantly different for MC pairs as compared to MCE groups and CPs, but not significantly different for MCE groups as compared to CPs. The presence of at least one adult male alters the calling rate and repertoire diversity significantly.

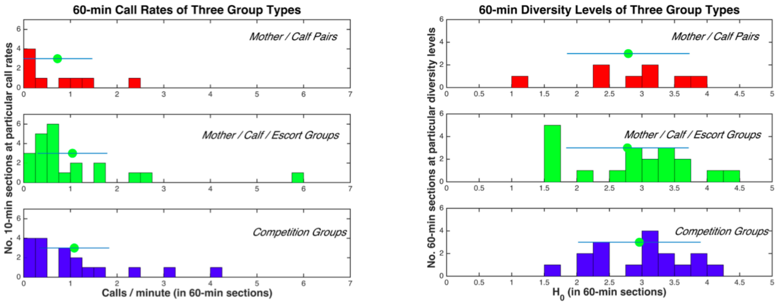


Figure 4.8: Call rate (left three subplots) and H_0 (right three subplots) histograms of 60-minute sections by group type: M/C pairs as red, M/C/E groups as green, and CPs as blue.

4.4.5 Repertoire Entropy Across Group Types

Since H_1 values were only measured for an entire tag, distributions were constructed for each group type and then compared. Recall that an H_1 value where all of the 48 Los Cabos call types are used with equal probability would be 5.5. A value of 0 would arise in the case of complete dominance by one call type in the repertoire. Figure 9 plots the entropy (H_1) distributions for each group type.

An ANOVA test indicates that the means of these three groups are significantly different from one another (p-value = 0.0086). However, the KS test indicates that the distributions could all have been sampled from the sample underlying population. The t-test again agrees with the ANOVA insomuch that the means of the MC pairs are not equal to the means of the MCE groups and CPs. Means from the MCE groups and CPs are equal, however. Again, the presence of at least one adult male in a tagged group seems to be a key factor in determining the entropy level on the tag.

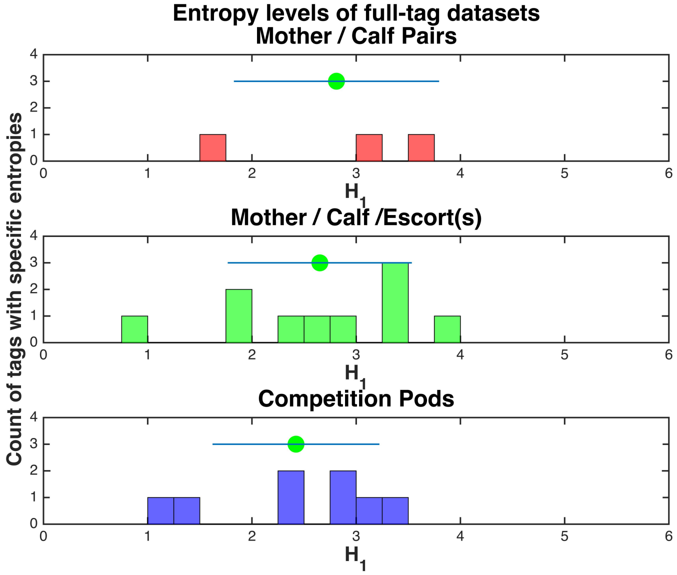


Figure 4.9: The entropy levels of each tag by separated in subplots by group type. Closer to 5 refers to a more uniform call repertoire, and closer to 0 indicates and more stereotyped repertoire.

4.4.6 Call Type Distributions Within and Across Group Types

Since H_1 does not consider *which* call types are used in larger or smaller proportions as compared to each other, distributions were made by plotting a bar for each of the 48 call type's proportional usage on a tag. These plots were made for each tag, and then combined for each group type. See Figure 10. When combined and plotted for group type, however, the call type proportions were normalized to the number of total minutes that each group type was recorded.

A two-sample Kolmogorov-Smirnov test was conducted through all pair-wise combinations within a group type. There exist three possible combinations for M/C pairs, and two of those pairs had significantly different call type distribution means from each other. Of the 45 possible combinations for M/C/E groups, nine distribution pairings had significantly different means from each other. Finally, of the 28 CP combinations, 18 significantly different pairings existed. See Table 2. Upon closer inspection, H=1 for the pairwise CP combinations of any 2014 tag compared to all other 2014 and the 2015 tags, but combi-

Table 4.2: Results from the KS tests for all pair-wise combinations between group types (bottom) and within each group type (top). H = 1 indicates that a pairing is significantly different from one another whereas H = 0 indicates that they are not.

KS Test summary	total combinations	combinations of h = 1	
M/C pairs	3	2	
M/C/E groups	45	9	
CP groups	28	18	
KS test results by group	H	p-value	kstat
M/C vs M/C/E(s)	1	0.0265	0.2917
M/C vs CP	1	0.007	0.3333
CP vs M/C/E(s)	0	0.9945	0.0833

nations of 2015 CP tags to each other yielded H=0. This may be due to the fact that two of the three 2014 competition pod tags had 14 individuals: a far larger number of animals than any other competition pod for both years.

