UNIVERSITY OF CALIFORNIA, SAN DIEGO

Habitat use of calling baleen whales in the southern California Current Ecosystem

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

in

Oceanography

by

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The dissertation of Elizabeth Vu is approved, and it is acceptable in quality and form for publication on microfilm and electronically:

Chair

University of California, San Diego

2015

DEDICATION

To Donald No Middle Initial Ross

EPIGRAPH

The cure for anything is salt water–
sweat, tears, or the sea.
—Isak Dinesen

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ACKNOWLEDGEMENTS

In fifth grade, I participated in my elementary school science fair, testing the effects of ambient noise, classical, and 90s pop music on the germination and growth of Viola spp. (common name: pansy garden flower). That my project, written in Sharpie on a piece of tri-fold cardboard, won accolades is sort of a miracle. Between fifth grade and my final year in graduate school, I've learned how to perform slightly more complex, acoustics-related research aided by an overwhelming amount of people:

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ABSTRACT OF THE DISSERTATION

Habitat use of calling baleen whales in the southern California Current Ecosystem

by

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Doctor of Philosophy in Oceanography

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Professor John Hildebrand, Chair

The extent to which temporal, spatial, environmental, and physiological factors influence baleen whale acoustic occurrence was investigated in the southern California Current Ecosystem, a highly productive, upwelling-driven ecosystem that hosts a large abundance of top predators. By combining data sets from ten years of passive acoustic monitoring and concurrent environmental sampling, this dissertation presents detailed intra-annual and mesoscale spatial patterns previously unknown. Analyses of temporal acoustic patterns revealed different acoustic occupancy by three species: blue whale (*Balaenoptera musculus*), humpback whale

(*Megaptera novaeangliae*), and fin whale (*Balaenoptera physalus*). The temporal separation between blue whale feeding and breeding call types showed a shift between behavioral states throughout the year. The temporal separation between blue and humpback whale reproductive calls showed different displays of reproductive calling behavior despite their overlapping migratory and seasonal reproductive cycles. Spatial patterns revealed different onshore and offshore occupancy, dependent on season, for each species. The reconciliation between acoustic and visual seasonal abundance demonstrated an increase in individual-level acoustic reproductive display during or approaching the mating season of each species. Analyses of habitat factors on call types from each species identified association of seasonality, bathymetry, sea surface temperature, and mixed layer depth with calling behavior. Generalized additive mixed models of acoustic calling revealed significant responses to seasonality and bathymetry at three different spatial scales, indicating the importance of these factors in explaining baleen whale distribution at broad scales. Lastly, a possible physiological driver of acoustic behavior was investigated by quantifying seasonal hormone concentrations in humpback whale blubber. The results of this research advance scientific understanding of yearlong acoustic cetacean occurrence in a productive oceanographic habitat and provide additional insight into the reproduction and migration of these species.

Chapter 1

Habitat use of baleen whales in the southern California region - Introduction

1.1 Introduction

Top predators are an essential part of their ecosystem underscored by their position atop the food chain. Therefore, it is essential to study top predators, assess their ecosystem function, identify drivers of their distribution and abundance, and consequently understand potential anthropogenic impact on their environment. The study of mobile, pelagic top predators begets many questions. How do we study animals that are often undetected and spend much time below the surface of the water? How can we learn more about their distribution, behavior, and preferred habitats? Simply put: where are they at certain times of the year and why are they there? This dissertation demonstrated the first steps taken to answer such questions.

Due to cetacean life histories and their ability to migrate long distances, cetacean distribution patterns and associated habitats vary spatially and temporally in numerous regions of the world such as the Eastern Tropical Pacific (ETP) (Ferguson et al., 2006; Reilly, 1990; Reilly and Fiedler, 1994), central North Pacific (Forney et al., 2015), California Current (Forney and Barlow, 1998), Antarctic (Sirovic and Hildebrand, 2011), North Atlantic (Baumgartner and Mate, 2005), and Gulf of Mexico (Davis et al., 1998). Species occurrence and distribution vary as a function of ecological variables that describe their habitat preferences (Guisan and Zimmermann, 2000; Guisan and Thuiller, 2005). Characterizing species-environment interactions is advantageous for gaining understanding of these distributions in a changing climate for the purposes of conservation and management.

Significant relationships between baleen whales and their habitat have been investigated on traditional feeding grounds. For example, humpback whales (*Megaptera novaeangliae*) off the coast British Columbia and the Bering Sea strongly associate with bathymetric features, such as depth, slope or distance to a specified isobath (Dalla Rosa et al., 2012; Moore et al., 2002b). Significant relationships also exist on traditional breeding grounds. For example, dynamic variables that favor seasonal productivity have influenced blue whale (*Balaenoptera musculus*) occurrence in the Costa Rica Dome (Ballance et al., 2006).

In this dissertation, I studied the feeding ground located in the California Current Ecosystem (CCE), a highly productive, upwelling-driven ecosystem that supports a large abundance of high trophic level predators, including cetaceans (Block et al., 2011). Cetacean occurrence and density in the CCE are significantly affected by a suite of habitat variables spanning many categories: static (e.g., bathymetric depth, slope), oceanographic (e.g., temperature, salinity) and variables which represent biological production (e.g., chlorophyll) (Barlow et al., 2009; Becker et al., 2012; Forney et al., 2012). Based on this evidence, the CCE and specifically, the southern California region are seen as an important feeding ground. However, as this dissertation will show, breeding-related behavior inferred from acoustic evidence diversifies the use of the region.

As a result of past habitat modelling in the CCE, many species-environment dynamics were identified. However, the scope of the studies have been limited in temporal scale. The temporal coverage had been incomplete due to the logistical constraints of sampling during certain times of the year. Past habitat models have largely focused on summer and fall seasons, when most visual surveys were conducted. In my dissertation, I incorporated continuous temporal coverage and improved understanding of overall habitat use by three baleen whale species, blue whales (*Balaenoptera musculus*), fin whales (*Balaenoptera physalus*), and humpback whales (*Megaptera novaeangliae*), in the southern California region. I employed Passive Acoustic Monitoring (PAM) methods and described the habitat of calling baleen whales. Because of the migratory nature of these exemplar species and inherent seasonality of their occurrence within regions, the near-continuous acoustic monitoring in the region was an important component for describing their seasonal distribution. I investigated the physical and biological ocean environment and their contribution to the presence and distribution of these species using habitat modeling methods. Environmental data were collected during the California Cooperative Oceanic Fisheries Investigations (CalCOFI) and the SIO Ocean Time Series CCE project.

Broadly, my dissertation research falls into three categories, first to characterize and quantify the patterns of acoustic call types over a full calendar year (using 10 years of available PAM data) across mesoscale spatial swaths extending past the continental shelf (Ch.2); second, to evaluate the possible environmental factors that predict acoustic occurrence and evaluate whether these results change based on the behavioral context of the call (Ch.3 and 4), and third, to investigate a possible internal physiological factor, hormone concentration, that may drive acoustic calling behavior (Ch.5).

1.2 Model species

The three baleen whale species chosen for study have been well researched in the southern California region and their vocalizations have been well characterized. Generally, baleen whales produce loud (>160 dB re: 1 Pa at 1 m), low frequency (<1 kHz), repetitive sounds. Their vocalizations can be categorized into call types which confer behavioral context, such as reproductive or foraging behavior.

1.2.1 Blue whales

Blue whale populations were depleted in the North Pacific by commercial exploitation (Clapham et al., 1999). Recent population estimates using both line-transect and capture-recapture methods in the California-Oregion-Washington region were between 2000 and 3000 animals (Barlow, 1995; Calambokidis et al., 2004) with population shifts likely occurring in and out of this region (Calambokidis et al., 2009). Blue whales in the eastern North Pacific are separate from populations in the central and western North Pacific based on differences in call types (Stafford et al., 1999, 2001; McDonald et al., 2006). The traditional view of their cyclic annual migration consists of feeding at mid- to high-latitudes during the summer and fall, followed by a southbound migration to tropical regions to give birth and mate in the winter and spring. This pattern is corroborated by the the visual evidence of feeding off California from May through November and migration to waters off Mexico and other regions within the eastern tropical Pacific in winter and spring (Reilly, 1990; Mate et al., 1999). While on the eastern North Pacific grounds, blue whales are feeding on dense patches of krill (Fiedler et al., 1998).

Blue whale vocalizations occur in the 20-100 Hz, low-frequency range. They are known to produce at least three call types in the eastern North Pacific (Oleson et al., 2007a; McDonald et al., 2006; Thompson et al., 1996; Rivers, 1997): A-, B-, and D-calls. A- and B-calls (∼10-20 second duration) consist of several components that are either pulsed (A-call) or tonal (B-call) in character, occur in repeated sequences, and are only produced by males. Therefore, they likely have a reproductive function, serving the purpose of mate attraction and long-range communication (McDonald et al., 2001; Oleson et al., 2007b). D-calls (down-sweep from 90-25 Hz, ∼1-4 second duration), are highly variable in frequency and temporal characteristics, are recorded from both males and females, and appear to have an identifiable behavioral context related to social interaction, particularly when animals are foraging (Oleson et al., 2007b). Previous studies have found evidence for social function between paired or closely associated calling whales, sometimes in alternating calling patterns between individuals (Thode et al., 2000; Berchok et al., 2006; Oleson et al., 2007b).

1.2.2 Fin whales

Fin whales, in contrast to blue whales, are present in the southern California area year-round, with peak occurrence in late summer and early fall (Barlow, 1995; Sirovic et al., 2012). Less is known about their residence in the area, with working hypotheses of a resident population, and/or complex within-area migration (Mizroch et al., 2009; Sirovic et al., 2015).

Fin whales produce at least two types of calls in this area: 20 Hz and 40

Hz (Sirovic et al., 2012). Each type lasts about 1 sec in duration and consists of downswept pulses. The 20 Hz calls sweep in frequency from 23 to 18 Hz (Watkins, 1981) and 40 Hz calls sweep from 62 to 48 Hz (Sirovic et al., 2012). The function of calls varies based on the pattern in which they are produced; regular sequences are attributed as song, sung by males, and therefore confer a reproductive function (Croll et al., 2002). Irregular, non-song sequences also occur and have a hypothesized social function.

1.2.3 Humpback whales

Humpback whales (*Megaptera novaeangliae*) are found in all major ocean basins and typically undergo seasonal migrations from feeding areas in high latitudes to warmer waters in tropical breeding areas in low latitudes (which is similar to the traditional view of blue whale migration). In the North Pacific Ocean, humpback whales feed primarily along the Pacific Rim from California to Russia and migrate to breeding areas along the coasts of Central America, Mexico, the offshore islands of Mexico, Hawaii, and the western Pacific (Calambokidis et al., 2001).

North Pacific humpback whale populations currently are estimated to be around 21,000 (Barlow et al., 2011) with the California population numbering around 1,000 individuals (Barlow and Forney, 2007). Their vocalizations have been well studied, especially song (Payne and McVay, 1971) although non-song calls have also been described for this species in other regions of the world (Dunlop et al., 2008; Stimpert et al., 2007). Humpback whales also have a dichotomy of calling behavior where males sing long, complex, repetitive song (Payne and McVay, 1971), with a still-uncertain reproductive function, while both males and females make social sounds.

1.3 Study region: southern California region and bight

The Southern California Bight (SCB) is the region from Point Conception to Ensenada, Mexico inshore of the Santa Rosa Ridge where the California land mass curves eastward, north of approximately 30^oN, and incorporating the Channel Islands. The SCB is a highly productive and complex region with many interacting oceanographic and bathymetric features including basins, ridges, troughs, banks, islands, and a slope along the 2,000 m isobath (Jackson, 1986; Hickey, 1992). There are various currents that dominate the region, including the equatorward flowing eastern boundary current, also known as the California Current (the eastern limb of the large-scale, anticyclonic North Pacific gyre), and the Southern California Eddy, an offshoot of the California Current that forms a large counterclockwise gyre within the SCB (Checkley and Barth, 2009; Lynn and Simpson, 1987). There is a confluence of various source waters, including the aforementioned cold, low salinity water of the California Current and the northward-flowing, warmer, high salinity waters from Baja California (which consist of the Davidson current and the California Undercurrent) (Hickey, 1979).

Oceanographic features, in the form of currents, counter-currents, frontal features, island wakes, mesoscale and sub-mesoscale eddies vary in strength seasonally and may result in high-productivity events (Jackson, 1986; Caldeira et al., 2005; Stegmann and Schwing, 2007). The variability in strength is mediated by several factors including the Aleutian Low and North Pacific High pressure systems (Checkley and Barth, 2009). The California Current is seasonally at its strongest and closest to shore in spring when there is predominantly equatorward flow. The poleward-flowing waters dominate in summer and fall and push the

California Current further offshore. The meeting of various currents forms strong mesoscale eddies, which have been shown to play an important role in zooplankton and fish larvae retention (Logerwell and Smith, 2001) and tend to be strongest in summer and fall. Finally, a major contributor to the productivity of the SCB and surrounding waters is equatorward wind in the late spring and summer which creates an offshore flow and upwelling of cold, nutrient-rich water near the coast (Checkley and Barth, 2009). The areas further offshore beyond the shelf break and outside of the SCB are less variable in oceanographic phenomena.

1.4 Data sources

In order to investigative the relationships between whale distribution and environmental factors, the following data sources were used.

1.4.1 Acoustic data collection instruments

Two passive acoustic data acquisition systems were used to record cetacean sounds.

Long-term passive acoustic data were collected using High-frequency Acoustic Recording Packages (HARPs; Figure 1.2) deployed in the southern California region. Each instrument contained acoustic sensors which were broadband (with a frequency range of 10 Hz to 100 kHz), low-power (50 mW) and had high sensitivity (more than -120 dB re 1V/uPa) (Wiggins and Hildebrand, 2007), which captured the vocalizations of low frequency and high-frequency-emitting animals. The instrument comprised a frame, flotation, and ballast and pressure cages which were bottom-mounted. The hydrophone was positioned above the instrument with a preamplifer. The package had a sampling rate of either 200 or 350 kHz and was calibrated for a flat response. HARP effort information for this dissertation is provided in Table 1.1.

While HARPs provided long-term coverage at one location, spatial coverage was obtained by using sonobuoys. Sonobuoys are expendable instruments which, upon deployment, inflate a flotation device with a radio transmitter, and release a hydrophone to depths ranging from 200 to 1000 feet (Ultra Electronics Inc.; Figure 1.3). Signals detected on sonobuoys were emitted via radio signals and were received using an omnidirectional VHF antenna (Diamond Antenna) and pre-amplifier (P160VDG preamplifier; Advanced Receiver Research) mounted on a mast of the ship. The preamplifier was connected to a 100 meter coaxial cable and signals were received with two ICOM radio receivers modified for low-frequency response (Greeneridge Sciences). Received signals were digitized with a sound board (Creative Labs Soundblaster Audigy and Realtek Corp. Avance Logic; both 24-bit), and signals were recorded on a personal computer using the software program LOGGER (Douglas Gillespie, International Fund for Animal Welfare). Sonobuoy models used in this study included DIFAR and Omnidirections models of 53F, 53E, 53D, and 57B at sampling rates of 4 to 48 kHz.

1.4.2 Environmental data collection platforms

Environmental data were collected from two platforms: the CalCOFI program, and an environmental mooring.

The CalCOFI program (calcofi.org; Figure 1.1) is a multi-agency partnership formed in 1949 to investigate the collapse of the sardine population off California. The program operates quarterly cruises and collects a large suite of hydrographic, environmental, and biological data covering a large area off the west coast of the United States in a systematic grid of monitoring stations. The core CalCOFI sampling scheme covers gridlines normal to the California coast covering the areas between San Diego and Avila Beach, CA and samples up to 600 km offshore, spanning the inshore and offshore regions off southern California. Since 2004, a marine mammal component was added to the CalCOFI program conducting visual and acoustic sampling of cetaceans along the designated CalCOFI grid lines. CalCOFI stations with numbers 45 and lower lie within the SCB. CalCOFI stations with numbers 53 and higher are outside of the Bight. CalCOFI stations with number 70 or higher lie to the west of the continental slope and occur in deep ocean water. Spacing between the transect lines and the distance between standard stations is 40 nm or 74 km. Nearshore stations are half or less of this spacing. Routine station occupations deploy a SeaBird CTD instrument with a 24-place rosette, each with 10-L PVC Niskin bottles. Sampling casts are made to 500 m depth, or shallower, depending on bottom depth. Continuous measurements of pressure, temperature, conductivity, dissolved oxygen and chlorophyll fluorescence are taken. In this dissertation, I used data from collection effort on the CalCOFI cruises in Table 1.2.

Long term environmental data to match the HARP data came from the CCE time series mooring maintained by the Scripps Ocean Time Series Group (mooring.ucsd.edu) since 2010. The moored insrument package included several sensors collecting the following habitat variable types: temperature, salinity, nitrate, oxygen, turbidity, among others (Figure 1.4). The temporal resolution of these data ranged from every 15 minutes to hourly. The mooring was located at CalCOFI Station 55 on Line 80 and was positioned close to the shelf break where localized upwelling processes are at their maximum. CCE times series effort information used for this dissertation is provided in Table 1.1.

1.5 Chapter summaries

In Chapter 2, I demonstrated the temporal separation between two call types of the blue whale, and between reproductive call types of the blue and humpback whale species. Because these two species both exhibit migratory cycles during overlapping time periods, it was expected that the seasonality of their call types were similar. However, there was a temporal shift in peaks of reproductive calling of these two species. While blue whale reproductive acoustic calls peaked once a year, humpback whale reproductive acoustic calling peaked twice a year, which implies that these two species use the southern California region in different ways. In Chapter 2, I also explored the spatial patterns of call types of all three species considered in this dissertation. The results of this chapter rejected the prevailing null hypothesis that calling behavior was consistent throughout the southern California region; there were various patterns in onshore and offshore contexts as well as northern and southern subregions. Finally, I discussed possible reasons for the non-overlapping prevalence of these call types and implications these temporal and spatial patterns may have on the reproductive pressures and the migration pathways of these species.

In Chapter 3, I explored the environmental factors that explain the seasonality of calling behavior of the blue, fin, and humpback whales. While a temporal factor (e.g. calendar month) was the best explanatory factor for all species, marginal explanatory power was provided by bathymetric and oceanographic factors. All species' acoustic presence was linked to depth. Blue whale call types were driven by sea surface temperature patterns and fin whales were driven by patterns in the mixed layer depth. Humpback whales were not linked to a physical oceanographic factor. This chapter discusses how these results compare and contrast to previous habitat models built for cetacean occurrence based on visual detection.