Pairwise KS tests were also performed for the three combinations of group types. As with previous results, M/C pairs are significantly different than M/C/E groups and CPs, and M/C/E groups are not significantly different than CPs in terms of the proportions of call types that they use. A few particular call types may be responsible for this difference. As seen in Figure 10, the first call type (the "whup") was used the most for all group types. The fifth call type (the "squelch" a call unique to Los Cabos) was used more often by CPs than by any group with a calf in it. The fourth, 11^{th}, 15^{th}, and possibly 23^{rd} call types are less extreme examples of call types used more often when no calves are part of the group. Conversely, the 34^{th} call type ("pulses") was used far more often in a group with a calf than in the CPs. The third, 6^{th}, 12^{th}, and 21^{st} call types are more mild examples of when a call type is used more often in a group with a calf compared to a group without one.

The results of each null hypothesis are as follows:

1. Null hypothesis 1 (that social call types from Cabo are the same as from all other humpback whale habitats) is rejected because humpback whales in Los Cabos only use 42 of the nearly 100 call types in the most recent iteration of the social call working group's

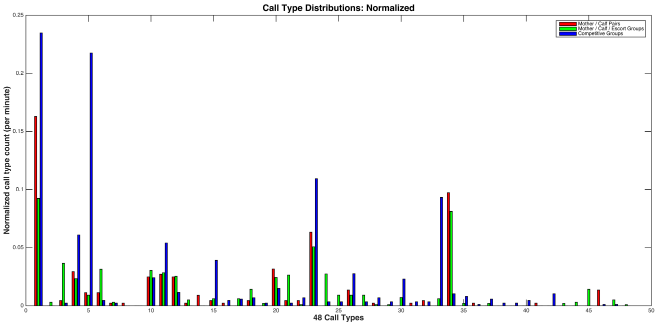


Figure 4.10: Distributions of call types used for each of the three group types, normalized to the amount of time each group type was recorded. M/C pairs are denoted in red, MCE groups in green, and CPs in blue.

global catalogue from Alaska, Australia, and Hawaii. Los Cabos also has at least six new call types in comparison to these other regions.

2. For M/C pairs and M/C/E groups, null hypothesis 2(A) (that calling rate is the same within a group type) is not rejected because the mean calling rates within each of these group types do not significantly differ from each other. For CPs, null hypothesis 2(A) is rejected because there is a significant difference in the mean calling rate across CP tags. Null hypothesis 2(B) (that calling rate is the same across group type) is rejected because the means of calling rates between groups with calves in them are significantly different from groups without calves, but their distributions are not. It may be that with a larger sample size, this hypothesis would in fact turn out to be true since the findings showed some non-significant trends.

3. For all group types, null hypothesis 3(A) (that repertoire diversity is the same within a group type) is not rejected because the mean H_0 values within each group type are not significantly different from each other. Null hypothesis 3(B) (that repertoire diversity is the same between group types) is rejected because groups with calves in them do not have the same amount of mean diversity in their call repertoires as groups without calves, but their distributions of repertoire diversity are not significantly different.

4. Null hypothesis 4 (that repertoire entropy is the same between group types)

Table 4.3: A summary of all ANOVA, KS tests, and Student's t-tests that were performed for all three group types and all four calling behaviors. "n/a" indicates that the test was not run and p-values are reported for significant results.

Group type	Test type	Calling rate	Diversity	Uniformity	Call type dist
Within MC	ANOVA	insignificant	insignificant	n/a	n/a
	KS test	n/a	n/a	n/a	H=1 for 2/3
	Student's t-test	n/a	n/a	n/a	n/a
Within MCE	ANOVA	insignificant	insignificant	n/a	n/a
	KS test	n/a	n/a	n/a	H=1 for 9/45
	Student's t-test	n/a	n/a	n/a	n/a
Within CP	ANOVA	p-value = 0.005	insignificant	n/a	n/a
	KS test	n/a	n/a	n/a	H=1 for 18/28
	Student's t-test	n/a	n/a	n/a	n/a
MC vs MCE	ANOVA	p-value = 0.049	p-value = 0.0002	p-value = 0.009	insignificant
	KS test	H = 0	H = 0	H = 0	H = 0
	Student's t-test	H = 1	H = 1	H = 1	H = 0
MC vs CP	ANOVA	p-value = 0.049	p-value = 0.0002	p-value = 0.009	insignificant
	KS test	H = 0	H = 0	H = 0	H = 1
	Student's t-test	H = 1	H = 1	H = 1	H = 0
MCE vs CP	ANOVA	p-value = 0.049	p-value = 0.0002	p-value = 0.009	insignificant
	KS test	H = 0	H = 0	H = 0	H = 0
	Student's t-test	H = 0	H = 0	H = 0	H = 0

is rejected because, even though every call type is not produced equally so as to create a uniform repertoire (i.e. $H_{1(eachgrouportag)} \neq 5.5$), the H_1 means are only significantly different between groups with calves in them versus groups without. Furthermore, the H_1 distributions are not significantly different between group types.

5. Null hypothesis 5 (that call type distributions are the same within and across group types) is rejected because the only call type distributions that are significantly different from each other are those from M/C pairs and CPs. Figure 10 illustrates that certain call types are used more often than others depending on group type, but not so much as to provide a significant difference between their distributions.

4.5 Discussion

It became evident during analysis that these 21 datasets did not capture the full range of calling behavior for humpback whales in Los Cabos. The more time whales were recorded, the more new call types were found, even though only six new call types of the 27 possibilities passed the threshold for being included in the catalogue. The complete list of single and composite calls (Table 1) that did not pass the threshold test will still be archived, however, in case they are found in other areas currently under investigation, such as Alaska (pers. comm. Michelle Fournet). Regardless of the incidence of new calls, this data suggests some level of intra-ground variability insomuch that there are call types used only in a specific breeding ground and, to our current knowledge, nowhere else.