The importance of bathymetric factors as shown in Chapter 3 underlies the importance of this variable in habitat models for these species. By focusing on one location and holding bathymetric factors constant, Chapter 4 presented habitat models built from a highly temporally resolved dataset that spans intra-seasonal time, thereby providing better resolution than provided in Chapter 3. Temporal factors were found to be the biggest drivers of the patterns observed in calling abundance. Temperature measurements taken at points below the sea surface were shown to be better environmental predictors when compared to temperature at surface. The importance of subsurface temperature measurements suggests the importance of features within the water column above and beyond widely-used sea surface properties. Finally, I tested the importance of a temporal environmental variability index in predicting whale calling abundance and found that there was no significant effect. Based on previous research highlighting the importance of environmental variability over space and time, my null results encourage further investigation of a better proxy for frontal systems or into relationships with prey directly.

In Chapter 5, I investigated a possible internal, physiological driver of calling behavior. Humpback whales are known to sing protractedly in the spring and fall when their behavioral efforts could be dedicated to procuring food resources on their feeding grounds. Furthermore, I showed in Chapter 3 that humpback song is best modelled by season and depth and failed to include a physical oceanographic factor. Therefore, I sought to investigate an alternative driver of the seasonal singing patterns. By quantifying a reproductive hormone, I showed that seasonal singing patterns matched the seasonal patterns observed in testosterone concentrations in their blubber and suggested a seasonal physiological conditioning that dictates calling behavior.

In Chapter 6, I synthesized the main contribution of this work to the larger research field and identified ways forward in which this work can further improve understanding of baleen whales in a transitional feeding ground.

(NB: Chapters 2-5 are meant to serve as publishable units and therefore contain some repeated information from introduction and methods presented in this chapter.)

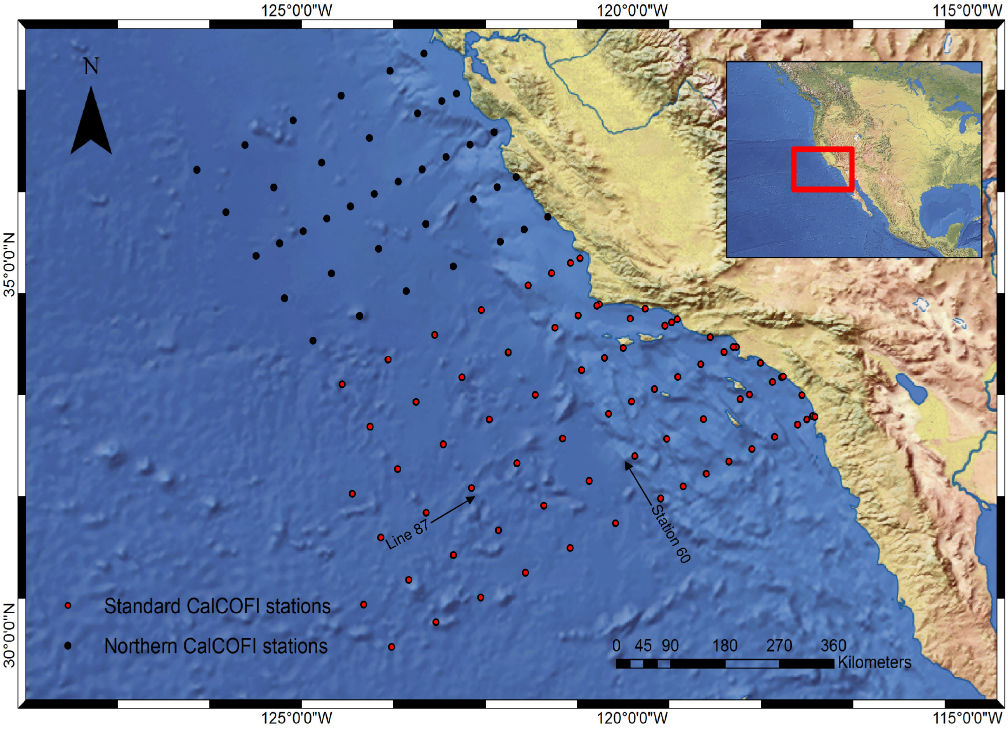

Figure 1.1: CalCOFI (California Cooperative Oceanic Fisheries Investigations) sampling grid with circles representing stations at which a suite of oceanographic sampling occurs on a quarterly time schedule. Northern stations were sampled on average once a year.

Figure 1.2: Schematic of a High Frequency Recording Package (HARP) used in recording the acoustic environment at Site C approximately 50 km off Point Conception at 34.3 ° latitude, -120.8 ° longitude at a depth of approximately 800m

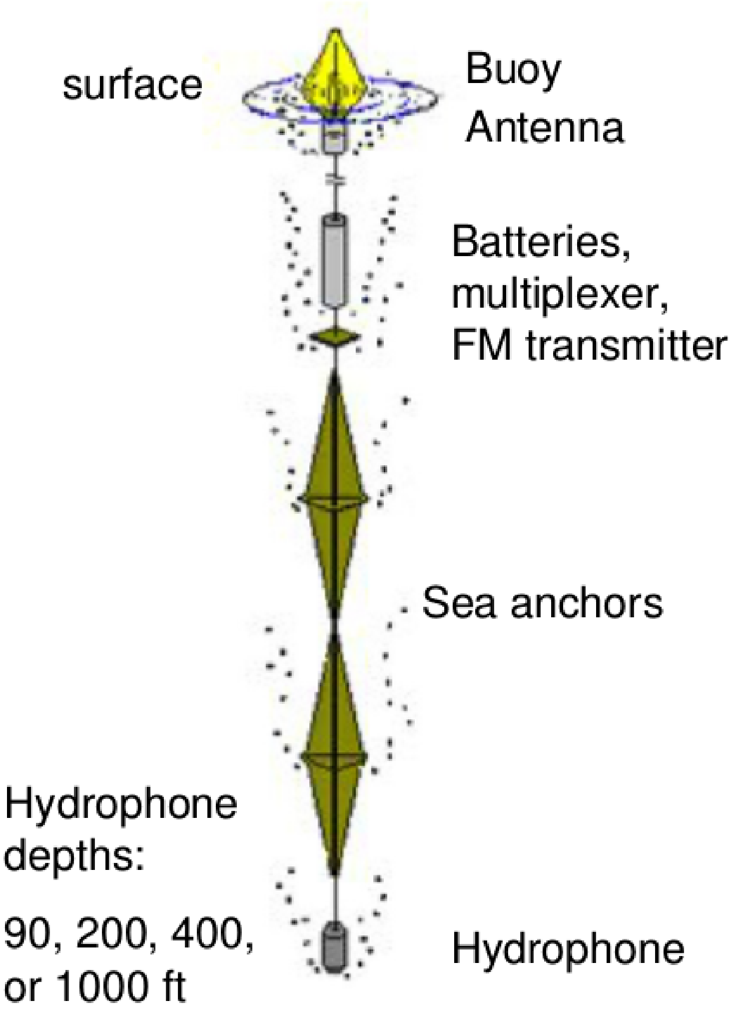

Figure 1.3: Schematic of a generalized sonobuoy used to obtain acoustic recordings from CalCOFI (California Cooperative Oceanic Fisheries Investigations) stations.

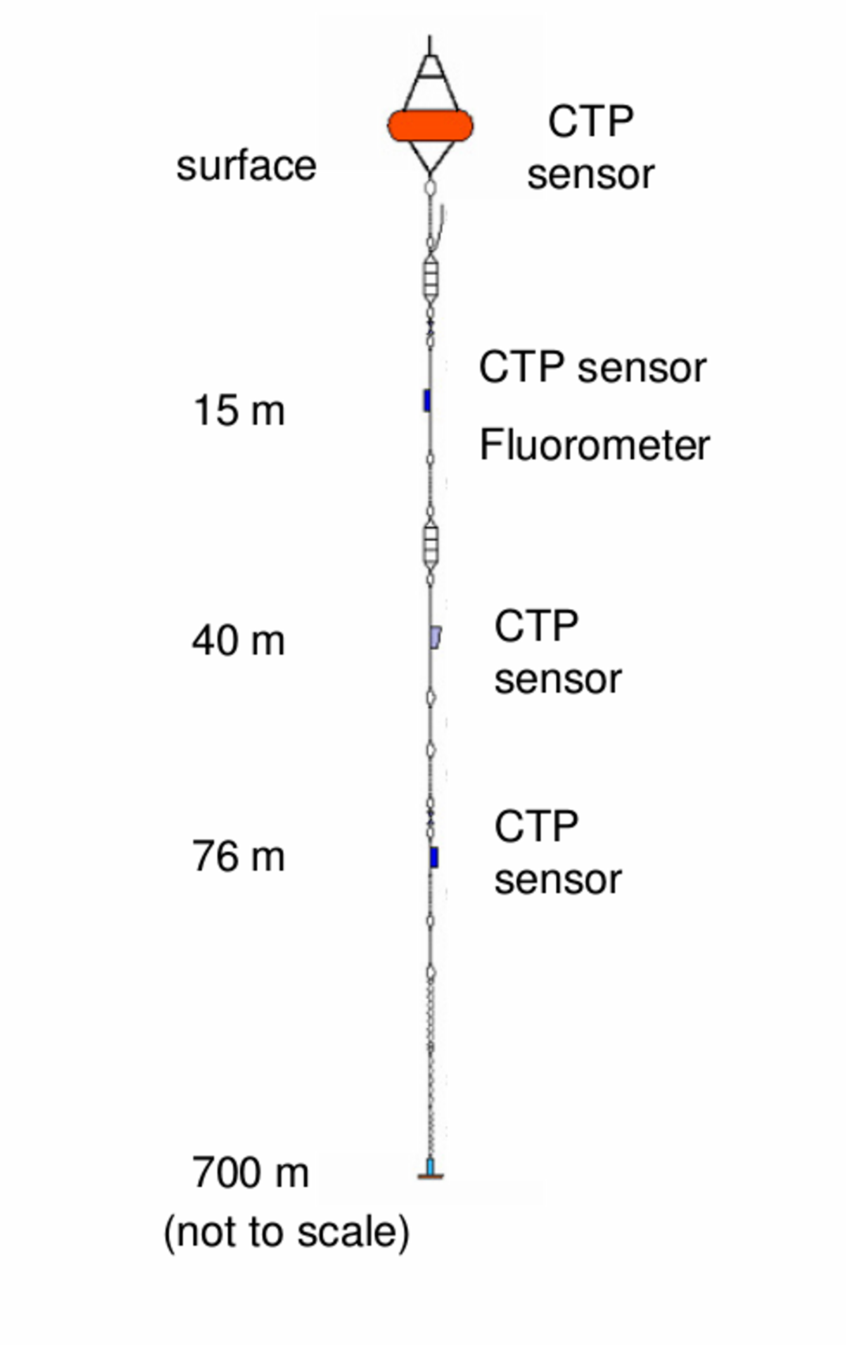

Figure 1.4: Schematic of the SIO Ocean Time Series Group CCE-2 mooring located approximately 50 km off Point Conception at 34.3 ° latitude, -120.8 ° longitude. Deployment of the mooring package occurred from 2010 to 2014

Table 1.1: Data collection effort (start and end dates) for HARP (acoustic) and CCE2 mooring (environmental) variables.

HARP			**CCE2 mooring**		
	Effort			**Effort**	
CINMS 12	3 Mar 2010	13 Jun 2010	CCE2-01	16 Jan 2010	5 Mar 2011
CINMS 13	24 Jun 2010	21 Sep 2010			
CINMS 15	16 Nov 2010	2 Mar 2011			
CINMS 16	5 April 2011	11 Jul 2011	CCE2-02	5 Mar 2011	14 Dec 2011
CINMS 17	27 Oct 2011	3 Mar 2012			
CINMS 18	25 Mar 2012	2 Aug 2012	CCE2-03	23 Mar 2012	10 Apr 2013
CINMS 19	2 Aug 2012	7 Dec 2012			
CINMS 20	18 Dec 2012	28 Apr 2013			
CINMS 21	2 May 2013	17 Jun 2013	CCE2-04	11 Apr 2013	1 May 2014
CINMS 22	22 Sep 2013	14 Jan 2014			

Table 1.2: Data collection effort (start and end dates) for CalCOFI cruises 2004-2012. Number of stations sampled during each cruise is provided. Cruises that sampled stations from the Northern CalCOFI lines are indicated.

Cruise	**Vessel**	**Year**	**Date**	**# stations**	**Northern stations**
CC0404	R/V New Horizon	2004	23 Mar - 8 Apr	32	
CC0407	R/V D. Starr Jordan		12-28 Jul	30	
CC0411	R/V Roger Revelle		2-19 Nov	50	
CC0501	R/V New Horizon	2005	4-20 Jan	27	
CC0504	R/V New Horizon		15 Apr - 1 May	31	
CC0507	R/V New Horizon		1-17 Jul	33	
CC0511	R/V New Horizon		4-21 Nov	24	
CC0602	R/V D. Starr Jordan	2006	2-27 Feb	28	*
CC0604	R/V New Horizon		1-18 Apr	25	
CC0607	R/V New Horizon		8-25 Jul	36	
CC0610	R/V Roger Revelle		21 Oct - 6 Nov	28	
CC0701	R/V D. Starr Jordan	2007	12 Jan - 3 Feb	31	*
CC0704	R/V D. Starr Jordan		27 Mar - 1 May	25	
CC0707	R/V New Horizon		28 Jun - 13 Jul	29	
CC0711	R/V New Horizon		2-18 Nov	24	
CC0801	R/V D. Starr Jordan	2008	7-30 Jan	22	
CC0804	R/V D. Starr Jordan		24 Mar - 1 May	18	
CC0808	R/V New Horizon		14-30 Aug	30	
CC0810	R/V New Horizon		14-30 Oct	20	
CC0901	R/V New Horizon	2009	8-23 Jan	26	
CC0903	R/V D. Starr Jordan		8-22 Mar	28	
CC0907	R/V McArthur II		14 Jul - 23 Aug	27	
CC0911	R/V New Horizon		6-23 Nov	25	
CC1001	R/V New Horizon	2010	12 Jan - 6 Feb	34	*
CC1004	R/V Miller Freeman		27 Apr - 17 May	8	*
CC1008	R/V New Horizon		30 Jul - 7 Aug	33	
CC1011	R/V New Horizon		28 Oct - 12 Nov	20	
CC1101	R/V New Horizon	2011	13 Jan - 6 Feb	24	*
CC1104	R/V B.M. Shimada		9-26 Apr	28	
CC1108	R/V New Horizon		27 Jul - 13 Aug	31	
CC1110	R/V New Horizon		16 Oct - 5 Nov	21	
CC1202	R/V New Horizon	2012	27 Jan - 12 Feb	25	
CC1203	R/V B.M. Shimada		24 Mar - 7 Apr	24	
CC1207	R/V Ocean Starr		2-27 Jul	25	
CC1210	R/V New Horizon		19 Oct - 5 Nov	17	

Chapter 2

Spatial and seasonal patterns of blue, fin, and humpback whale acoustic presence in the southern California Current Ecosystem

2.1 Introduction

The dynamic California Current Ecosystem (CCE) is one of the most productive marine environments in the North Pacific Ocean (Block et al., 2011; Santora et al., 2012), hosting several top predators during part of their seasonal migrations. While these top predators (which include sharks, cetaceans, sea birds, and pinnipeds) are ostensibly attracted to the region for the productivity and high densities of prey, an underlying seasonal cycle dictates the occurrence of large whales, particularly the blue (*Balaenoptera musculus*), humpback (*Megaptera novaeangliae*), and fin whale (*Balaenoptera physalus*). Despite nuanced complexities in migration patterns, all three species follow general basin-wide seasonal migrations, whereby they spend winter breeding months in low latitude breeding grounds and summer months in higher latitudes (i.e. temperate and sub-polar) feeding grounds (Reilly and Thayer, 1990; Mate et al., 1999; Calambokidis et al., 2001; Edwards et al., 2015). However, the specific timing of their movements to and from these regions, and the extent to which they stay in each of these regions, is poorly understood.

Furthermore, their movements over regional mesoscales spanning different bathymetric conditions are poorly understood. Past work has correlated increased sightings and numbers of cetaceans with bathymetric features like depth and slope (Baumgartner et al., 2001; Hamazaki, 2002; Yen et al., 2004). While the mechanisms by which cetaceans are directly responding to these features are poorly understood, these broad environmental features are easily obtained and are useful for predictive distribution models. In this study, I investigated the temporal and spatial patterns of whale presence on a feeding ground using a variety of available acoustic records.

2.1.1 Blue whale visual and acoustic presence in the northeastern Pacific Ocean

Blue whales are known to spend the winter and early spring months in Mexican waters and offshore Central America near the oceanographic feature known as the Costa Rica Dome (Reilly, 1990; Stafford et al., 1999, 2001; Bailey et al., 2009). As the year progresses to late spring, summer, and fall months, this population of blue whales are seen and heard off of Baja California, California, Oregon, Washington and the Gulf of Alaska (Calambokidis et al., 1990, 2004, 2009; Oleson et al., 2007c; Burtenshaw et al., 2004; Trickey et al., 2015; Debich, 2014; Stafford, 2003). Whether all individuals participate in the yearly migration and go to the same locations within the ocean basin is less clear. To determine such year-round presence, there has been an increase in year-round acoustic monitoring effort in known blue whale feeding grounds (Debich, 2014; Trickey et al., 2015) to augment the historic acoustic records from breeding grounds (Stafford et al., 1999; Watkins et al., 2000).

Blue whales are known to produce at least three call types in the eastern North Pacific [Oleson et al., 2007b, McDonald et al., 2006, Thompson et al., 1996, Rivers, 1997]: A-, B-, and D-calls. These vocalizations occur in the 20-100 Hz, low-frequency range. A- and B-calls (∼10-20 second duration) are pulsed and tonal in character, respectively, occur in repeated sequences, and are only produced by males. Therefore, they likely have a reproductive function in mate attraction and long-range communication (McDonald et al., 2001; Oleson et al., 2007b). D-calls (down-sweep from 90-25 Hz, 1-4 second duration) are highly variable in frequency and temporal characteristics, are recorded from both males and females, and are produced in a social, foraging context (Oleson et al., 2007b).

It is known, from year-round acoustic monitoring near the eastern tropical Pacific, that a peak in reproductive calling (i.e. B-calls) occurs in February and March (Stafford et al., 2001). As the whales migrate along the west coasts of Central and North America, fewer calls are detected in one region and increased calling is detected in another. As the year progresses, blue whale D-calls are recorded off southern California from April to November while B-calls are recorded from June to January (Oleson et al., 2007a). Acoustic monitoring in other higher-latitude feeding areas show either similar patterns (e.g.,(Debich, 2014; Stafford, 2003)) or an extension of peak reproductive calling behavor into December, January, and February such as off Washington (Burtenshaw et al., 2004; Trickey et al., 2015).

2.1.2 Humpback whale visual and acoustic presence in the northeastern Pacific Ocean

Based on visual evidence, eastern Pacific Ocean humpback whales are found in warmer, tropical breeding areas in low latitudes (e.g., mainland and Baja Mexico, and Central America) during the winter breeding period (Steiger et al., 1991; Calambokidis et al., 2000; Rasmussen et al., 2012). As the year progresses, they migrate northward and feed primarily along the Pacific Rim off California/Oregon/Washington (Calambokidis et al., 2001, 1996) during the summer feeding period.

Humpback whales have dichotomous calling behavior where males sing long, complex, repetitive song (Payne and McVay, 1971) with a still uncertain reproductive function, while both males and females make social sounds (Dunlop et al., 2008). Although the structure and function of their vocalizations, especially song, have been well studied, the only instances of year-round acoustic effort in the eastern Pacific Ocean report a winter and early spring presence in low latitudes (Watkins et al., 2000), bimodal (October, April) peaks in acoustic presence off central California (Helble, 2013), and opportunistic singing detection during migration (Norris et al., 1999; Charif et al., 2001).

2.1.3 Fin whale visual and acoustic presence in the northeastern Pacific Ocean

Fin whales, in contrast to blue and humpback whales, are present off southern California year-round, with peak occurrence in late summer and early fall (Barlow, 1995; Sirovic et al., 2012). Less is known about their residence in the area, with working hypotheses of a resident population, and/or complex within-area migration

(Sirovic et al., 2015). Recent visual surveys suggest that fin whales use nearshore waters in the winter and spring and shift to offshore waters in the summer and fall (Douglas et al., 2014; Campbell et al., 2015).

Fin whales produce at least two types of calls in this area: 20 Hz and 40 Hz (Sirovic et al., 2012). Each call lasts about 1 sec in duration in a downswept pulse. The 20 Hz calls sweep in frequency from 23 to 18 Hz (Watkins, 1981) and 40 Hz calls sweep from 62 to 48 Hz (Sirovic et al., 2012). The function of calls varies based on the pattern in which they are produced; songs consist of stereotypic sequences of the down-swept 20 Hz pulses organized into regularly repeated sequences. Sung by males, they likely confer a reproductive function (Croll et al., 2002). Irregular, non-song sequences also occur and have hypothesized social function.

2.1.4 Hypotheses

The goal of this study is to investigate the seasonality and spatial variability in detections of blue, humpback and fin whale calls based on two acoustic datasets collected in the southern CCE from 2004 to 2014.

Regarding temporal patterns, I tested the following hypotheses:

H_o: Blue, fin, and humpback whale call types are detected equally across all seasons.

H_{1a}: Blue, fin, and humpback whale call patterns are variable across all seasons.

H_{2a}: There is a temporal separation between foraging (D-calls) and reproductive (B-calls) calls for blue whales

H_{3a}: There is a temporal separation between reproductive call types for blue and humpback whales.

Regarding spatial patterns:

H_o: Blue, fin, and humpback whale call types are detected equally in onshore/offshore regions.

H_1: Blue, fin, and humpback whale call types are variable in spatial distribution off southern California.

2.2 Methods

2.2.1 Study area and data collection

I used two sources of acoustic data from different research platforms in the southern California region: 1) expendable sonobuoys deployed off research ships that provide wide area coverage and 2) a bottom-moored acoustic recorder at a single location to provide excellent temporal resolution.

Sonobuoy Recordings

Baleen whale acoustic presence (humpback song, blue whale D-calls, blue whale B-calls, fin whale 20 Hz pulses; Figure 2.3) was manually detected from recording effort aboard 35 cruises from 2004 to 2012 (Figure 2.2). Acoustic data were collected as a part of the marine mammal component of the CalCOFI program (California Cooperative Oceanic Fisheries Investigations; calcofi.org; Figure 2.1), a multi-agency partnership formed in 1949 to investigate the collapse of the sardine population off California. The program operates quarterly cruises (spanning 17 to 30 days in duration) and collects a large suite of hydrographic, environmental, and biological data covering a large area off the west coast of the United States in a systematic grid of monitoring stations. The core CalCOFI sampling scheme covers gridlines normal to the coast covering the areas between San Diego and

Avila Beach, CA and samples up to 600 km offshore, spanning the inshore and offshore regions of the southern California region (Figure 2.1). In 2004, a marine mammal component was added to the CalCOFI program adding visual and acoustic sampling of cetaceans along the designated CalCOFI grid lines. Spacing between the transect lines and the distance between standard stations is 40 nm (74 km). Nearshore stations are half or less of this spacing.

During cruises, acoustic data were collected from Directional Frequency Analysis and Recording (DIFAR) and omnidirectional sonobuoys (Ultra Electronics Inc.) at CalCOFI stations that were occupied during daylight hours (with the exception of the fall cruise in 2004 when additional personnel allowed for night time monitoring). Equipment permitting, two sonobuoys were deployed at each CalCOFI station to ensure data reception. DIFAR (AN/SSQ 53 D/E/F) sonobuoys contained a directional hydrophone with a bandwidth from 10 to 2,400 Hz. Omnidirectional (AN/SSQ 53 B) sonobuoys contained a hydrophone with a bandwidth from 10 to 20,000 Hz. Upon deployment, sonobuoys inflated a flotation device and released a hydrophone to a pre-set depth ranging from 90 to 1000 feet. Signals recorded on sonobuoys were transmitted via a single radio carrier frequency and were received using an omnidirectional VHF Diamond Antenna and P160VDG preamplifier (Advanced Receiver Research) mounted on a mast of the ship. The preamplifier was connected to a 100 meter coaxial cable and signals were received with two ICOM radio receivers modified for low-frequency response (Greeneridge Sciences). Received signals were digitized with a sound board (Creative Labs Soundblaster Audigy and Realtek Corp. Avance Logic; both 24-bit), and signals were recorded on a personal computer using the software program LOGGER (Douglas Gillespie, International Fund for Animal Welfare). Sonobuoys were programmed to scuttle automatically after a maximum of 8 hours after deployment. Sonobuoy models used in this study included DIFAR and Omnidirections models of AN/SSQ 53F, 53E, 53D, and 57B with sampling rates between 4 and 48 kHz.

Fixed Station Recordings

Acoustic data were collected from a site (hereafter Site C) located off southern California approximately 50 km off Point Conception (34.3 ° N, -120.8 ° W) at a depth of approximately 800m (Figure 2.1) from 2010 to 2014. This site corresponds to the longstanding sampling station of the CalCOFI grid Line 80/Station 55, located on the continental shelf and exposed to consistent upwelling conditions.

The acoustic data were recorded using a High frequency Acoustic Recording Package (HARP) moored to the sea floor over a series of 10 deployments (Figure 2.2). The instrument contained a hydrophone which is broadband, low-power (50 mW) and high sensitivity (more than -120 dB re 1V/uPa) (Wiggins and Hildebrand, 2007), allowing captures of low-frequency and high-frequency vocalizations. The instrument also comprised a frame, flotation, ballast, and pressure cages which were bottom-mounted. The hydrophone was positioned above the instrument with a preamplifer and a calibrated system to allow for a flat response across all frequencies. Data were sampled by HARPs at 200 kHz, except 2 deployments that were sampled at 320 kHz.

2.2.2 Acoustic data processing and analyses

Sonobuoy acoustic analyses

On average, each sonobuoy deployment lasted between 1 and 8 hours. For this study, the presence or absence of at least one call detection within the first two hours of the recording was noted for each call type studied. Because of the variable quality of recordings, manual methods were used. Acoustic data were analyzed visually via spectrograms using the Matlab-based custom software Triton version 1.81 by a single experienced analyst. To minimize variation in the analyst's ability to accurately define call types within the spectrogram, I standardized viewing window parameters (e.g., contrast and brightness of the call, the size of the window, duration shown in each window, and visible bandwidth) and the analysis parameters (e.g., FFT length and percent overlap) to ensure consistent time and frequency resolution across sonobuoy recordings. The original data had sampling rates between 4,800 and 48,000 Hz and were decimated from its original form to a uniform bandwidth ranging from 10-2,400 Hz. Decimated files were scrutinized in 60s windows between 0-200 Hz for fin whale and blue whale calls, and between 0-500 Hz for humpback whale calls, in 1 Hz bins with 90% temporal overlap. Even though humpback whale song units can be detected at a much higher frequency range, at least parts of the calls can be seen at lower frequencies between zero and 500 Hz. Whenever a partial humpback call was detected, the analysis window was expanded up to 1000 Hz to ensure that humpback calls were correctly identified and no false positives were logged. The quality of recording data was annotated as 'Poor', 'Medium', or 'High' for each hourly presence. The quality of data was assessed based on the presence of background noise (e.g. ship noise, flow, swells, etc.) and technical problems (e.g. radio interference, patchy signal, instrument failure, etc.). Data denoted with 'Poor' quality had noise interruptions for greater than $\sim$ 60% of the hour, 'Medium' quality data was free of noise between 40% and 60% of the hour, and the score of 'High' was given to data clear of noise for less than 20% of an hour.

Detector analyses for HARP recordings

Automatic detectors were used to determine the presence of blue whale calls and manual detection was used for annotating humpback whale calls in HARP recordings. All call detections were annotated for subsequent seasonal and daily call count analyses.

Before any analyses were conducted, all data were decimated by a factor of 100 to create an effective acoustic bandwidth from 10 to 1000 Hz (for 200 kHz sampled data) or 10 to 1600 Hz (for 320 kHz sampled data). For subsequent data analyses, long-term spectral averages (LTSAs) with 5 s temporal and 1 Hz frequency resolution were created for each deployment using custom software developed in MATLAB (ver. 2007b, Mathworks, Inc.).

The Generalized Power-Law (GPL) detector, originally designed for humpback whale vocalizations (Helble et al., 2012), was modified to allow for the detection of the highly variable blue whale D-call, constraining the parameters to fit the downswept nature of the call. The GPL detector was run over four years of acoustic record from 2010 to 2014. Because of the generalized nature of the detector and ubiquitous self-noise from the recorder, D-call detections yielded an order of magnitude more false detections than true detections. Therefore, in order to minimize the bias from false detections, each HARP deployment was verified by a human analyst to exclude false detections, thereby reducing the false alarm rate to zero. A groundtruthing process was implemented to determine the true positive (recall) rate for the detector. We randomly selected a subsample of 24 hours for each deployment for manual detection and confirmation. The D-call recall rate was between 67% and 85% for the 10 HARP deployments (Table 2.1).

B-calls were automatically detected using spectrogram cross-correlation (Mellinger and Clark, 2000). Spectrogram correlation for B-calls is a viable option due to the stereotypical frequency and temporal characteristic of the the call. However, seasonal and interannual shifts in call frequency has been shown to occur (McDonald et al., 2009). For this study, multiple detector templates and detection thresholds were determined amongst the multiple deployments in order to account for the shift in frequency content of the call. A kernel, or reference function, was developed from approximately 30 hand-picked B-calls with each call separated by at least 24 hours to ensure independence of calls for each deployment. This kernel was determined from the peak frequency of the third harmonic of the B-calls measured automatically at five time periods within the call (0, 1.5, 3, 4.5, 10 seconds) using customized MATLAB-based software. The deployment-specific template was run on a subset of data (containing at least 200 hand-picked calls) at various threshold values in order to obtain the optimum threshold value that minimized false detections, minimized missed calls, while maximizing true detections. The optimal threshold was manually chosen to minimize the tradeoff between precision and recall (Table 2.1). Finally, the automatic detector was run on all files using the appropriate kernel and threshold. Detections from February to May were always verified by a human analyst due to the scarcity of calls during these months. False detections were deleted from the record for these months. All detections times and threshold scores were stored in the Tethys metadata database (Roch et al., 2013).

Manual acoustic analyses for HARP recordings

A human analyst reviewed Longterm Spectral Averages (LTSAs) for all HARP deployments to annotate hourly presence of humpback whale song activity lasting at least one theme (Payne and McVay, 1971) or longer. Acoustic annotations were logged via custom software Triton version 1.81. When necessary, close inspection of call spectrograms confirmed detection annotations. To calculate the spectrograms, fast Fourier transforms (FFTs) of the time series of waveforms were performed with 2,000 or 3,200 samples, 90% overlap, and Hamming window.

2.2.3 Statistical analyses

Temporal distribution of call types

Statistical evaluation of the temporal distribution of each blue and humpback whale call type was performed on the available four year data set. Each call detection was indicated by the Julian day on which it occurred and was treated as one in a sample of calls for each call type. This variable was assigned an angular value based on its position on an imaginary annual circle. The mean value (and 95% confidence interval) of each call type was calculated from the angular values. Essentially, this 'mean' value represented the time of year of peak calling. Seasonal length (number of days between first and last call detection) and seasonal midpoint (the calendar date of the halfway point between first and last detections of each call type) were also calculated for each call type. For length and midpoint determinations, the first detection after March 1st was considered the first detection of the year based on historical knowledge of typical first arrival dates of these species on the feeding grounds.

To test for significant differences in the yearly distribution of call types (i.e. the homogeneity of seasonal mean), I used the non-parametric Watson-Wheeler test which is robust against departures from the circular von Mises distribution (Batschelet, 1981). To accept the alternative hypotheses (H_{2a}, H_{3a}), we must reject the null expectation that the seasonal distributions of call types have the same mean. Analyses were modeled after that demonstrated in previous analyses done for blue and fin whales (Oleson et al., 2007c; Sirovic et al., 2012). All statistical analyses were performed using the ‘circular’ package in R version 3.1.2.

Spatio-temporal analyses

Probability of detection (number of detections / number of sonobuoy deployments) was calculated for each call type across the CalCOFI grid in stratified groups: CalCOFI stations with numbers 45 and lower lie within the Southern California Bight; CalCOFI stations with numbers 53 and higher lie to the west of the bathymetric ridge and are outside of the Bight; offshore (and onshore) categories were designated as stations higher and equal to 60 (and lower than 60); northern/southern lines occur above/below CalCOFI Line 87 (with the southern category inclusive of Line 87).

Additionally, an extension of the generalized linear model (GLM) (McCullagh and Nelder, 1989) was used to model the relationship between blue, humpback, and fin whale acoustic presence and distance from shore in transformed space. GLMs (Equation 2.1) and generalized linear mixed models (GLMMs; Equation 2.2) are expressed in the following equations:

$$GLM : g(E(Y)) = X_m\beta \tag{2.1}$$

$$GLMM : g(E(Y)) = X_m\beta + Z_j\gamma \tag{2.2}$$

where E(Y) are the estimates of the non-normal response variable (i.e. baleen whale acoustic detections), g is the link function with a given distribution function, Xβ is the linear predictor consisting of a linear combination of unknown parameters β with independent fixed variables X, and Zγ is the component incorporating the random variable Z. We modelled a binomial family distribution with logit link function.

Distance from shore and season (and their interaction) were the only covariates considered. Distance from shore was estimated by measuring the distance from the mainland shore via the CalCOFI Line transect that intersected the coastline. The line represented the shortest perpendicular distance to the mainland shore, but not necessarily the shortest distance to a shoreline (in some cases Channel Islands which may be closer). Probability of detection was calculated in sections stratified by north/south and onshore/offshore for visualization, but the regression analysis was performed on pooled areas over all years with year modelled as a random effect. A negative coefficient for the fixed term (distance) indicated increased acoustic presence as distance from shore increased and it also indicated the degree to which whales were likely to occur onshore or offshore. All statistical analyses were performed using R version 3.1.2.

2.3 Results

2.3.1 Seasonal occupancy

We observed seasonal variability in the occurrence and abundance of blue whale B-calls and D-calls, and humpback whale song throughout 2010 to 2014 at Site C (Figure 2.4). Seasonal length was longest for blue whale D-calls (335 days) and shortest for B-calls and humpack song (272 days each; Table 2.2). Blue whale D-calls were heard predominantly in the summer months with the mean (i.e. peak day of occurrence) in early July. B-calls were heard during the summer and fall months with the mean (i.e. peak) in mid-September. Humpback song had two peaks 1) in the spring and 2) the fall with means in late March and early November, respectively (Figure 2.4; Table 2.2). There were significant differences in the means of the seasonal distribution of blue whale B-calls and D-calls (Watson-Wheeler test, W = 26889, $p < 0.001$; Table 2.3). There were also significant differences between hourly presence of B-calls and humpback whale song (Watson-Wheeler test, W = 2944, $p < 0.001$; Table 2.3). Seasonal midpoints of blue whale B-calls and D-calls were ∼1 month after the estimated mean (i.e. peak) in calling, which indicates a long right tail of the calling distribution (Table 2.2).

2.3.2 Spatio-temporal analyses

Relationships for various call types to distance to shore were different for each season (Table 2.4). For blue whales, both call types showed increased probability of detection in the summer and fall months (Figure 2.6; Figure 2.8) with higher B-call probability of detection closer to shore in the SCB during the summer and fall months (Figure 2.5). In contrast, for blue whale D-calls, there was no significant spatial pattern, with persistent habitat use nearshore and offshore throughout the year (Figure 2.7; Table 2.4). For fin whales, there was significant nearshore presence except during the winter months (Figure 2.9). Fin whales were acoustically present year-round and showed an increase in probability of detection during the fall and winter months (Figure 2.10). For humpback whales, there was a shift in distribution offshore from summer to winter (Figure 2.11). with the highest probability of detection during the winter and spring months (Figure 2.12).

2.4 Discussion

2.4.1 Seasonality of call types

This study offered the first detailed view into the temporal and spatial variability of different call types of three different species on a southern California feeding ground. Our study demonstrated that resident and migrant baleen whales were associated with bathymetric features although the nature of these relationships varied across species and call types. These spatial patterns highlighted the need for year-round monitoring as relationships between call types and distance to shore varied between seasons.

The probability of detection was not equal for any call types across all seasons. Blue whale D-calls were detected longest over the year but were less abundant than B-call counts. There was a temporal shift from a prevalence in D-calls in spring through summer to B-calls in summer to late fall, which has been shown in previously studies conducted almost a decade earlier (Oleson et al., 2007c). This shift from foraging to reproductive calling represented a shift in behavioral state for blue whales as the summer transitioned to fall.