In terms of testing the 2^{nd} through 4^{th} null hypotheses, neither call rate nor H_0 distributions were significantly different from each other when applied to a non-parametric test (i.e. none passed the KS test). However, the means of the distributions from groups containing adult males were significantly different from groups not containing adult males (i.e. they passed both the ANOVA and Student's T-test) indicating that calls vary for groups with adult males vs. groups without. Larger group sizes may be one explanation for higher calling rates, more diverse repertoires, and less uniform entropies, because M/C pairs are only two individuals, M/C/E groups (in this study) ranged from three to five whales, and competition pods (in this study) ranged from four to fourteen whales. If each whale calls just as much as another individual whale and uses its own subset of call types, then large groups would naturally have more variability in calling rate, repertoire diversity, and entropy than a pair of whales. A second explanation for this finding is that sample sizes are insufficient. Even when breaking tag data into 60-minute segments, three M/C pairs are unlikely to create a distribution that represents the entire Los Cabos M/C population's calling behavior.

It is of note that, until Zoidis et al. (2008), calves were not thought to vocalize and textbooks and other sources said they did not. Perhaps verifying that they called was so difficult because they vocalize less often (have a lower calling rate) than all groups with at least one grown male. It is also possible that the sounds attenuate so quickly, that previous recording methods were not focused enough on groups with calves, or the hydrophone was not in proximity at the time of the call, or the techniques were not designed to detect calf calls. The findings of this paper indicates that calls may exist and occur even if they have not been documented previously or are thought not to occur. In 2015, this author working in collaboration with A.M. Zoidis collected tag acoustic data from both Hawaii and México in order to assess inter-ground variability. These data will be further analyzed in a future study.

Interestingly, the calling rates of CPs are found to be between the calling rates found with M/C pairs and M/C/E groups. This may be because when escorts are with M/C pairs, they are generally in a different behavioral state than males in competitive groups, which are aggressively chasing females or competing with other males. When with a M/C group, escorts may be less active and in a lower energy state than males in aggressive and fast-moving competitive pods. Whales in competitive groups are usually positioned close to each other, traveling at high speeds at the surface, engaging in physical battles in which they hit or charge one another and vie for position at the front of the group as primary escort. It is possible that, with all the energy expended while swimming with an aggressive pack, extra energy for vocalizing may be not available, or, that with all the bodily noise being produced, the production of social calls at a certain call rate is futile since they would be masked. Another possibility is while it is never been verified, it may be that the distances escorts maintain from the other conspecifics when with M/C pairs varies from the distances males maintain from each other while fighting in competitive groups such that maintaining vocal contact between escorts, mothers, and calves occurs at a different call rate. These speculations illustrate how difficult it is to deduce causative factors for whale behaviors. Finally, differences in calling rate, H_0, and H_1, could be due to the attenuation of sound through water in social calls. If calves produce less intense calls than grown males, (Zoidis et al. 2008 documented amplitudes that were verified to have been produced by calves), then fewer calls from a calf would have passed the 6 dB SNR threshold for this project. Furthermore, some of the calls that did not pass the SNR threshold may have been different types than the ones that passed. More intense calls from grown males, however, would have passed the 6 dB SNR threshold and increased both the calling rate and the call types detected creating an uneven distribution of adult male calls in the study samples.

With regards to call type distributions, different group types would be expected to show different call distributions if each call type had its own communicative function for a particular behavior. For example, calls indicative of aggression would more likely be used in CPs than in M/C pairs. Even though the overall call type distributions were not significantly different between group types, it was interesting that five (of the 48) call types were used more often by CPs than by groups with a calf, and four call types were used more often by groups with a calf than without one.

4.6 Conclusion

The goal of this project was to establish a baseline understanding of call types used and of calling behavior displayed on a breeding ground that, to date, has not been documented for humpback whale social calls. Humpback whales in Los Cabos may use many more call types than sampled to date, but further study is needed since we have not deployed enough tags to obtain a truly random and representative sample of that subpopulation. It is also possible that the act of approaching and tagging an animal may result in oversampling individual whales that are habituated to boats, resulting in an under sampling of animals that avoid boats and thus may use different call types or calling behaviors. This study is merely a starting point in understanding the small-scale (“intra-group” and “inter-group”) variability of humpback whale communication on a breeding ground.

The largest contribution to the humpback whale social call research community resulting from this project is the compilation of a single catalogue for audio and visual samples of call types from many humpback whale social call datasets. This catalogue represents the most calls collected to date. The social call catalogue working group collaborating on this work will continue to meet and cooperate to establish terminology and to define measurement and analysis standards so future datasets are comparable. With this degree of collaboration, social call research will flourish.

4.7 Acknowledgements

This project never would have had legs to stand on without Ann Zoidis for teaching me social calls from the very beginning through data agreements, extensive meetings, and incredible in-water field experiences to facilitate my understanding of the vast behavioral contexts one must consider when interpreting vocalizations. Special thanks to Rebecca Dunlop for sharing audio examples of her Australian social sounds to kick start my training in social call detection and classification. While moving forward, the other original members of the social call catalogue group (Chris Gabriele, Alison Stimpert, Melinda Rekdahl, Michelle Fournet, and Ann Bowles) provided eyes and ears for verifying new sounds and refining terminology. I am forever indebted to the rest of the Universidad Autónoma de Baja California Sur marine mammal research team (Pamela Martínez-Loustalot, Diana López, Juan Carlos Salinas, Hiram Rosalez-Nanduca, and Carlos Alberto López) for their countless hours and patience while not only learning to tag whales, but also refining the method during bilingual "adventures". Thank you to William Burgess for always responding to the inevitable urgent questions about the acoustic tags. Finally, the datasets would not have been effectively analyzed without a GUI developed and refined by Drs. Aaron Thode and Jit Sarkar and the conviction of the following volunteers: Pushpita Bhattacharya, Jacob Dodd, India Dove, Patricia Fernandez Waid, Deborah Gardner, Gina Horath, Kent Kubo, Celeste Medina-Ontiveros, Melissa Nguyen, Edgar Ramírez Manriquez, Kaitlyn Woolling, and Adam Zeman. The Ocean Foundation provided funding for this project.

Chapter 5

Conclusion

The cumulative findings of this work provide novel tools in three areas of bioacoustics: ambient acoustic environment characterization, density (population) estimation, and breeding-ground based social call behavior. By answering each of the three objectives in the Introduction of this dissertation, new information was gleaned and novel management tools were provided for use in the vital breeding grounds of the Eastern North Pacific gray whale and the North Pacific humpback whale.

5.1 Laguna San Ignacios ambient acoustic environment: a general summary

Chapter 2 answered the questions: "how does one quantify the presence of human (anthropogenic) noise in an overall acoustic environment for management purposes?" And, "what other factors besides intensity, or "loudness", should be taken into consideration?" It turns out that the main contributors to an ambient acoustic environment are not necessarily the "loudest" (and thereby the most obvious assumption), but rather the ones that put at least a moderate amount of energy into the environment the most often. Using bottom-mounted recorders, eight years of acoustic data from the most heavily-trafficked area by pangas (Punta Piedra in the Middle Zone) were analyzed. Additionally, a few select years from the Lower and Upper Zones were analyzed areas that were hypothesized to have different acoustic features merely because both humans and gray whales use them differently.

I originally expected that tides, wind, whales, and pangas would be the most dominant sound sources. Each of these sources occurs on a different schedule though: some are "quiet" and continuous while others are sonorous and sporadic. Therefore, a statistical method plotting different hourly-averaged PSD percentiles was developed to investigate at which intensities and for what percentage of time each sound source ensonified the environment. With this method, the first long-term baseline acoustic study of LSI has been added to its rich photo ID and population monitoring studies. Adding acoustic measurements to these other datasets provides a more complete understanding about the critical gray whale breeding ground as a whole. A few of the observations in this baseline study were:

1. Pangas are not as much of a dominant sound source as originally thought. Rather, crepuscular snapping shrimp inundated the gray whale "nursery", creating what we have coined "acoustic camouflage". And dusk-centric croaker fish, that were not even initially expected to have much acoustic influence, dominated the acoustic environment in the Lower Zone.

2. Gray whale calls are not as prolific as initially expected. Acoustic propagation effects in the lagoon are not suited for optimal gray whale call transmission. Regardless, gray whales call at a rate that would only be detectable from a percentile higher than the 99^{th} using our statistical method.

3. The effects of wind and tide were not detectable with the method used nor in the frequencies explored. These physical phenomena practically define life on land at Laguna San Ignacio, but are not equally strong acoustic forces underwater.

4. Laguna San Ignacio's ambient acoustic environment is temporally stable. Even

with a fluctuating gray whale population and tourism levels, the acoustic environment in the Middle Zone has not changed much over nearly a decade. Whether this is a result of good conservation practices by the whale-watching pangueros or not, it at least lends credence to the fact that this study is truly a representative baseline account of the lagoon.

5. Mary Lou Dahlheim's original hypothesis in her master's thesis that gray whales occupy an "acoustic spectral niche" centered at 300 Hz was supported. As the noise minimum in the lagoon tends to hover near 300 Hz, it makes sense that gray whales would produce calls close to that frequency for the best likelihood of transmitting their signals the greatest distances without masking effects.

Snapping shrimp, fish, and pangas were the dominant sound sources in the lagoon's *multiple* ambient acoustic environments. As a contribution to the larger acoustics community, this work is evidence that the percentile statistical method (only used in a strait, a continental shelf, and a firth to date) holds fast in a sub-tropical lagoon environment as well. It is therefore a robust tool for understanding many acoustic environments and, as it becomes more widely used, can serve as a common metric for comparing environments across the globe.

Looking forward, new questions arise from the results of this chapter. Is it possible that vessel traffic will become so heavy in the future that the sound from pangas will exceed that of the croaker fish and snapping shrimp? We will only know by continued passive acoustic monitoring in the same locations. If so, will the vessel noise create an adaptive pressure on the gray whales and how will they respond? Gray whales have coevolved with the snapping shrimp and croaker fish for millennia, but will they be able to adapt to such a relatively sudden change in their habitat at the hands of humans? If not, what maladaptive responses will sanctuary managers need to watch for? Luckily, Laguna San Ignacio has a highly devoted team of researchers monitoring it annually, and the past eight years have experienced relatively stable acoustic environments. Gray whales likely encounter a larger range of acoustic environments as they migrate and inhabit their feeding grounds, so for the near future, the lagoon seems to truly be their sanctuary.