As blue whales arrived on the southern California feeding ground, they did not sing. Instead, they produced D-calls and engaged in foraging behavior. Since blue whales are thought to also feed on breeding grounds (Reilly, 1990), feeding effort and reproductive success during the winter/early spring breeding season in the eastern tropical Pacific may set the stage for how these whales use the southern California region in summer/fall. For example, if feeding effort was not fruitful during the winter months, whales will arrive in southern California nutrient-deprived, which may dictate their energy budget towards foraging rather than singing. Similarly, if a whale had spent most of the breeding season engaged in song (and precluded from foraging), then their first arrival on feeding grounds would be dedicated to getting food. As feeding success increases over the course of a feeding season, an increase in singing occurs.

The acoustic monitoring effort in the southern California region indicated that although there were strong seasonal patterns, at least some calls were detected year round. Our acoustic results extended the known seasonal presence of blue whales in the Southern California Bight by showing early detection of D-calls in April and late detection of B-calls in December. Although the occurrence of D-calls has not been studied as extensively as B-calls, these results suggest that monitoring of both call types is required to accurately assess the seasonal distribution of blue whales on feeding grounds. Monitoring of both call types also addresses the bias towards males as it includes call types known to be produced by females as well as males.

Despite similar seasonal durations of B-calls and humpack whale song, there was a temporal separation between reproductive call types for two different species. A prevalence in humpback whale song occurred in late March, with a shift in prevalence of blue whale B-calls in September, then a return to higher levels of humpback whale song in November. The bimodal peak in humpback whale singing reflected the same pattern shown in a separate ocean basin (Vu et al., 2012) with elevated singing during the shoulder seasons surrounding the winter breeding season.

As humpback whales arrived back on the feeding grounds in the spring, they were singing at high rates. As the summer approached, singing diminimished presumably as the whales were focusing on foraging activity. The temporal separation in song by blue whales and humpback whales was evident when blue whale singing started in summer after spring humpback whale singing diminished. The second peak in humpback whale song occurred in fall as singing ramps up again before the humpback whales leave for their breeding grounds. At the same time, blue whales continued in pervasive singing through fall. The decrease in blue whale singing coincided with their departure from the area.

2.4.2 Spatial patterns in calling

The spatial patterns of acoustic detections changed with season. Blue whales produced B-calls closer to shore during the summer and fall, though there was no spatial difference in D-call production. Seasonal probability of detection did not always match the seasonal patterns of whale abundance based on visual-based effort. Within the southern CCE, specifically southern California, blue whales are seen in highest numbers in summer, decrease in numbers in the fall, and are virtually absent in winter/spring from the study area (Figure 2.14) (Campbell et al., 2015; Douglas et al., 2014; Forney and Barlow, 1998; Forney et al., 1995). Our results similarly show higher probability of acoustic detection during the summer/fall than in winter/spring, although there was a non-zero probability of detection during these months for both D-calls and B-calls, which highlights the usefulness of acoustic monitoring during these less-sampled months. The sustained reproductive calling in the fall coinciding with the slight decrease in abundance indicated a seasonal increase in individual-level calling during the summer to fall transition.

While humpback whales are seen all year, they occur in higher proportion onshore during the summer months (85%; inshore of the 200m isobath) and lower in fall (15%; Forney and Barlow (1998); Douglas et al. (2014)). Most calling occurred offshore during the winter and spring months. This suggests that while humpback whale song may be an inappropriate proxy for population estimates, much can be learned about spatial use of the region by migrating singing whales. It remains unclear whether the humpback whales heard in the offshore waters of southern California in winter and spring are part of the California feeding population or whether they represent other subpopulations. The peak acoustic probability of detection observed for humpback whales during winter and spring may represent both 1) migrants travelling from wintering grounds south of southern California in Mexico and Central American to summer feeding grounds north of southern California such the US West Coast, Canada, and Alaska and 2) individuals that feed off southern California for an extended period of time (Calambokidis et al., 1996). Our results showed that an increase in humpback whale song detection occurred in the onshore region from winter to spring. This slightly higher probability of acoustic detection in the Southern California Bight for springtime humpback song suggested that males that arrived more onshore in spring were still singing when they got to southern California. Humpback whale visual and acoustic seasonal detection did not match in southern California. While visual effort showed consist humpback year-round presence (Figure 2.14) (Campbell et al., 2015; Douglas et al., 2014; Forney and Barlow, 1998), the highest probability of detection occurred during winter and spring while the lowest occurred in summer and fall. Higher acoustic presence during the winter and spring indicated a change in individual-level calling rate as humpback whales transition from fall to winter.

Fin whales are generally acoustically encountered year-round. They are more often heard closer to shore, except in winter, when they are heard both onshore and offshore. During the winter, fin whales are not heard in the Santa Barbara Channel. Their absence has been documented previously using visuals- and acoustics-based methods (Redfern et al., 2013; Sirovic et al., 2015).

Fin whales visual and acoustic seasonal detection did not match in southern California. Fin whales were visually detected throughout the year, with higher levels of abundance in summer and fall (Figure 2.14) (Campbell et al., 2015; Douglas et al., 2014; Forney and Barlow, 1998). The high fin whale detection rates in fall and winter reported in this study corroborate previously published patterns in the southern California region which shows acoustic detection all year with notable decreases in calling from April to July (Sirovic et al., 2012). However, they do not perfectly overlap the abundance patterns from visual effort. High acoustic presence persists through winter when fin whale abundance dips, indicating a change in individual-level calling rate as fin whales transition from fall to winter.

All three species display an increase in calling on the individual level during the fall (blue whales) or winter months (fin and humpback whale). The increase in singing coinciding with the seasonal winter mating period for the three species is likely an indication of an increase in reproductive activity. Blue whales curiously increase their reproductive activity in the fall, a few months earlier than the increase in singing seen in fin and humpback whales in the winter. This suggests that blue whales may be subject to different reproductive pressures requiring additional time dedicated to reproductive behavior such as singing. Blue whales are known to have the lowest testes to body size ratio (Brownell and Ralls, 1986) and likely do not use sperm competition as their main strategy for reproductive success. Instead, other forms of reproductive display may be employed to display male intrasexual dominance or intersexual pair bonding. Therefore, earlier and more protracted singing, as seen in our study, may be necessary for blue whales, but such a hypothesis requires more investigation.

The prevalence of song on feeding grounds suggests that the production and function of song is flexible. The duration over which singing occurs is much longer than the window for which mating must occur in order to start a 11-12 month gestation period that leads to calving in low-latitude tropical areas during the winter. With low reports of calving in the summer and fall (Tomilin, 1957), it is apparent that the majority of births still occur during the breeding season. Early singing may occur for a number of reasons which include status maintenance (conferring male-male interactions) and/or appealing to females before breeding season leading to reproductive success later in the season when females are reproductively responsive (conferring female-male interactions). Whether the function of song is to appeal to females or establish dominance amongst males, early singing by whales allows for a head start on long-term assessment and association (Oleson et al., 2007c), and eventually, high reproductive success.

2.4.3 Hypothesized migration patterns

Historic and recent acoustic recordings collected across the North Pacific Ocean give insight to long-term whale presence (Watkins et al., 2000; Curtis et al., 1999; Stafford et al., 1999, 2001; Burtenshaw et al., 2004; Oleson, 2005; Sirovic et al., 2015) and can be used to gain a better understanding of baleen whale distribution and migration patterns. Based on the insights from this study regarding temporal and spatial patterns in the southern California region, together with the vast literature on population structure for blue and humpback whales in the Northeast Pacific Ocean, we propose migration patterns shown in Figure 2.16 and Figure 2.15.

The acoustically-detected seasonal occupation of Site C within the larger landscape of known calling patterns in the ocean basin indicates that the southern CCE is a part of the blue whale migratory cycle but not necessarily the main northern limit. Singing blue whales are detected in higher latitudes, such as in the Gulf of Alaska in summer to fall. Due to the timing of the acoustic peaks in Gulf of Alaska (Debich, 2014), there is likely a separate subpopulation that occupies that area although some individuals from the CA population have been re-sighted in the area (Calambokidis pers. comm.). Individuals also occur off the Oregon/Washington coast (e.g., 47 30.04N, 125 21.26W, depth 1,384 m; (Burtenshaw et al., 2004; Trickey et al., 2015)). Because acoustic peaks are always shifted in time from southern California, there is a northward shift in distribution as the year progresses. These whales also have acoustic peaks off OR/WA after most of their population leaves the WA/OR/CA area, which is evidence that at least some animals stay longer in the area, but are not detected visually because of less effort in area. Therefore, the hypothesized route includes the California/Oregon/Washington region as a single feeding region with whales mostly found along CA, but they travel throughout.

There is increased singing activity in the winter at eastern tropical Pacific breeding grounds (Stafford et al., 2001). Therefore, blue whales leave the California/Oregon/Washington region by Jan and migrate southward, probably far offshore (past the detection range of the CalCOFI grid) due to few B-call detections during the winter months in southern California (with supporting evidence from satellite tagged blue whales which show that these migratory paths can indeed occur far offshore (Bailey et al., 2009)). The fact that the whales from Gulf of Alaska are also not detected in their southbound migration in the offshore CalCOFI stations further supports far offshore pathways. Few offshore CalCOFI detections in spring also support the notion of a far offshore, unknown migratory pathway in the northbound direction.

Similarly, Site C is not the northern limit for humpback whales with seasonal occupancy in OR/WA, off the coast of Canada, and the Gulf of Alaska (Calambokidis, 2008). There is evidence of onshore singing in southern California during spring when humpback whales arrive and very little singing in summer and fall when they are proportionally more abundant onshore based on visual effort. Offshore singing detection increases in fall and winter as shown in the southern California acoustic record (this study) and off Washington coast (Trickey et al., 2015). The heavy offshore southern California humpback song presence in winter and spring is most likely from migrating whales during their southbound winter and northbound spring migrations. There are at least three subpopulations which can contribute to this offshore song detection: Offshore Mexico, Mainland Mexico, and Central America (Steiger et al., 1991; Calambokidis, 2008) but it was not within the scope of this work to differentiate between the songs of each subpopulation.

2.4.4 Data limitations

Interannual variation

The analyses of patterns of seasonal duration and timing were based on pooled acoustic detections over four years and did not account for interannual variability. The observed interannual variation from 2001 to 2003 (Oleson et al., 2007c) suggested that the specific timing of migration fluctuated. The time series used in this study contained gaps in data collection which correspond to critical times during which certain call types start, peak, or end and therefore we could not determine the specific time of arrival in every year. However, pooling all four years of call detections yielded blue whale calling patterns that were similar to patterns seen in previous years (Oleson et al., 2007c; Sirovic et al., 2015). In other studies, dynamic oceanographic variables such as temperature and fronts were shown to explain baleen whale presence (Becker et al., 2010; Tynan et al., 2005). Since environmental factors were not considered in this chapter, I did not explore the full extent to which habitat could influence calling patterns within the region, and explain interannual variation of call patterns. I explore environmental factors in the next chapter.

The analyses looking at the relationship between call types and distance from shore consisted of mixed effects models with year-specific random effects used to explicitly model between-year variation in the data. I modeled this random effect to account for interannual variation without specific expectations for the trajectory of the trend. I was instead interested in testing whether or not including year as a random effect was significant and adequate to capture the between-year variation. Therefore, I tested the random effects variance components equal to zero and found that including a random effect was necessary. However, more extensive analyses would be needed in order to answer specific questions about interannual long-term trends.

Potential effects of noise

Site C, which has been included in other published studies (Sirovic et al., 2015; McKenna, 2011) was exposed to the highest average low-frequency noise levels (i.e., 86 dB re $1\text{Pa}^2/\text{Hz}$ at 40 Hz with maximum levels at 117 dB) when compared to a sample of other sites in the Southern California Bight. Only 25% of measured sound levels at this site were below 80 dB re $1\text{Pa}^2/\text{Hz}$ at 40 Hz (McKenna, 2011). Although not in a shipping lane, the site is exposed to both local ships passing to/from the Los Angeles/Long Beach port and distant ships travelling across the basin. Therefore, this site is subject to variability in noise which can affect the probability of detection over time and bias call counts (e.g. as shown in (Helble, 2013)).

2.5 Acknowledgments

The authors gratefully acknowledge the efforts of all those involved in the collection of these data, especially SWAL lab engineers and numerous field volunteers, including but not limited to: Melissa Soldevilla, Liz Henderson, Nadia Rubio, Greg Campbell, Lisa Munger, Megan McKenna, Erin Oleson, Jessica Burtenshaw, Karli Merkens, Katherine Whitaker, Josh Jones, Hannah Bassett, Lauren Roche, Anne Simonis, Amanda Debich, Katherine Whitaker. Sarah Johnson assisted with manual acoustic detection of CalCOFI recordings. Ally Rice helped validate the B-call detector used in this study. Tyler Helble customized his GPL detector to allow for D-call detection capablity. Marie Roch and her lab developed Tethys, which allowed for ease of managing the large number of acoustic detections. We gratefully acknowledge the funding support of Frank Stone, Ernie Young, Linda Petitpas, Bob Gisiner, and Curt Collins at the Chief of Naval Operations, division N45, the Office of Naval Research, and the Naval Post Graduate School.

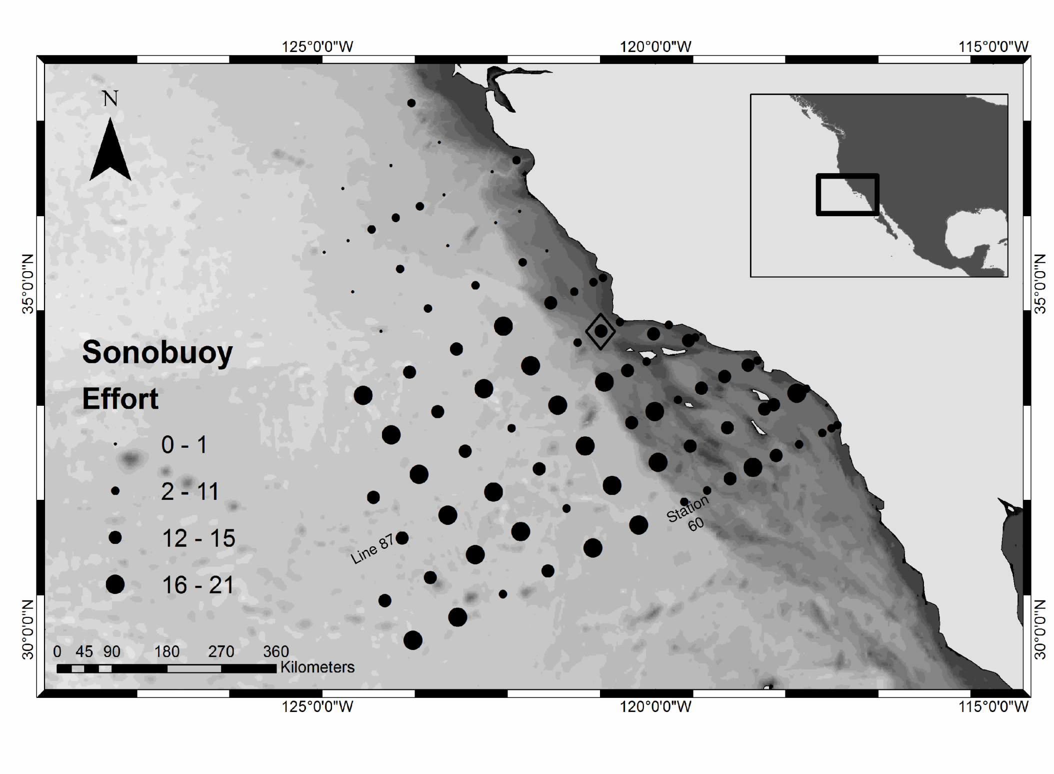

Figure 2.1: Locations of sonobuoy recording effort (number of deployments) within the CalCOFI sampling grid from 2004 to 2012. Location of High Frequency Recording Package (HARP) approximately 50 km off Pt. Conception is marked by the diamond.

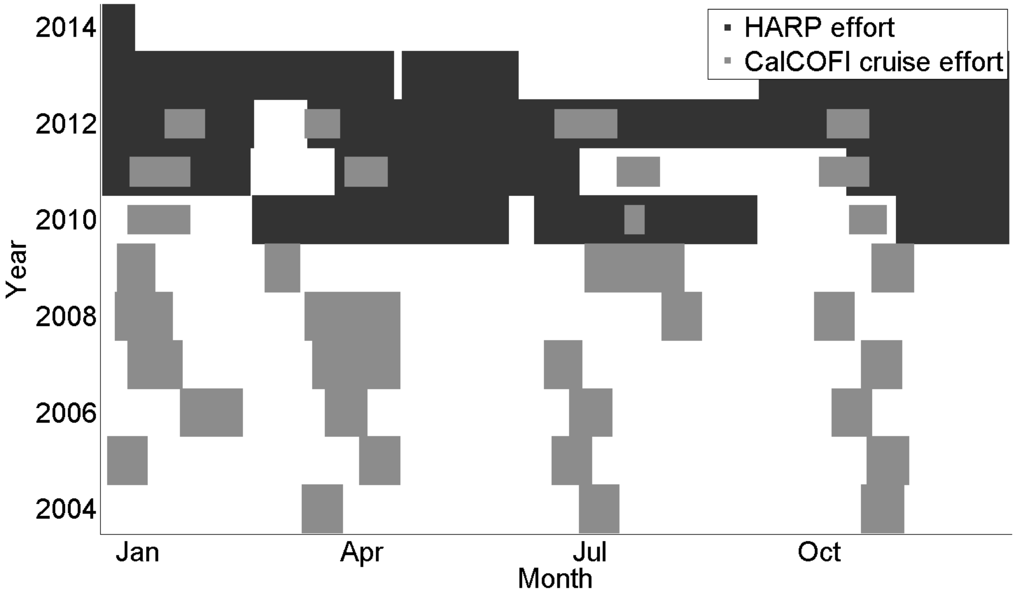

Figure 2.2: Dates of CalCOFI (California Cooperative Oceanic Fisheries Investigations) cruises and High Frequency Recording Package (HARP) recording effort.

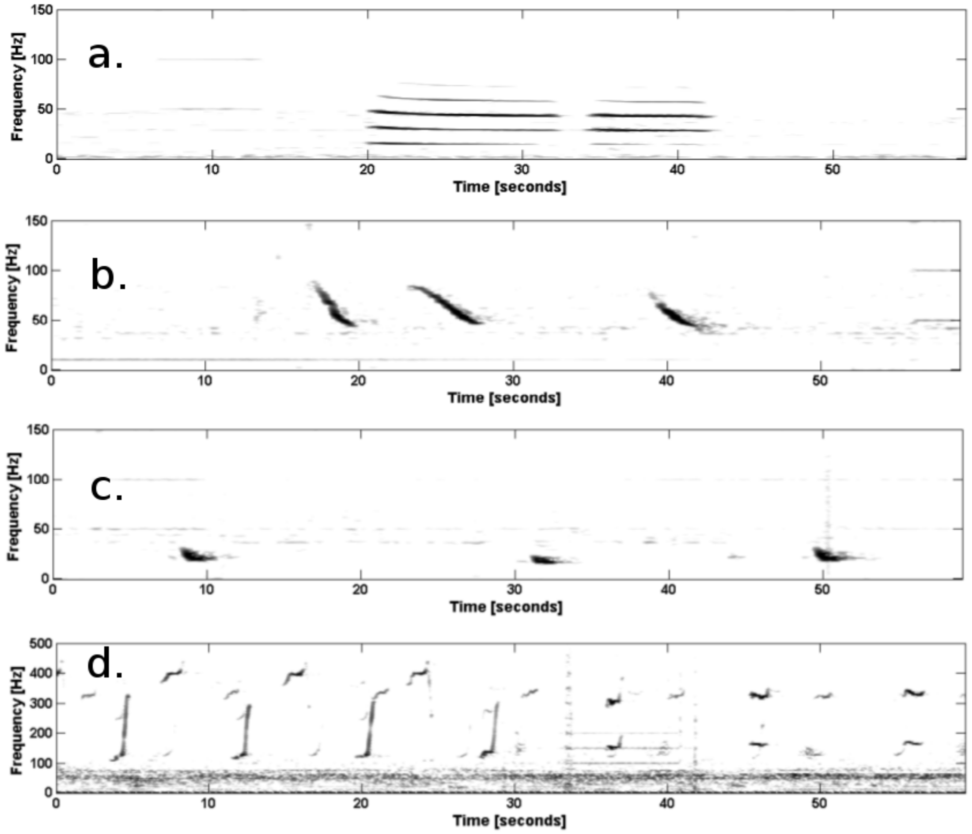

Figure 2.3: Spectrogram of (a) tonal blue whale B-calls with a series of harmonically-related components (the third harmonic is used for detection due to its high SNR) (b) downswept blue whale D-calls, which exhibit more variability in frequency range and duration than B-calls (c) fin whale 20 Hz pulses and (d) humpback whale song. Spectrograms were constructed to display signals in 1 Hz bins with 90% temporal overlap.

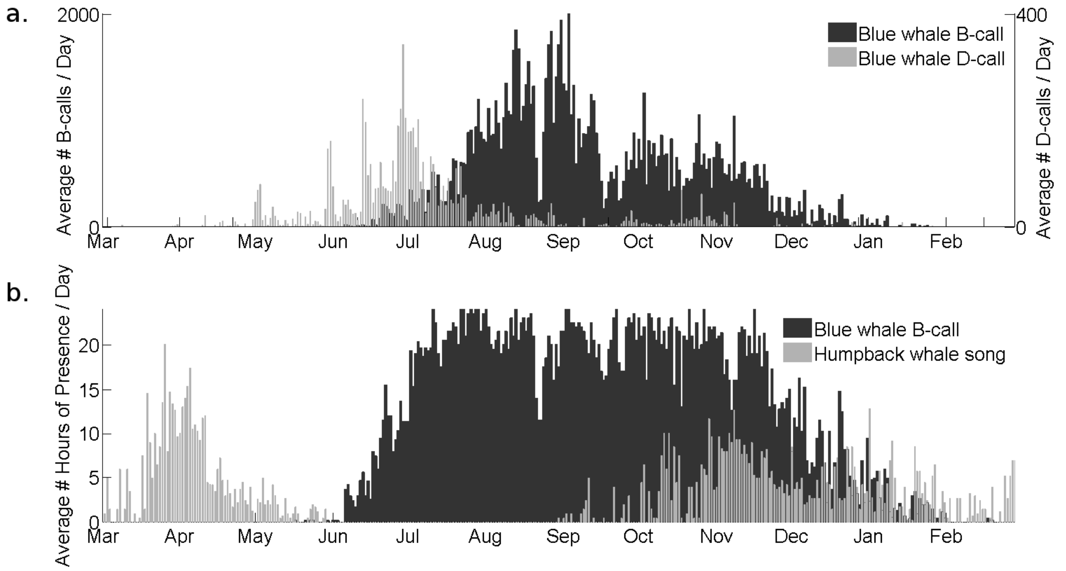

Figure 2.4: Four year average seasonality of (a) blue whale B-call and D-call (detections/day) and (b) humpback whale song (hourly bins/day) at Site C.

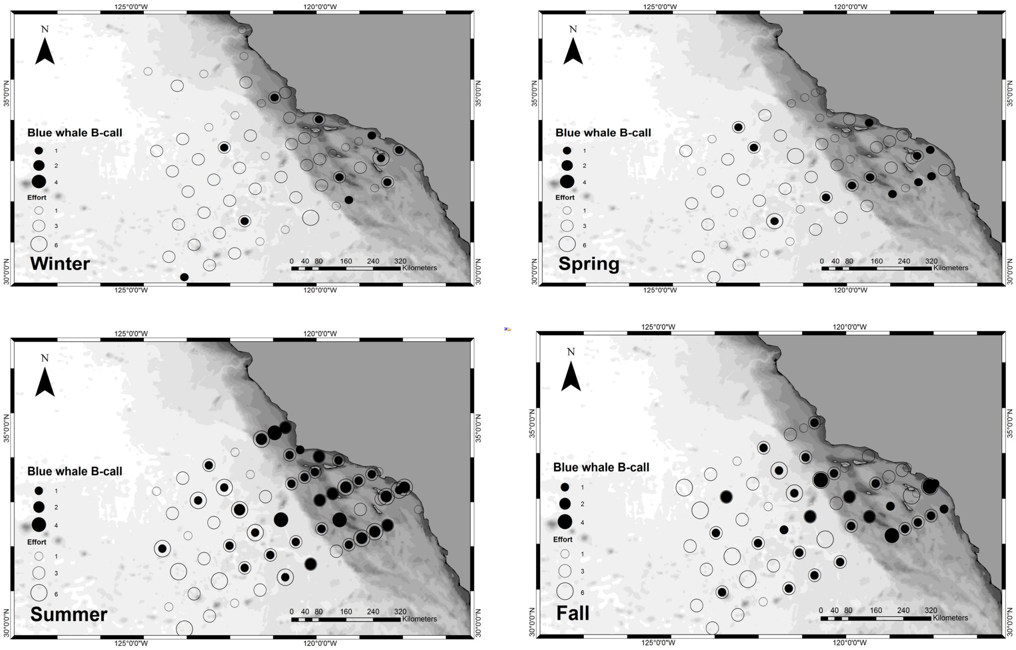

Figure 2.5: Total detections of blue whale B-calls in southern California during each season. Each detection represents confirmed acoustic presence in the first two hours of recording effort per sonobuoy deployment. Sonobuoy effort represents number of deployments at each station over 9 years of effort.

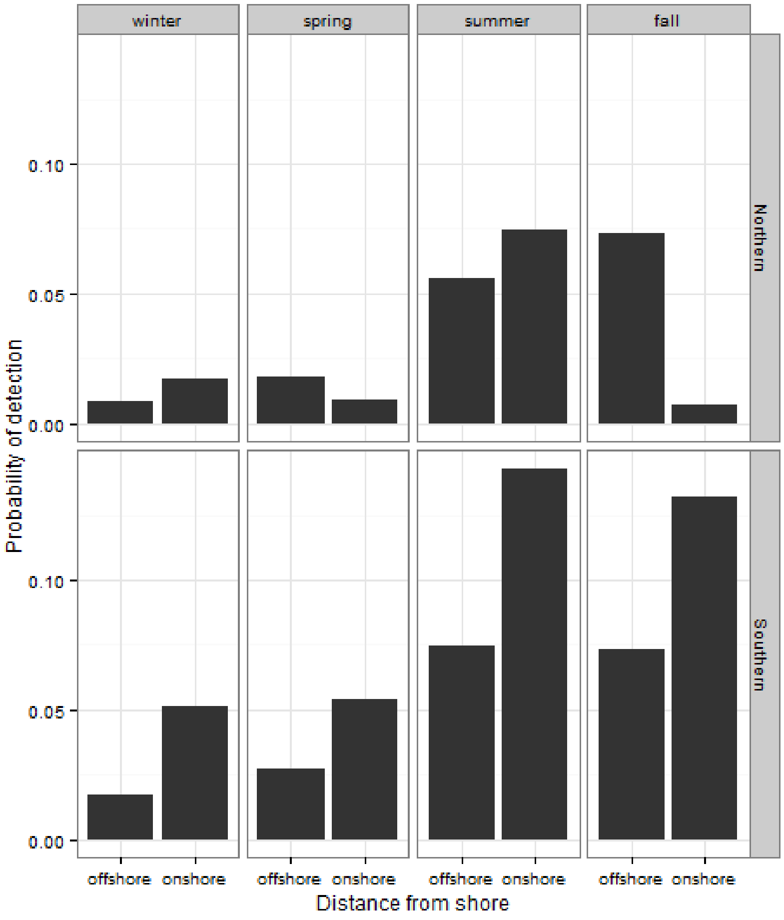

Figure 2.6: Probability of detection for blue whale B-calls stratified into the following categories: by season, northern/southern, and onshore/offshore contexts. CalCOFI stations with numbers 45 and lower lie within the Southern California Bight; CalCOFI stations with numbers 53 and higher lie to the west of the bathymetric ridge and are outside of the Bight; offshore (and onshore) categories were designated as stations higher and equal to 60 (and lower than 60); northern/southern lines occur above/below CalCOFI Line 87 (with the southern category inclusive of Line 87).

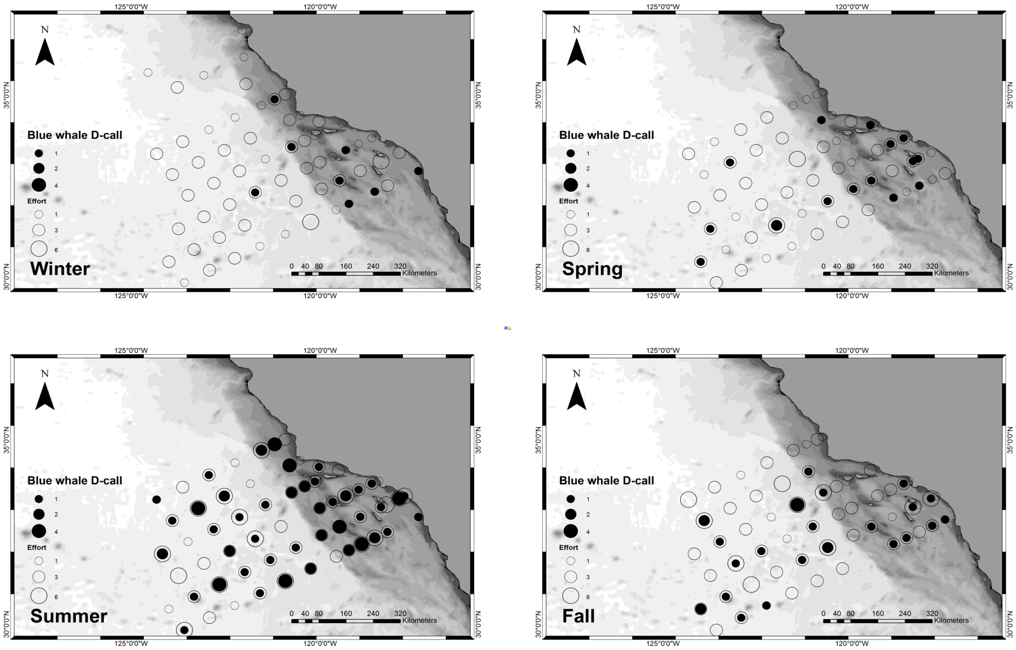

Figure 2.7: Total detections of blue whale D-calls in southern California during each season. Each detection represents confirmed acoustic presence in the first two hours of recording effort per sonobuoy deployment. Sonobuoy effort represents number of deployments at each station over 9 years of effort.

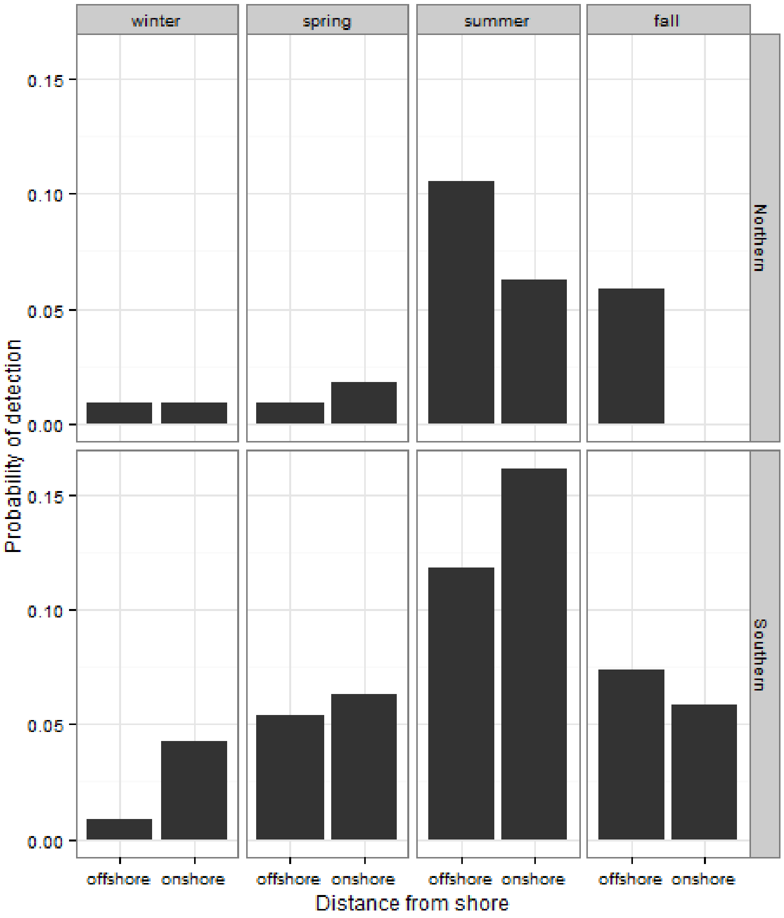

Figure 2.8: Probability of detection for blue whale D-calls stratified into the following categories: by season, northern/southern, and onshore/offshore contexts. CalCOFI stations with numbers 45 and lower lie within the Southern California Bight; CalCOFI stations with numbers 53 and higher lie to the west of the bathymetric ridge and are outside of the Bight; offshore (and onshore) categories were designated as stations higher and equal to 60 (and lower than 60); northern/southern lines occur above/below CalCOFI Line 87 (with the southern category inclusive of Line 87).

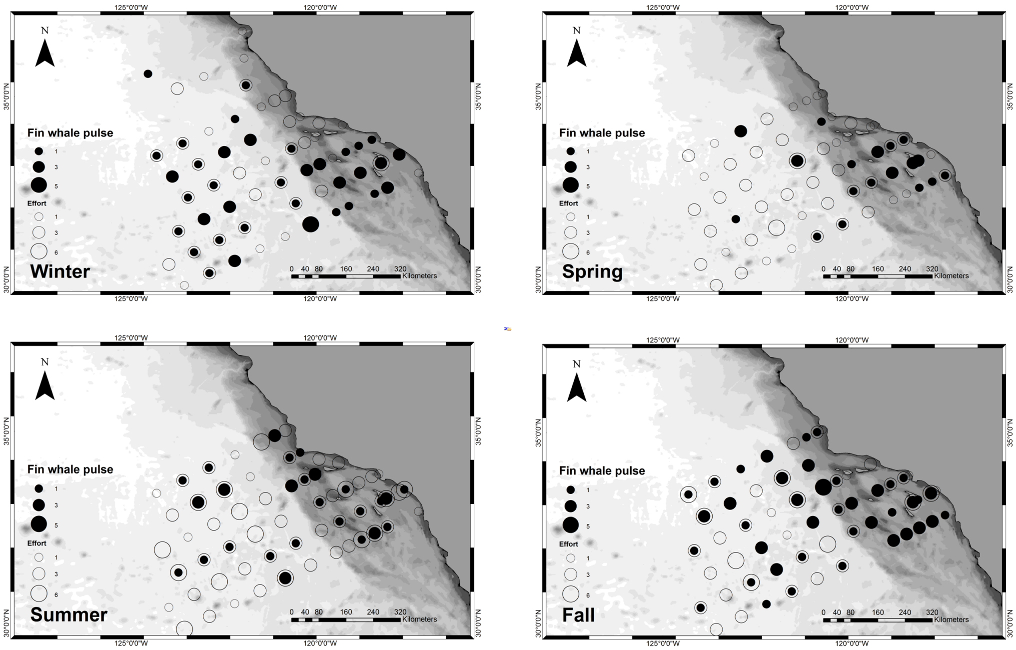

Figure 2.9: Total detections of fin whale 20-Hz pulses in southern California during each season. Each detection represents confirmed acoustic presence in the first two hours of recording effort per sonobuoy deployment. Sonobuoy effort represents number of deployments at each station over 9 years of effort.