5.2 How to estimate humpback whale population size with a single recorder: a Los Cabos case study

Chapter 3 answered whether researchers can use the intensity of sounds produced by a single species, if the sounds are produced continuously and are the dominant source in the environment, to measure population size. In short, the answer is yes. But the exact relationship of sound intensity to the number of whales present that are producing that amount of sound is unique to each ambient acoustic environment. This dependence of sound intensity per whale relies heavily on the habitat's physical characteristics like bathymetry and water depth, but also on the behavior of the whales themselves.

In the case of Chapter 3, which used humpback whales in the Los Cabos region, the physical characteristics of the environment could be accounted for in the analytical model, and many of the assumptions about the behaviors of the singers were negligible with a small changes in population size. The analytical model thus relied on what we called the "sensitivity" term and its spatial density variables. After testing the analytical model against empirical data (visual surveys compared to night-time singing intensities) and a GLM, its credibility held true for most bandwidths in the humpback whale song spectrum. One of the most surprising outcomes of this chapter was that, while trying to understand some discrepancies between the analytical and empirical results, it became evident after adjusting the spatial density variables in the "sensitivity term, that humpback whales likely adjust their spacing (pack more closely) as the population grows. Other results were:

1. Humpback whales in Los Cabos sing on a diel cycle like they do on the Hawaiian breeding grounds. These night-time peaks were at least 115 dB re 1 μPa across the Los

Cabos region.

2. The sound intensity per animal relationship, at least for the Los Cabos region, is roughly that sound intensity increases as the square root of the number of whales sighted. Since a relationship can be established, and it is in agreement with what the analytical model predicted for evenly spaced animals, we can deduce that past theories saying singing humpback whales space themselves apart as are setting up territories is supported.

3. The KIP model is not foolproof: there are many combinations of singing behavior and packing that can give the same results. Shifts in singing like increasing source levels, decreasing inter-unit intervals, changing the male:female ratio of whales in the area, and actually modeling a non-flat bathymetry could counteract or tweak the analytical model and empirical results as they stand.

The scientific contribution that this chapter gives to the acoustics community is field-based evidence that continuously-vocalizing whale species population size can, in fact, be measured from a single recorder using a technique that hitherto was only put forth theoretically. It could also be applied to fin whales and blue whales other endangered species whose populations need to be closely monitored.

Looking forward, new research goals arise from this work. Is the Los Cabos region case a fluke (no pun intended) insomuch that this analytical model agreed so well with the empirical data? There are other humpback whale breeding grounds across the globe, some in areas where large acoustic arrays would be costly to deploy (i.e. the Indian Ocean and the Revillagigedos Islands). If this work can be replicated in the other breeding areas, perhaps a single bottom-mounted recorder can truly be a powerful and cost-effective population estimation tool for researchers and sanctuary managers alike. Furthermore, if historical acoustic datasets exist that are accompanied by concurrent visual surveys, can this method be adapted to estimate past population sizes of blues, fins, and humpbacks?

5.3 Social calls made by humpback whales in Los Cabos: how often and how varied?

Chapter 4 answered questions about how stereotyped humpback whale social calling behavior is in Los Cabos, Mexico, and provided evidence that these social calls may be behaviorally contextual as their rate of emission, diversity and entropy vary between social group types. A low level of variability in these calling features was expected within a social group type, and a higher level of variability was expected between group types. In fact, distributions of calling rate, repertoire diversity, and call types used were not always significantly different between group types. The most significant trend was how calling rates and repertoire diversity changed with the size of the group being recorded on the tag. Certain group types, however, (like competitive groups vs. mother/calf/escort groups) had opposing trends. For example, competitive groups decreased their repertoire diversity as the breeding season progressed, while mother/calf/escort groups increased the variety of calls they used.

As a contribution to larger-scale social call studies, this chapter provides an expected baseline amount of variation in small group types in a particular breeding ground. As data become available to compare social call acoustic structure and behavior across different breeding grounds, or feeding grounds and migration routes, any biogeographic variability that exists can be related to this smaller scale variability. Furthermore, this research can provide a reference for future studies on characterizing how humpback whales call in other acoustic environments (such as in the presence of intense anthropogenic noise). One of the most exciting outcomes of this chapter was the creation of an international social call catalogue working group that continues to meet at Acoustical Society of American and Society for Marine Mammal conferences. .

5.4 Conclusion summary

Success stories in the world of conservation management do exist, and increasing their frequency is a large motivating factor for my research. With a mix of dedicated effort by local people and passionate interest by scientists and tourists alike, governments cannot only be persuaded to federally manage critical habitats for an endangered species, but can also serve as an example to the rest of the world. Laguna San Ignacio is one such success story. That being said, new tools to facilitate conservation efforts are needed. Monitoring population sizes with both minimal equipment and the least invasive techniques are optimal. Countries bordering the waters that provide vital habitat space for many endangered marine species have insufficient budgets for a slew of fancy equipment and teams of researchers. Even countries with large budgets tend to place science and conservation on the back burner. For highly vocal cetacean species, hopefully using a single recorder, a couple of years of visual data collection, and an established post-processing technique, can provide a more cost-effective (not to mention fuel-efficient) technique for population size estimation than the visual survey and towed acoustic array methods employed to date. The baseline calling behavior variability as presented in Chapter 4 could also serve as a management tool insomuch that sanctuaries could strive to mitigate any anthropogenic sound source that alters calling behavior (assuming that altered behavior is a stressor to the whales).