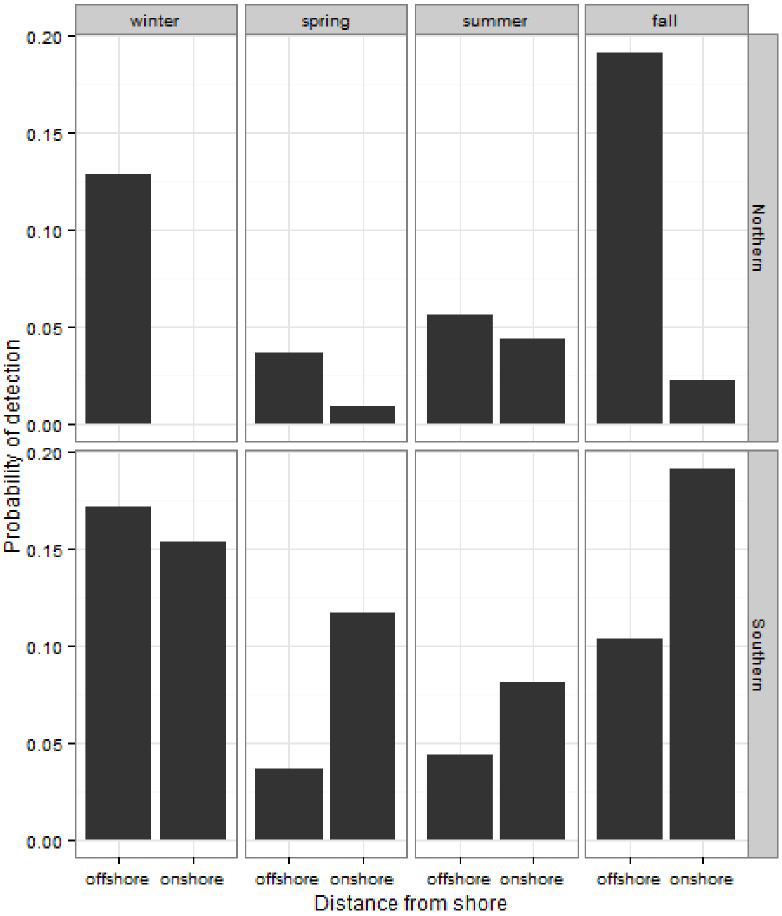

Figure 2.10: Probability of detection for fin whale 20 Hz pulses stratified into the following categories: by season, northern/southern, and onshore/offshore contexts. CalCOFI stations with numbers 45 and lower lie within the Southern California Bight; CalCOFI stations with numbers 53 and higher lie to the west of the bathymetric ridge and are outside of the Bight; offshore (and onshore) categories were designated as stations higher and equal to 60 (and lower than 60); northern/southern lines occur above/below CalCOFI Line 87 (with the southern category inclusive of Line 87).

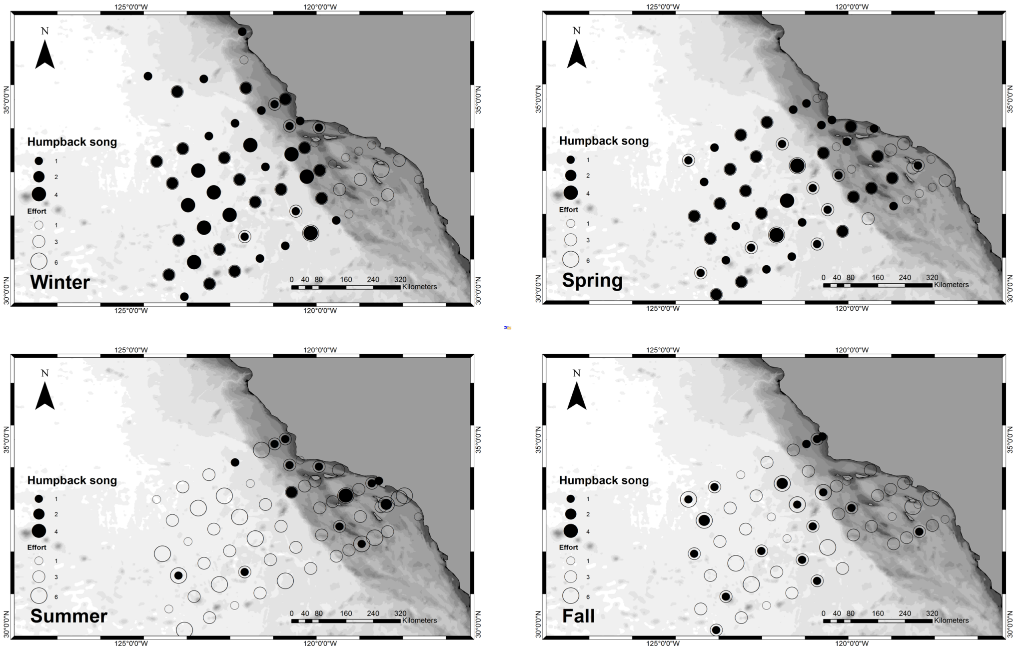

Figure 2.11: Total detections of humpback whale song in southern California during each season. Each detection represents confirmed acoustic presence in the first two hours of recording effort per sonobuoy deployment. Sonobuoy effort represents number of deployments at each station over 9 years of effort.

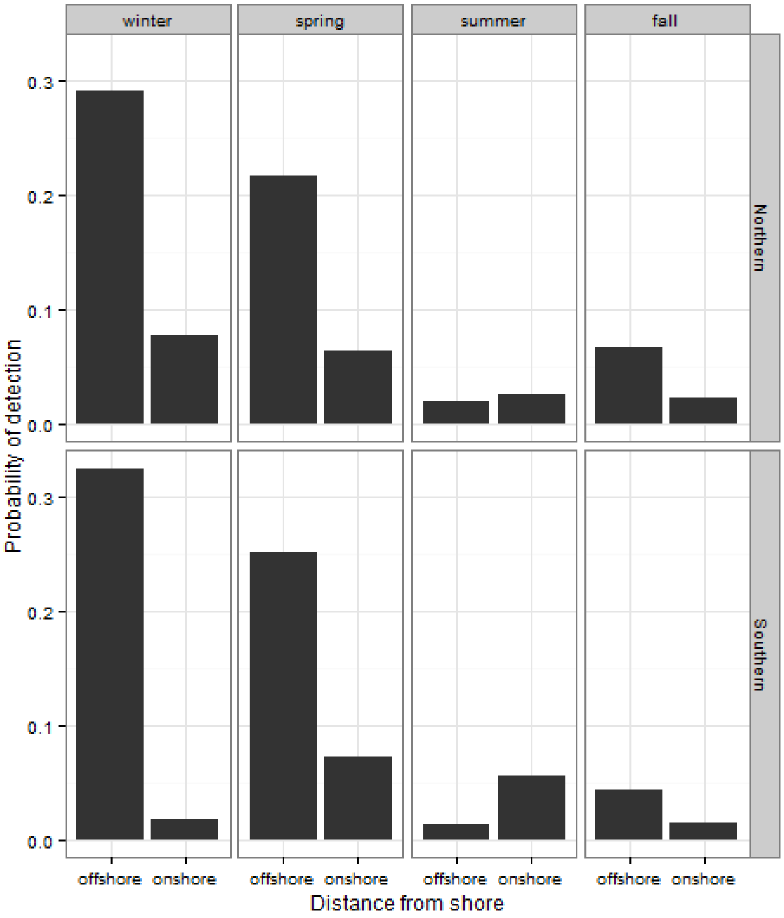

Figure 2.12: Probability of detection for humpback whale song stratified into the following categories: by season, northern/southern, and onshore/offshore contexts. CalCOFI stations with numbers 45 and lower lie within the Southern California Bight; CalCOFI stations with numbers 53 and higher lie to the west of the bathymetric ridge and are outside of the Bight; offshore (and onshore) categories were designated as stations higher and equal to 60 (or lower than 60); northern/southern lines occur above/below CalCOFI Line 87 (with the southern category inclusive of Line 87).

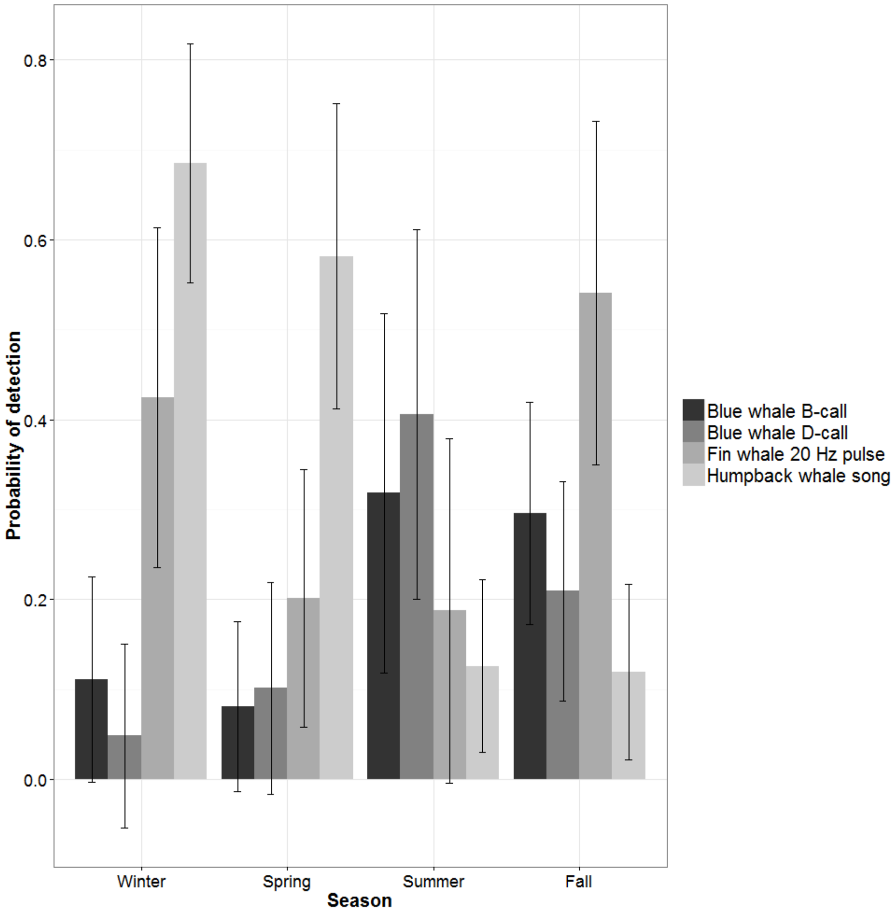

Figure 2.13: Nine year average probability of detection of blue whale B-calls and D-calls, fin whale 20 Hz pulses, and humpback whale song within the CalCOFI sampling grid. Error bars represent 95% confidence intervals.

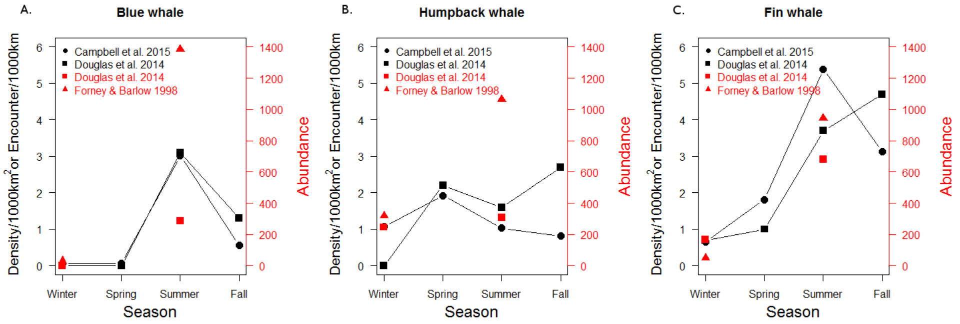

Figure 2.14: Various seasonal indices of abundance, density, or encounter rate based on visual detection for A. blue whales, B. humpback whales, and C. fin whales in the southern California region.

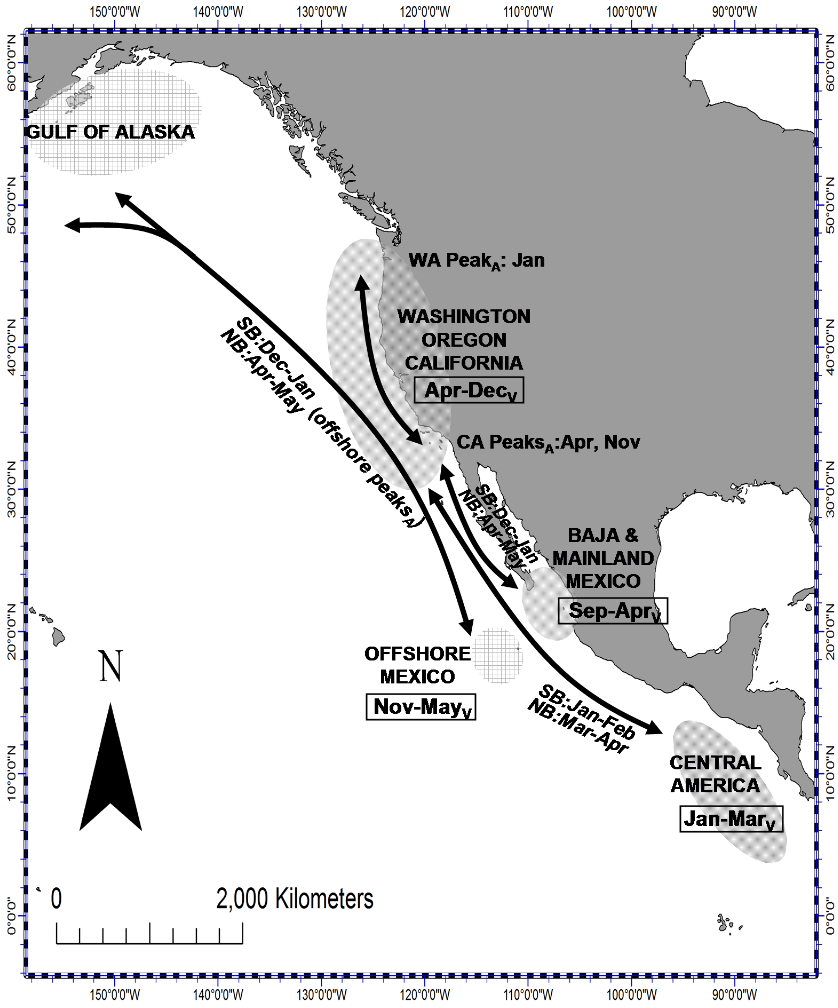

Figure 2.15: Hypothesized migrational movements and timing in breeding and feeding regions in the northeastern Pacific Ocean for humpback whales based on acoustic and visual records from this study and (Steiger et al., 1991; Calambokidis et al., 2000, 2001; Calambokidis, 2008; Trickey et al., 2015; Helble, 2013; Norris et al., 1999) and E. Jimenez [pers. comm.]. 'A' subscript refers to 'acoustic' and 'V' subscript refers to 'visual' dates of occupancy in each region. WA is Washington state, SB refers to southbound migration, NB refers to northbound migration. Hatched areas refer to subpopulations within the northeast Pacific Ocean although interchange between areas has been documented. Lines represent connections between feeding and breeding grounds and do not represent actual migration pathways.

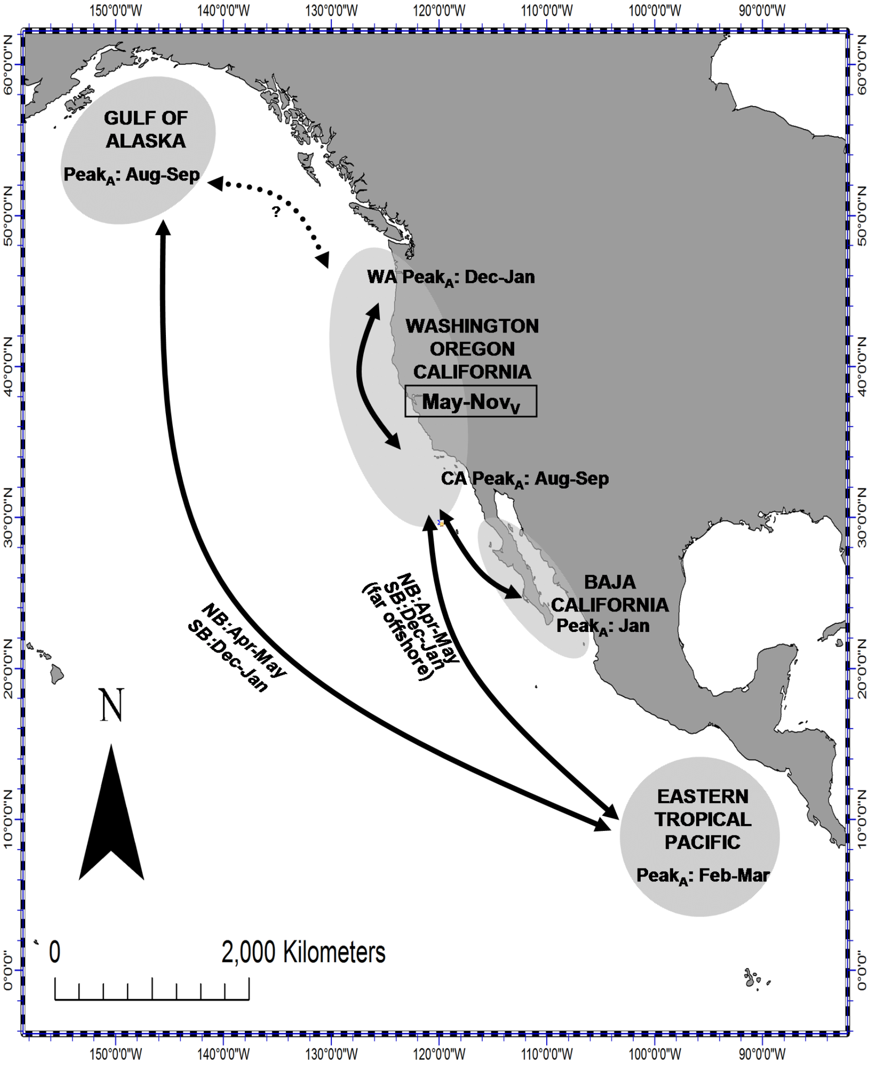

Figure 2.16: Hypothesized migrational movements and timing in breeding and feeding regions in the northeastern Pacific Ocean for blue whales based on acoustic and visual records from this study and (Reilly, 1990; Stafford et al., 2001; Etnoyer et al., 2006; Pardo et al., 2013; Trickey et al., 2015; Debich, 2014) and E. Oleson [pers. comm.]. ‘A’ subscript refers to ‘acoustic’ and ‘V’ subscript refers to ‘visual’ dates of occupancy in each region. WA is Washington state, SB refers to southbound migration, NB refers to northbound migration. Hatched areas refer to a possible subpopulation within the northeast Pacific Ocean although interchange between areas is possible. Lines represent connections between feeding and breeding grounds and do not represent actual migration pathways.

Table 2.1: Precision (fraction of true positives over true positives and false positives) and recall (fraction of true positives over true positives and false negatives) rates for each HARP deployment for B-call and D-call detection efforts. *A detection kernel used from a previous deployment. **No true detections present and recall rate could not be calculated.

HARP			
	B-call		**D-call**
	Precision	Recall	Recall
CINMS 12	.86*	.83*	.71
CINMS 13	.86	.87	.67
CINMS 15	.93	.95	**
CINMS 16	.81	.84	.72
CINMS 17	.94	.93	**
CINMS 18	.89	.84	.67
CINMS 19	.88	.88	.67
CINMS 20	.97	.95	**
CINMS 21	.88	.64	.85
CINMS 22	.92	.82	**

Table 2.2: Seasonal length, midpoint, and mean for each call type pooled over 4 years. Seasonal length was determined by number of days between first and last detection. Seasonal midpoint was calculated as the halfway point between first and last detections of each call type. Seasonal mean (i.e. 'peak' of the year) is the calendar date of the mean of the circular distribution of detections. For length and midpoint, the first detection after March 1st was considered the first detection of the year based on historical knowledge of typical first arrival dates of these species on the feeding grounds.

Call Type	Seasonal Length (days)	Seasonal Midpoint (Calendar Day)	Seasonal Mean (Calendar Day) [95% CI in days]
B-calls & D-calls	355	Aug 26	Sep 13 [<1]
B-calls	274	Oct 5	Sep 16 [<1]
D-calls	335	Aug 16	Jul 4 [1]
B-call (hourly presence)	274	Oct 5	Sep 17 [3]
Humpback song (hourly presence)	272	Sep 1	Jan 21 [7]
		(fall peak)	Nov 8 [3]
		(spring peak)	Mar 26 [3]

Table 2.3: Results of Watson-Wheeler tests of homogeneity of means comparing the seasonal timing between blue whale and humpback whale call types for four years of acoustic listening effort from 2010 to 2013. Reported values of W, the statistic of the test, and p-values are provided for each comparison.

Comparison	N	Watson-Wheeler Test	
		W	p-value
B-call vs. D-call	255,896 ; 20,165	26889	<.001
B-call vs. Humpback song	8,921 ; 3,671	2944	<.001
B-call vs. Fall peak humpback song	8,921 ; 1,841	1323	<.001
B-call vs. Spring peak humpback song	8,921 ; 1,830	3699	<.001

Table 2.4: Test results of logistic regression analysis of spatial variability. Drop-in-deviance statistics (D), associated p-values (p) and the model coefficients (C) are reported for each season. Significance: *$0.05 > p > 0.01$,**$0.01 > p > 0.001$,*** $p < 0.001$

Blue whale B-call	D	p	C
Winter	2.70	$p = 0.10$	-0.0061
Spring	4.46	$p = 0.03$*	-0.0073
Summer	22.67	$p < 0.001$***	-0.0093
Fall	8.28	$p = 0.004$**	-0.0059

Blue whale D-call	D	p	C
Winter	4.73	$p = 0.03$*	-0.0109
Spring	1.02	$p = 0.31$	-0.0029
Summer	2.75	$p = 0.10$	-0.0027
Fall	0.37	$p = 0.54$	0.0013

Fin whale pulse	D	p	C
Winter	0.03	$p = 0.86$	-.00004
Spring	11.01	$p < 0.001$***	-0.0099
Summer	7.56	$p = 0.006$**	-0.0060
Fall	13.50	$p < 0.001$***	-0.0069

Humpback whale song	D	p	C
Winter	27.97	$p < 0.001$***	0.0142
Spring	5.53	$p = 0.02$*	0.0047
Summer	9.43	$p = 0.002$**	-0.0095
Fall	0.16	$p = 0.69$	0.0010

Chapter 3

Year-round habitat modelling of blue, fin, and humpback whale acoustic presence on a southern California feeding ground

3.1 Introduction

The environment in which animals occur is often heterogeneous and therefore is expected to influence the distribution of animals based on preferential environmental factors. Habitat models are a widely used tool for explaining and predicting the likely occurrence of animal species both on land and in the oceans (Guisan and Zimmermann, 2000; Redfern et al., 2006). These models merge a variety of environmental information with knowledge on the presence of a given species with the aim of finding a relationship between the environment and the likelihood a species could be found in it. This approach is used extensively in the marine environment where visual information on the presence of a given species is frequently difficult to obtain given the difficulty of working in a vast ocean characterized by often inclement weather, and the fact that marine animals spend most or all of their time underwater and out of sight. Marine mammals are a highly mobile taxon for which the presence and seasonal behavior are of importance for both monitoring and management of species. Therefore, the modelling of their habitat has been done extensively throughout the Pacific (Becker et al., 2012; Reilly and Fiedler, 1994; Forney et al., 2015) and Atlantic (Hamazaki, 2002; Baumgartner et al., 2001) Oceans, and elsewhere (Hedley and Buckland, 2004).

The dynamic California Current Ecosystem (CCE) is one of the most productive marine environments in the North Pacific Ocean (Hickey, 1979; Block et al., 2011). Such productivity appears to drive the occurence of a large number of marine mammal species. Three species, the blue whale (*Balaenoptera musculus*), fin whale (*Balaenoptera physalus*) and humpback whale (*Megaptera novaeangliae*), are known to routinely visit the CCE as part of their seasonal migration cycles. The blue and humpback whale species perform basin-wide migrations, whereby they spend winter breeding months in low latitude breeding grounds and summer months in higher latitudes (e.g. temperate and sub-polar) feeding grounds (Reilly and Thayer, 1990; Mate et al., 1999; Calambokidis et al., 1990, 2001). While there is an underlying, migration-driven seasonal cycle which dictates the occurrence of these species, the particular details of how the dynamics of the environment influence the occurrence of these species on a seasonal timescale is less well known. This study used acoustic evidence to investigate the environmental factors that influence baleen whale occurrence off southern California on an intra-annual timescale.

3.1.1 Regional oceanography

The confluence of an eastern boundary current and complex bathymetric features create a highly productive region in the southern part of the CCE. The Southern California Bight (SCB) is the region from Point Conception to Ensenada, Mexico inshore of the Santa Rosa Ridge where the California land mass curves eastward, north of approximately 30^oN, and including the Channel Islands. The SCB is a highly productive and complex region with many interacting oceanographic and bathymetric features including basins, ridges, seamounts, canyons, banks, islands, and a slope along the 2,000 m isobath (Jackson, 1986). There are various currents that dominate the region, including the equatorward flowing eastern boundary current, also known as the California Current (the eastern limb of the large-scale, anticyclonic North Pacific gyre), and the Southern California Eddy, an offshoot of the California Current that forms a large counterclockwise gyre within the SCB (Checkley and Barth, 2009; Lynn and Simpson, 1987). The southern CCE contains a confluence of various distinct source water masses with varying hydrographic properties which can be used to track water origins of the major currents (Simpson, 1984). These source waters include the aforementioned cold, low salinity, fresh water of the California Current reflecting its subarctic origins. The western edge of the California Current becomes increasingly warm and salty upon mixing with North Pacific Gyre waters. There is also the northward-flowing, warmer, high salinity, high nutrient, and low oxygen waters (consisting of the Davidson current and the California Undercurrent) with origins in the Equatorial Pacific (Hickey, 1979; Castro et al., 2001). Finally, there is coastally upwelled water which is characterized as cold, salty, high nutrient and low oxygen (Sverdrup, 1938).

Oceanographic features, in the form of currents, counter-currents, frontal features, island wakes, mesoscale and sub-mesoscale eddies vary in strength seasonally and may result in high-productivity events (Jackson, 1986; Caldeira et al., 2005; Stegmann and Schwing, 2007). The variability in strength is mediated by several factors including the Aleutian Low and North Pacific High pressure systems (Checkley and Barth, 2009). The California Current is seasonally at its strongest and closest to shore in spring when there is predominantly equatorward flow. The poleward-flowing waters dominate in summer and fall and push the California Current further offshore. The meeting of various currents forms strong mesoscale eddies, which have been shown to play an important role in zooplankton and fish larvae retention (Logerwell and Smith, 2001) and tend to be strongest in summer and fall. Finally, a major contributor to the productivity of the SCB and surrounding waters is equatorward wind in the late spring and summer which creates an offshore flow and upwelling of cold, nutrient-rich water near the coast (Checkley and Barth, 2009). Along the continential slope, an upwelling regime dominates the overall oceanography of the region. The areas further offshore, outside of the SCB are less variable in oceanographic phenomena.

3.1.2 Seasonality of baleen whale occurrence and distribution

Blue whale presence inferred from visuals and acoustics in the northeastern Pacific Ocean

Blue whales spend the winter and early spring months in Mexican waters and offshore Central America near the oceanographic feature known as the Costa Rica Dome (Reilly, 1990; Stafford et al., 1999, 2001; Bailey et al., 2009). As the year progresses to late spring, summer, and fall months, this population of blue whales are seen and heard off of Baja California, California, Oregon, Washington and the Gulf of Alaska (Oleson et al., 2007c; Burtenshaw et al., 2004; Trickey et al., 2015; Debich, 2014; Stafford, 2003; Debich, 2014; Trickey et al., 2015).

Acoustic information on blue whales has been useful for the study of seasonal occurrence and distribution of these elusive animals. Blue whale vocalizations occur in the 20-100 Hz, low-frequency range. They are known to produce at least three call types in the eastern North Pacific (Oleson et al., 2007a; McDonald et al., 2006; Thompson et al., 1996; Rivers, 1997): A-, B-, and D-calls. A- and B-calls (∼10-20 second duration) are pulsed or tonal in character, respectively, and occur in repeated sequences. They are only produced by males and, therefore, likely have a reproductive function, serving for mate attraction and long-range communication (McDonald et al., 2001; Oleson et al., 2007b). D-calls (down-sweep from 90-25 Hz, ∼1-4 second duration) are highly variable in frequency and temporal characteristics, are recorded from both males and females, and are produced in a foraging context (Oleson et al., 2007b).

In the eastern tropical Pacific, a peak in reproductive calling (i.e. B-calls) occurs in February and March (Stafford et al., 2001). As the year progresses, blue whale D-calls are recorded in the southern California area from April to November while B-calls are recorded from June to January (Oleson et al., 2007a). Acoustic monitoring in other areas of the higher-latitude feeding areas show either similar patterns (e.g. in Gulf of Alaska; Debich (2014); Stafford (2003)) or an extension of peak reproductive calling behavior into December, January, and February as off Oregon and Washington (Burtenshaw et al., 2004; Trickey et al., 2015).

Humpback whale presence inferred from visuals and acoustics in the northeastern Pacific Ocean

North eastern Pacific Ocean humpback whales are found in warmer, tropical breeding areas in low latitudes (e.g., mainland and Baja Mexico, and Central America) during the winter breeding period (Steiger et al., 1991; Calambokidis et al., 2000). They feed primarily along the Pacific Rim in California/Oregon/Washington (Calambokidis et al., 2001, 1996) during the summer. Humpback whales are known to have dichotomous calling behavior where males sing long, complex, repetitive song (Payne and McVay, 1971), inferring a reproductive function, while both males and females make social sounds (Dunlop et al., 2008). Although the structure and function of their vocalizations, especially song (Payne and McVay, 1971), have been well studied, the only reports of year-round acoustic effort and presence for this population include a winter and early spring presence in low latitudes (Watkins et al., 2000), bimodal (October, April) peaks in acoustic presence off central California (Helble, 2013), and opportunistic singing detection during migration (Norris et al., 1999).

Fin whale visual and acoustic presence in the northeastern Pacific Ocean

Fin whales, in contrast to blue whales, are present in the southern California area year-round, with peak numbers in late summer and early fall (Barlow, 1995; Sirovic et al., 2012). Less is known about their residence in the area, with working hypotheses of a resident population, and/or complex within-area migration (Sirovic et al., 2015). Recent visual surveys suggest that fin whales use nearshore waters in the winter and spring and shift to offshore waters in the summer and fall (Douglas et al., 2014; Campbell et al., 2015). Fin whales produce at least two types of call in this area: 20 Hz and 40 Hz. Each call lasts about 1 sec in duration in a downswept pulse. The 20 Hz calls sweep in frequency from 23 to 18 Hz (Watkins, 1981) and 40 Hz calls sweep from 62 to 48 Hz (Sirovic et al., 2012). The function of these calls may be inferred from the pattern in which they are produced; songs consist of stereotypic sequences of the down-swept 20 Hz pulses organized into regularly repeated sequences. These patterns are sung only by males and therefore confer a reproductive function (Croll et al., 2002). Irregular, non-song sequences also occur and have hypothesized social function.

3.1.3 Behavioral context

The majority of quantitative models of cetacean distribution based on habitat are typically built from visual survey data conducted from a shipboard platforms (Forney, 2000; Hamazaki, 2002). Because visual surveys were primarily used, past habitat models largely ignore the behavioral state of the whale. Behavioral state is a valuable addition to understanding species presence and area usage since it provides an insight into the biological importance of a given region to the species in question. Although high biological productivity and visual evidence of feeding events support the idea that the southern California region is a recognized feeding area (Barlow et al., 2011), reproductive calling also occurs (Oleson et al., 2007c), suggesting mixed used of habitat and potential for flexible switching between reproductive, social, and foraging behavior.

In addition to visual effort, an increasing number of research programs have considered acoustics as an additional component of their research due to the proliferation of long-term passive acoustic recording capability, rendering these type of data more readily available (Barlow and Taylor, 2005; Swartz et al., 2003). Furthermore, standalone acoustic programs allow high resolution data at a considerably reduced cost when compared to visual-based logistical cost constraints. Therefore, the incorporation of acoustic data to characterization of cetacean distribution and habitat is a natural step towards building robust models (Hastie et al., 2005; Soldevilla, 2008; Merkens, 2013) which include detections of (vocalizing) animals not at the surface.

3.1.4 Environmental influences on baleen whale distribution

Significant species-habitat relationships occur on traditional breeding grounds. For example, dynamic variables that favor seasonal productivity have influenced blue whales occupancy in the Costa Rica Dome (Ballance et al., 2006; Reilly, 1990). Significant species-habitat relationships also have been shown to occur on traditional feeding grounds. For example, humpback whales off the coast British Columbia and the Bering Sea strongly associate with bathymetric features, such as depth, slope or distance to a specified isobath (Dalla Rosa et al., 2012; Moore et al., 2002a). Extensive research in the CCE has shown that cetacean occurrence and density is significantly affected by a suite of habitat variables spanning the same aforementioned categories: static (bathymetric depth, slope), oceanographic (temperature, salinity) and variables which represent biological production (e.g., chlorophyll) (Barlow et al., 2009; Becker et al., 2012; Forney et al., 2012).

Despite the extensive research performed for these regions, the scope of these studies have been limited in temporal scales. The temporal coverage has been incomplete due to the difficulty of sampling during certain times of the year. Past habitat models have largely focused on summer and fall seasons, when most visual surveys are conducted and thereby missing scarce, but valuable winter and spring coverage. This study used year-round acoustic detections of blue, fin, and humpback whales in order to investigate the environmental factors which best predict the occurrence of these species. This study also addressed the behavioral state of the whale in order to test which environmental predictor variables are important in different behavioral contexts associated with specific call types.

3.1.5 Hypotheses

I investigated the hypotheses that the inclusion of readily available oceanographic predictor variables results in better descriptive models of baleen whale calling occurrence than the null model. I expected to find that the foraging calls types were best modelled using environmental variables that are associated with high productivity. I expected to find an overlap in habitat variables selected for blue whales and humpback whales for analogous reproductive call types.

3.2 Methods

Baleen whale presence inferred from their calls was modelled using a variety of environmental variables. Multivariate models were considered. Several steps were employed in order to align the available data for optimal use in the habitat modelling method of choice (Figure 3.3). Description of data collection, analyses, and modelling methods are described in the sections below.

3.2.1 Study area and data collection

Baleen whale acoustic presence (humpback song, blue whale D-calls, blue whale B-calls, fin whale 20 Hz pulses; see Figure 3.2) was manually detected from recording effort aboard 35 cruises from 2004 to 2012. Acoustic data were collected as a part of the marine mammal component of the CalCOFI program (California Cooperative Oceanic Fisheries Investigations; calcofi.org; Figure 2.1), a multi-agency partnership formed in 1949 to investigate the collapse of the sardine population off California. The program operates quarterly cruises (spanning 17 to 30 days in duration) and collects a large suite of hydrographic, environmental, and biological data covering a large area off the west coast of the United States in a systematic grid of monitoring stations. The core CalCOFI sampling scheme covers gridlines normal to the California coast covering the areas between San Diego and Avila Beach, CA and samples up to 600 km offshore, spanning the inshore and offshore regions of the southern California region. Since 2004, a marine mammal component was added to the CalCOFI program, adding visual and acoustic sampling of cetaceans along the designated CalCOFI grid lines. CalCOFI stations with numbers 45 and lower lie within the Southern California Bight. CalCOFI stations with numbers 53 and higher lie to the west of the bathymetric ridge and are outside of the Bight. Spacing between the transect lines and the distance between standard stations is 40 nm (74 km). Nearshore stations are half or less of this spacing.

During cruises, acoustic data were collected from Directional Frequency Analysis and Recording (DIFAR) and omnidirectional sonobuoys (Ultra Electronics Inc.) at CalCOFI stations that were sampled during daylight hours (with the exception of the fall cruise in 2004 when additional personnel allowed for night time monitoring). Equipment permitting, two sonobuoys were deployed at each CalCOFI station. DIFAR (AN/SSQ 53 D/E/F) sonobuoys contained a directional hydrophone with a bandwidth from 10 to 2,400 Hz. Omnidirectional (AN/SSQ 57 B) sonobuoys contained a hydrophone with a bandwidth from 10 to 20,000 Hz. Upon deployment, sonobuoys inflated a flotation device and release a hydrophone to a pre-set depth ranging from 90 to 1000 feet. Signals recorded on sonobuoys were transmitted via a single radio carrier frequency and were received using an omnidirectional VHF Diamond Antenna and P160VDG preamplifier (Advanced

Receiver Research) mounted on a mast of the ship. The preamplifier was connected to a 100 meter coaxial cable and signals were received with two ICOM radio receivers modified for low-frequency response (Greeneridge Sciences). Received signals were digitized with a sound board (Creative Labs Soundblaster Audigy and Realtek Corp. Avance Logic; both 24-bit), and signals were recorded on a personal computer using the software program LOGGER (Douglas Gillespie, International Fund for Animal Welfare). Sonobuoys were programmed to scuttle automatically after a maximum of 8 hours after deployment. Sonobuoy models used in this study included DIFAR and Omnidirections models of AN/SSQ 53F, 53E, 53D, and 57B with sampling rates between 4 and 48 kHz.