This dissertation focused on three rather disparate aspects of bioacoustics: ambient acoustic environment characterization, density estimation modeling and testing, and social call classification and characterization. This work was largely applied, provided countless exciting opportunities to learn new and unique skill sets, and conducted basic yet foundational research in the areas I believe could benefit the most quickly from the new discoveries and tools presented here: marine sanctuaries.

Appendix A

The Kuperman-Ingenito-Perkins (KIP) model

A propagating acoustic field in an ocean with a relatively flat bathymetry can be modeled as the weighted sum of a set of normal modes:

$$p(f, z_w, z_r, S) = (S(f)/\rho) * \sqrt{2\pi/r} * \sum_m (e^{\imath k_{r,m} r}/\sqrt{k_{r,m}}) \psi_{m(z_w)} \psi_{m(z_r)} \tag{A.1}$$

where S is the *linear* source intensity (in W/m^2, *not* dB re 1 μPa) of a sound produced at water depth z_w and horizontal range r. Additionally, ρ is the water density, k is the medium wavenumber at frequency f, ψ_m and $k_{r,m}$ are the mode depth function ("mode") and horizontal wavenumber for index m, and z_r is the receiver depth. Roughly speaking, a mode represents a particular "multipath" that can travel a sustained horizontal distance in the ocean. The normal mode formulation is the most compact way to express the acoustic field for relatively low-frequency sounds in a shallow-water environment, with one caveat: in an actual ocean environment a continuous wavenumber contribution to the field exists at close ranges, and is an important contributor to the ambient noise field. This near-field contribution can be modeled using normal modes by adding a "false bottom" some distance beneath the actual ocean/sediment interface (Perkins et al., 1993). This process yields a set of highly-attenuated "leaky" modes that approximates this near-field contribution. Therefore, to remove the need to simulate a "false bottom", the simulations discussed in Section 2.4 model an environment with a sediment layer overlying a granite bedrock.

Kuperman & Ingenito (1980) showed that the cumulative noise field generated by a collection of temporally and spatially uncorrelated noise sources, each modeled with Eq. (A1), and all randomly distributed with respect to range and azimuth relative to the receiver, produces an analytical solution for sources distributed out to infinite range. Perkins et al. (1993) extended this result for noise sources distributed over a finite range, producing the following equation for the ocean waveguide ambient noise power spectral density detected at the origin by a set of random sources distributed within a circular region of radius *R* surrounding the origin:

$$I(f, z_w, z_r, R) = q^2\{(\iota\pi/(\rho^2 k^2))\Sigma_{n,m} * ((\Psi_{n(z_w)}\Psi_{m(z_w)}\Psi_{n(z_r)}\Psi_{m(z_r)})/$$

$$(\mathrm{k}_{r,m}^2 - (k_{r,n}^*)^2))[2 - (\sqrt{k_{r,m}/k_{r,n}^*}) + \sqrt{k_{r,n}^*/k_{r,m}})e^{-\iota(k_{r,m}-k_{r,n}^*)R)}\}(\mathrm{A.2})$$

Here q^2 represents a source strength in terms of units of source intensity spectral density per unit area. The term in curly brackets is the propagation term *P* in Eq. (1), and consists of a double sum of various weightings of normal modes. Note that this "regional radius" *R* does *not* represent the range between an individual singing whale and the receiver; rather, it represents the farthest range that any singing whale could be present at the time of the measurement.

As noted in previous literature, the double sum in Eq. (A2) can be approximated by a single sum by noting that the off-diagonal terms ($n \neq m$) are typically much smaller than the diagonal terms ($n = m$). The *P*term in Eq. (1) then becomes

$$P(f,z_w,z_r,R) \approx (1/(\rho^2k^2))\Sigma_m(\psi_{m(z_w)}\psi_{m(z_r)})^2/(2\kappa_m\alpha_m) * [1-(\kappa_m/\sqrt{\alpha_{m^2}+\kappa_{m^2}}e^{-2\alpha_m})] \tag{A.3}$$

or defining

$$U_m \equiv [\psi_m(z_w)\psi_m(z_r)]^2, andT_m \equiv \kappa_m/\sqrt{\alpha_{m^2}+\kappa_{m^2}}:$$

P(f,z$_w, z_r, R) \approx Q\sum_m(U_m(z_w,z_r))/(2\kappa_m\alpha_m)[1-T_me^{-2\alpha_mR}]$(A.4)

Here κ_m and α_m are the real and imaginary parts of the horizontal wavenumber $k_{r,m}$ of mode $m : k_{r,m} = \kappa_m + \iota\alpha_m$. The imaginary term expresses the attenuation factor (how rapidly the mode decays with horizontal propagation distance) for the mode in question. Figure A1 reproduces Fig. 3(a), but uses all terms in the double sum (Eq. A2) instead of just the “diagonal terms (Eq. A3). A comparison of the figures shows that the dB contours of the simplified expression are virtually identical to the complete expression of Eq. (A2), although the contours display more fine-scaled structure with R. When δ_{CD} is estimated in the (bandwidth-integrated) manner shown in Fig. 4, the resulting sensitivity estimates are unchanged.

To compute the term dP/dR in Eq. (5b) we take the partial derivative of Eq. (A3) with respect to R and find

$$\partial P/\partial R = \Sigma_m(U_m/\kappa_m)T_me^{-2\alpha_mR} \tag{A.5}$$

Thus the second term in Eq. (5b) [or third term in Eq. (4)] becomes

$$(\upsilon R/2P)\partial P/\partial R = (\upsilon R\Sigma_m(U_m/\kappa_m)T_me^{-2\alpha_mR})/(\Sigma_m(U_m/(2\kappa_m\alpha_m))[1-T_me^{-2\alpha_mR}]) \tag{A.6}$$

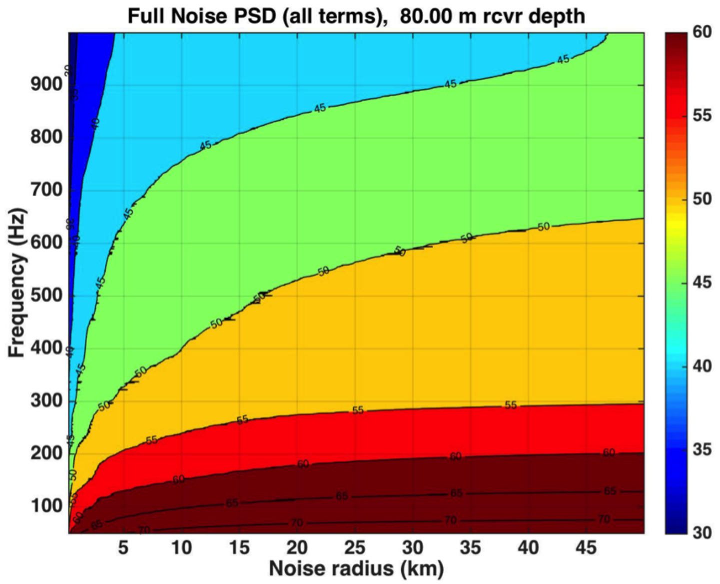


Figure A.1: Reproduction of Fig. 3(a), but using all double summation terms in Eq. (A2) instead of the single-summation approximate form of Eqs. (A3) and (A4).

and approaches a maximum value of $\upsilon/2$ (1/2 when υ=1) for situations where both R and α_m are small. Similar expressions can be obtained for the full double-sum expression for P in Eq. (A2).

Eqs. (A1-A6) have assumed that the receiver is placed at the center of the noise area A. When the receiver location is placed at an offset ΔR meters with respect to the geographic center of the noise-producing region, Eq. (A2) is modified to become

$$I(f,z_w,z_r,R) = q^2\{(\iota\pi)/(\rho^2k^2)\Sigma_{n,m}(\Psi_{n(z_w)}\Psi_{m(z_w)}\Psi_{n(z_r)}\Psi_{m(z_r)})/$$

$$(\mathrm{k}_{r,m}^2-(k_{r,n}^*)^2)[2-J_0[(k_{r,m}-k_{r,n}^*)\Delta R](\sqrt{(k_{r,m})/(k_{r,n}^*}+\sqrt{(k_{r,n}^*)/(k_{r,m})})e^{-\iota(k_{r,m}-k_{r,n}^*)R)}]$$

$$\}\ (\mathrm{A.7})$$

One sees that, in cross-modal terms (where $n \neq m$), the term associated with T_m is modified by a zeroth-order Bessel function J_0. However, the approximate single-sum expressions in Eqs. (A4)-(A6) remain unmodified, since $J_0(0)$=1. Thus if an acoustic receiver lies anywhere within the boundary of the singing region, Fig. 3(a) will look roughly the

Table A.1: Best-fit coefficient (δ) and R2 values for the GLM in Eq. (6), for different combinations of visual counts and acoustic metrics using the 100-1000 Hz bandwidth. Like Table 3, this combines both years of data. The predictor variables with the highest R^2 were "all" whales visual count with the nightly average (D) acoustic metric. Based on these results, this predictor variable pairing was further tested for the highest R^2 values across multiple bandwidths (Table 3).

Acoustic Metric	Visual Count	R^2	p-value	d slope (SD)	Intercept (SD)
A	All	0.33	1.70 e-3	0.45 (0.13) dB	114 (1.26) dB
	No-m/c	0.31	2.70 e-3	0.45 (0.14) dB	114 (1.30) dB
	Solos	0.14	1.89 e-1	0.25 (0.18) dB	117 (1.24) dB
B	All	0.26	3.00 e-3	0.31 (0.10) dB	115 (0.93) dB
	No-m/c	0.25	3.50 e-3	0.32 (0.10) dB	115 (0.95) dB
	Solos	0.14	4.99 e-2	0.26 (0.12) dB	117 (0.87) dB
C	All	0.14	6.48 e-2	0.31 (0.16) dB	105 (1.54) dB
	No-m/c	0.15	5.64 e-2	0.38 (0.09) dB	105 (1.55) dB
	Solos	0.28	3.70 e-3	0.38 (0.09) dB	105 (1.22) dB
D	All	0.42	1.24 e-4	0.25 (0.13) dB	115 (0.84) dB
	No-m/c	0.40	2.09 e-4	2.38 (0.98) dB	115 (0.86) dB
	Solos	0.18	5.36 e-2	1.74 (0.71) dB	117 (0.85) dB
E	All	0.42	1.25 e-1	1.09 (1.14) dB	30 (12.40) dB
	No-m/c	0.41	1.75 e-1	4.43 (1.17) dB	29 (12.68) dB
	Solos	0.38	5.60 e-1	2.38 (0.98) dB	19 (10.10) dB

same. Only the fine scale structure of the contour lines will shift. These results also imply that narrowband empirical measurements of sensitivity are robust to the receiver location within the singing area.

Appendix B

Generalizing the model for variations in source level, singing depth, broadband vocalizations, and spatial density gradients

Equation (1) is defined for power spectral density (or intensity integrated across a narrow frequency band) and assumes a group of randomly distributed animals that share the same source levels and singing depths. Here we show that the key consequences of the model are retained when these assumptions are relaxed.

A better model of humpback whale singing behavior consists of defining a probability density function $p(S,z_w)$ such that out a total population $N_{singers}$, the number of animals singing between depth $z_w \pm \Delta z/2$ with (linear) source intensity spectral densities between $S \pm \Delta S/2$ will be $\sim N_{singers}\, p(S,z_w) \Delta z \Delta S$. If we can factor $p(S,z_w)$ into $p(S)p(z_w)$ (i.e. assume that source level is statistically independent of singing depth), then a little thought shows that Eq. (1) remains valid if S is replaced by

$$\overline{S} = \int_0^\infty S p(S) dS \tag{B.1}$$

and Eq. (A4) remains valid if is replaced by

$$\overline{U_m} \equiv [\psi_m(z_r)]^2 \int_0^\infty p(z_w)\psi_m^2(z_w)dz. \tag{B.2}$$

Note that Eq. (B1) is defined over the *linear* source level, so if a source level distribution is presented in terms of dB, S will likely be dominated by the upper tail of the distribution.

With these modifications one can proceed through Eqs. (2) to (5) and find that δ in Eq. (7) is still independent of $\overline{S}$. If $p(S,z_w)$ cannot be factored (e.g. source levels decrease as they sing deeper), then δ will depend on the functional relationship between S and z_w.

Another correction to Eq. (1) is the incorporation of a broadband integration into the intensity measurement (instead of the narrowband integrations shown in Fig. 4). If the time-averaged spectrum from a singing whale, including periods of silence between units, is independent of its broadband source level, i.e. $S(\omega)$ is independent of $\sqrt{\int_{\omega_1}^{\omega_2} d\omega \mid S(\omega) \mid^2}$, then the definition of the sensitivity in Eq. (3) can be expanded to involve an incoherent summation across a bandwidth defined by frequencies ω_1 and ω_2. Thus, using Eqs. (3) and (A6), an example of the sensitivity for the constant density scenario becomes

$$\delta_{broadband} \equiv \partial(I_{dB,broadband})/\partial(10log_{10}N) =$$

$$\mathrm{Q}_{indiv} + (\upsilon R \textstyle\int_{\omega_1}^{\omega_2} (\overline{Q(\omega)}/k^2)[\Sigma_m(\overline{U_m}/\kappa_m)T_m e^{-2\alpha_m R}]d\omega)/$$
$$(\textstyle\int_{\omega_1}^{\omega_2} (\overline{Q(\omega)}/k^2)[\Sigma_m(\overline{U_m}/2\kappa_m\alpha_m)[1 - T_m e^{-2\alpha_m R}]]d\omega)$$

(B.3)

Here $\overline{Q_\omega} = S(\omega)/\sqrt{\int_{\omega_1}^{\omega_2} d\omega \mid S(\omega) \mid^2}$. As before, the sensitivity δ from a broadband noise intensity measurement will be independent of the distribution-averaged individuals source levels $S_{dB,broadband}$. The difference from before, though, is that the modal terms are now weighted by $\overline{Q_{\omega}}$ (the normalized source spectrum).

Finally, the propagation term P in Eq. (1) is independent of azimuth in a range-independent environment. An immediate consequence of this fact is that Eq. (1) is a solution not only for constant spatial densities of animals, but is also a solution for scenarios where animals are distributed along a linear spatial gradient. Let $\sigma(r,\Theta)$ = N/A(N) be the spatial density of singing animals at range r and azimuth Θ from the sensor. Then Eq. (1) shows that the contribution to the ambient noise field from an annular ring of sources between r and r+dr is proportional to $\int_0^{2\pi}\sigma(r,\Theta)rdrd\Theta$. For an arbitrary linear spatial gradient $\sigma = \sigma_0 + mrcos\Theta$ (where σ_0 is the spatial density directly over the sensor and m is the linear spatial gradient), one finds

$$\int_0^{2\pi}\sigma(r,\Theta)rdrd\Theta = \int_0^{2\pi}\sigma_0 rdrd\Theta. \tag{B.4}$$

Since Eq. (B4) holds for any annular ring of radius r, Eq. (1) is a solution for a distribution of noise sources with a linear spatial gradient, provided the spatial density used in Eq. (1) is the spatial density of noise sources directly above the sensor.

In summary, the expanded definition of δ in Eq. (B3) remains independent of the population's source level distribution and duty cycle under the following two assumptions: (1) the source levels generated by a population are statistically independent of their singing depths, and (2) the spectral shape of the animals' song spectrum (averaged across the entire duration of the song, including silent periods) is independent of the broadband source level. Extensions of the theory to cover a distribution of duty cycles (periods of rest) are straightforward. The sensitivity is also unaffected by the presence of a linear spatial gradient in the spatial distribution of singers. Although, there remain major assumptions that cannot be relaxed: (1) the songs must be temporally uncorrelated over the measurement window, (2) the singing area is a circular wedge, and (3) the bathymetry under the singing region is flat.

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