3.2.2 Sonobuoy signal processing

Each sonobuoy deployment lasted between 1 and 8 hours. For this study, the presence/absence of at least one call detection within the first two hours of the recording was noted for each call type studied. Acoustic data were analyzed visually via spectrograms using the Matlab-based custom software Triton version 1.81 by a single experienced analyst. To minimize variation in the analyst's ability to accurately define call types within the spectrogram, I standardized viewing window parameters (e.g., contrast and brightness of the call, the size of the window, duration shown in each window, and visible bandwidth) and the analysis parameters (e.g., FFT length and percent overlap) to ensure consistent time and frequency resolution across sonobuoy recordings. The original data had sampling rates between 4,800 and 48,000 Hz and were decimated from its original form to a uniform bandwidth ranging from 10-2,400 Hz. Decimated files were scrutinized in 60s windows between 0-200 Hz for fin whale and blue whale calls, and between 0-500 Hz for humpback whale calls, in 1 Hz bins with 90% temporal overlap. Even though humpback whale song units can be detected at a much higher frequency range, at least parts of the calls can be seen at lower frequencies between zero and 500 Hz. Whenever a partial humpback call was detected, the analysis window was expanded up to 1000 Hz to ensure that all humpback calls were correctly identified and no false positives were logged. The quality of recording data was annotated as 'Poor', 'Medium', or 'High' for each hourly presence. The quality of data was assessed based on the presence of background noise (e.g. ship noise, flow, swells, etc.) and technical problems (e.g. radio interference, patchy signal, instrument failure, etc.). Data denoted with 'Poor' quality had noise interruptions for greater than ~60% of the hour, 'Medium' quality data was free of noise for between 40% and 60% of the hour, and the score of 'High' was given to data clear of noise for less than 20% of an hour.

3.2.3 Environmental data processing and analyses

Routine CalCOFI stations included deployment of a SeaBird CTD instrument with a 24-place rosette, each with 10-L PVC Niskin bottles. Sampling casts were made to 500 m depth, or shallower, depending on bottom depth. Continuous measurements of pressure, temperature, conductivity, dissolved oxygen and chlorophyll fluorescence are taken during the casts.

A final candidate list of variables to be considered in the model selection process was determined by eliminating all collinear variables as necessary. Elimination of collinear covariates were conducted by analyses of pairwise correlation coefficients and variable inflation factors (version R 3.1.2, package RandomForest). The final variables included in the model were temperature at surface, salinity at surface, concentration of chlorophyll at surface, the magnitude of the thermocline, and mixed layer depth (Table 3.1). Depth (m) and bottom slope (in degrees) were derived from bathymetric data using Spatial Analyst in ArcGIS.

Acoustic detection range

We included an additional ‘weighted detection range’ co-variate in order to account for the station-specific differences which might result in different propagation characteristics and, consequently, different detection ranges at the various CalCOFI sampling stations. We assigned a range of 0-1 for ‘weighted detection range’, with 0 representing no detection capability and 1 representing maximum detection range. We created five categories with weighted values of 0, .25, .5, .75, and 1.0, representing shallow and deep environments, as well as environments where sound could be blocked by heavily sloped bathymetry and/or above-surface land masses (such as the coastline or the Channel Islands). Each stations was analyzed and assigned a weight based on depth and distance to nearlest shore. The process for assigning weighted detection range resulted in similar values for blue whale D-calls and humpback song, and for blue whale B-calls and fin whale pulses due to the similarity of source levels and frequency characteristics of the call types.

3.2.4 Modelling framework

Acoustic and environmental measurements from the same station sampling were modelled using a generalized additive mixed modelling (GAMM) framework to identify the most significant habitat variables that explain the calling presence of these whales in southern California. GAMMs allow for investigation into the relationships between whale detections and environmental factors via a non-linear framework (Hastie and Tibshirani, 1990). Generalized additive models (GAMs) incorporate fixed effects and represent an extension of the generalized linear model (GLM), but do not constrain the relationship between y and x to be linear or of any particular function. GAMMs allow for additional model terms to represent the random effects. These models can be represented by:

$$GAM : g(E(Y)) = X_m\beta + f_1(x_1) + f_2(x_2) + ... + f_m(x_m) \tag{3.1}$$

$$GAMM : g(E(Y)) = X_m\beta + f_1(x_1) + f_2(x_2) + ... + f_m(x_m) + X_i\alpha \tag{3.2}$$

where E(Y) are the estimates of the normal or non-normal response variable (e.g. baleen whale acoustic detections) and g is the link function with a given distribution function. The link function addresses the non-normally distributed response data. $X_m\beta$ represents an intercept parameter, $X_i\alpha$ represents a random term, and the f_m smoothing functions can be parametric or non-parametric (e.g. functions comprised of smoothing splines or LOESS smoothing functions).

Call detection during a two hour monitoring period was approximated with a binomial family and a logit link. A cyclic cubic regression smooth was applied to the seasonal temporal variable, which allows for the last month of the year to be smoothly connected with the first. The other functions were constructed with cubic regression smoothing splines with shrinkage, which allows for third order polynomials to be fit on segments of data and allows for the smoothness selection to approach zero term completely. Each spline was applied with a maximum of 3 degrees of freedom in order to prevent overfitting and an overly complex model which may be difficult to interpret ecologically (Forney, 2000; Ferguson et al., 2006). All iterations of models were used with year as a random effect to account for the sampling constraint of repeated stations (i.e. nested) within each year of sampling. Because there is no formalized way to estimate deviance explained for GAMMs (Wood, 2006), we followed the approach used by (Gilman et al., 2012) of fitting an equivalent GAM to derive the measure of GAM goodness-of-fit, taking the residuals, and fitting an intercept-only model with year as the random term. If the random term is significant, as determined by likelihood ratio tests, we then can assume the goodness-of-fit for various parameters in the GAM equivalent of each final model as the minimum deviance explained. All GAMs and GAMMs were fitted using the mgcv package for R version 3.1.2. An added modelling parameter of setting Gamma to 1.4 allowed for an additional check on overfitting (Wood, 2006).

3.2.5 Model selection

Due to a priori knowledge of the seasonality of whale presence as well as the spatial heterogeneity of calling within the study grid, we constructed 'base' models with a seasonal factor and its interaction to depth (a crude proxy for distance to shore) for all call types. Based on the exploratory analyses of these base models, we chose to augment the models with permutations of the set of variables listed in Table 3.1. The best-fit models were compared using the Aikake Information Criterion (AIC) values defined as:

$$AIC = -2(log(likelihood)) + 2K \tag{3.3}$$

where K represents the number of parameters included in the model fit. Models with the lowest AIC values were chosen as the final model. On occasion, post-hoc analyses of the 'best' fit models showed insigificant model terms in the final model. Therefore, a backwards selection process was implemented to inspect candidates for removal in order to achieve a model with only significant terms. We provide plots of partial model fits of each parameter on the entire 9-year dataset for qualitative evaluation. These partial fits demonstrate the influence of individual significant predictor variables on cetacean acoustic presence in final models.

3.2.6 Spatial considerations

Spatial autocorrelation is a concern when modelling environmental variables to baleen whale distribution. The acoustic range of baleen whale call types is potentially on the order of 10's of km. Additionally, the degree to which marine mammals are clustered or dispersed may lead to erroneous conclusions if they do not align with the scale of spatial features of interest. To address possible effects of spatial autocorrelation, the model selection process was performed on datasets binned at three different spatial scales. In the first category, we treated each sampled station as a single unit of effort. Next, we pooled stations into adjacent clusters of 4 which represented approximately 80 x 80 km spatial bins. Last, we pooled clusters of 9 stations resulting in approximately 120 x 120 km grids (Figure 3.4). We expect the central tendancy of the results at these three spatial scales to be the same if spatial autocorrelation is not a concern.

3.3 Results

Using a suite of seasonal, bathymetric, and oceanographic covariates to explain the acoustic presence of four call types, the temporal factor of month was shown to be the biggest contributor to explained variance in the selected models. All three species revealed strong seasonal forcing but not all call types were predicted by the physical oceanography of the region (Table 3.2). Humpback whales showed a seasonal trend in habitat use, with an interaction of depth (and correponding onshore/offshore distribution) on season. Blue whales producing B-calls displayed an increasing trend with shallower depths. In contrast, calling fin whales had nonlinear relationships with depth throughout the year.

On average, the selected final models correctly classified ∼18% of observations. Explained variance was highest for humpback whale song (23%) which included only seasonal and depth covariates. Blue whale D-calls were best explained with month (11%). Blue whale B-call and fin whale models significantly improved in goodness-of-fit with the addition of oceanographic covariates. Specifically, the explained variance using the best-fit model with only temporal predictors was never greater than 14%. When oceanographic covariates were included, explained variability in calling presence increased from 10% to 19% for fin whale pulses.

3.3.1 Blue whale B-call

The final selected model for the blue whale B-calls included sea surface temperature (SST), depth, and detection range (R^2=.17). B-call acoustic presence decreased with increasing depth and leveled off with increasing temperature (Figure 3.5). A linear fit between detection range and acoustic presence showed that B-calls were more likely to be detected at the offshore stations.

3.3.2 Blue whale D-call

The final selected model for the blue whale D-calls included only a temporal factor: month (R^2=.11). The highest probability of D-call acoustic detection was in the summer months (Figure 3.6).

3.3.3 Humpback whale song

The final selected model for the humpback whale song included month, depth, and their interaction across the four seasons (R^2=.23). There was a strong seasonal signal during the winter and spring cruises (Figure 3.8). The positive, near-linear relationship with depth indicates these whales are heard in winter and spring offshore. No additional oceanographic covariates were significant for the humpback whale song model.

3.3.4 Fin whale 20 Hz

The final selected model for the fin whale 20 Hz pulses included month, depth, their interaction, and the seasonal anomaly of mixed layer depth (MLD) (R^2=.19). There was a slight preference for the shelf edge during fall and winter months (Figure 3.7). An additional oceanographic variable was significant; the seasonal anomaly for MLD was chosen with negative anomalies predicting higher probability of detection (Figure 3.7).

3.3.5 Spatial scale

While the smallest spatial scale allowed for model selection of oceanographic terms, these terms were dropped as spatial scales increased (except for B-calls, which retained SST throughout the range of spatial scales). The best predictors across all call types (except for B-calls) were either season, depth, or both (with their interaction; Table 3.3).

3.4 Discussion

These results offer a new seasonal look at distribution and habitat use patterns of blue, fin, and humpback whales. This study demonstrates that calling baleen whales are strongly associated with time of year and bathymetric features, though responses varied across species. All call types, except for B-calls, were associated with month. All call types, except for D-calls, were associated with depth. Humpback whale song was not influenced by an additional oceanographic variable; season and depth were the best predictors. Overall, the hypothesis that the inclusion of readily available oceanographic explanatory variables (not including seasonal or bathymetric variables) would result in better explanatory models of baleen whale occurrence was only supported by the inclusion of SST and MLD as important explanatory variables of blue whales and fin whales, respectively.

A comprehensive study which aimed to predict cetacean densities from habitat modelling (Barlow et al., 2009) showed that more oceanographic and biologically relevant variables were important for predicting cetacean densities in the CCE than determined for this study. In that study, all three species' encounter rate models were determined by, at minimum, bathymetric factors (depth, slope, and distance to the 2000 m isobath), SST, and Beaufort sea state. For predicting the encounter rate of fin whales and humpback whales, CV(SST) was additionally important. Blue whale encounter rate was predicted by the aforementioned variables as well as MLD, chlorophyll, and salinity. These models, built from a multi-year, bioregion-wide dataset of line-transect visual surveys, stand in contrast to the simpler models built from passive acoustic data in the current study. However, the explained deviance for the visual-based models ranged from 9% (fin whales) to 22% (blue whales) and 33% (humpback whale) which are similar values to that determined in the current study (Figure 3.2) and therefore highlights the need to explore other possible influences that can account for the yet unexplained variance. These visual-based surveys were conducted during the summer and fall months and lack the year-round temporal coverage that is needed to sample humpback and fin whale individuals that still occur in the CCE during the winter and spring months.

3.4.1 SST as a seasonal proxy

D-calls were explained by the seasonal factor while the final model for B-calls did not include the monthly seasonal factor. The lack of a seasonal factor was peculiar since month was a strong variable for the rest of the call types. Instead, the main explanatory variable for B-call occurrence was SST, showing higher detection odds in warmer waters and reaching a plateau at around 16^{o}C and higher. SST values exhibited a strong seasonal forcing with the winter and spring months associated with colder SSTs and the summer and fall months with warm SSTs. Upon further investigation, if the B-call model was forced to include the seasonal factor, the only other significant variable in the best-fit model would be depth. If season was removed from model selection, SST was the dominant explanatory variable. SST seasonal anomaly is not significant. Therefore, it can be assumed that for B-calls only, information contained in the SST times series encompasses the variability of seasonality (and therefore serves as a seasonal proxy), but the SST time series doesn't outperform the monthly seasonal covariate for the other call types.

3.4.2 Influence of SST

Past studies in the northern Pacific Ocean have shown blue whales and SST to be negatively correlated with a preference for colder temperatures from upwelled, nutrient-rich waters (Croll et al., 1998; Fiedler et al., 1998). In polar regions, there is a positive correlation between blue whale calling distribution and temperature due to sea ice formation (Sirovic and Hildebrand, 2011). Past work in the CCE has shown that there was the greatest number of fin whale encounters in moderate-temperature waters of 1419^{o}C (Becker et al., 2010) while humpback whales seem to prefer colder temperatures (Becker et al., 2010). The functional relationship between SST and blue whale call types in this study show a positive relationship with a plateau above 16°C. The increased sampling during times of the year when blue whales are not usually around has lead to the the best-fit model to included a seasonal factor. To account for this seasonality while testing whether cold SST might matter in the southern CCE, SST seasonal anomaly, which was calculated by taking out the monthly average across all years, was included as a candidate predictor variable. It was not shown to be significant for any of the call type models. We could not, therefore, find evidence of co-location of blue, fin, or humpback whale occurrence in colder SST like that found in past studies.

3.4.3 Influence of mixed layer depth

Anomalously low or shallow MLDs were associated with fin whale 20 Hz pulses. Shallow MLDs appear when there is low water turbulence. The biological consequence of having a shallow MLD may include higher average illumination over the mixed layer depth, with a consequent increase in phytoplankton growth rate integrated over the mixed layer, granting sufficient nutrients provided from deeper waters. Generally, there is balance, defined by a compensation depth (Sverdrup, 1953) where the chances of biological productivity is maximized. An anomalously low MLD would lead to better conditions for phytoplankton blooms and overall productivity of a region, which may lead to an increased occurrence of (acoustically-active) fin whales.

Stratification was suggested to influence right whale (*Eubalaena glacialis*) occupation in the lower Bay of Fundy. Right whales were observed during periods of high surface stratification (Murison and Gaskin, 1989) explained by high prey accumulation at the boundary layer between the water masses at the edge of the mixed layer. This explanation serves as an alternative mechanism from that described above which uses Sverdup's Critical Depth hypothesis to explain blooms during times of more shallow mixed layer depths. Although mixed layer depth, stratification, and other water property-related indices are important, the underlying mechanism to explain its importance to the whale may differ and further investigation is warranted.

3.4.4 Influence of bathymetry

Both humpback whale and fin whale habitat models included significant terms for depth stratified by season. Humpback whales were predicted further offshore during the winter and spring cruises and significantly closer to shore during the summer cruises. Fin whales, on the other hand, showed a nonlinear relationship with a slight peak in occurrence at intermediate depths (∼2000m, near shelf edge). The best model for B-calls did not include seasonally stratified depth terms. Instead, there was an overall trend of higher detection at shallower depths.

Becker et al. [2010] showed blue and humpback whales were most likely visually detected closer to shore. While our models for acoustic occurrence for blue whales concurred with that result, humpback whales were shown to be more acoustically active further from shore during the winter and spring. Only during the summer was there a higher detection of song onshore. The difference in these models highlight the potential insight gained from including year-round data. If we had modelled humpback whale acoustic occurrence using only summer and fall CalCOFI cruises, we would have had similar results to Becker et al. [2010] regarding whale/depth relationships. However, the offshore acoustic occurrence, likely driven by migrating whales engaged in reproductive display, influences our best-fit models to account for the interaction between season and depth in our yearlong view. The dual use of the CalCOFI region as a feeding ground stop-over and/or a region to pass through can be further elucided by independent satellite tag data. This method allowed researchers in Australia to discern between two core areas identified as breeding habitat where one served as a main wintering ground and the other a migration route (Smith et al., 2012). Satellite or other tagging and tracking technology would allow for us to determine the offshore animals as moving or migrating or if there may be an additional reason why offshore presence is heavy.

Slope was shown to be important for blue and humpback whales (Barlow et al., 2009) presumably due to the topographically induced conditions for prey aggregation. However, slope was not included in the best-fit models of this study. The mismatch in spatial scales over which an acoustic detection and its associated slope were measured may account for why slope was significant for any of the call types. Acoustic detections of the call types in this study may be from individuals up to several tens of kilometers away. Acoustic detections, therefore, represent a potentially large integrated area, which potentially encompasses a wide range of slope measurements. Consequently, the slope measured over each individual CalCOFI station may not align in space with the unknown location of the caller. In contrast, visual detection and slope measurement is well matched in space and its inclusion in habitat models predicting visual encounter rate is appropriate.

3.4.5 Influence of biological variables

Chlorophyll was not found to be a significant predictor for any of the call types as shown in other studies using visual- and acoustics-based methods (Burtenshaw et al., 2004; Smith et al., 1986). However, the only other known studies linking passive acoustic detection and habitat (Sirovic and Hildebrand, 2011; Moore et al., 2002b) have found no evidence of a linkage to chlorophyll. Instead the important patterns included warmer SST, deeper depths, less prey biomass (Sirovic and Hildebrand, 2011), and cold SST and oceanic fronts (Moore et al., 2002b). Nevertheless, hypotheses for how whales and chlorophyll are linked need to be refined as there may be top-down control by zooplankton depleting chlorophyll concentration, mitigated by whales feeding on zooplankton.

Results of studies that incorporated a seasonal index into their habitat models resembled these results, showing that species were largely influenced by temporally variable parameters subject to seasonality (in addition to depth and topographical variables) (Anderwald et al., 2012; Henderson et al., 2014). A study that included the spring to summer transition showed changes in habitat preferences between these two seasons in the northern CCE for humpback whales (Tynan et al., 2005), highlighting the need for investigating habitat in as many seasonal periods as possible. For highly mobile, pelagic, migratory, and long-lived species like those in the present study, seasonal indices were shown to be, unsurprisingly, the most important predictor, and therefore should be included in future models whenever possible.

3.4.6 Function of call types

I found no evidence for my hypothesis that foraging calls types were influenced by environmental variables associated with high productivity. Because D-calls have been shown to be generated primarily during foraging behavior, the models predicting D-calls were hypothesized to represent foraging habitat. However, month was the only selected explanatory variable for D-calls. The best model for predicting B-calls, on the other hand, are highly predicted by SST, not only standing in as a proxy for season, but also explaining some amount of variance above the nested model of the seasonal month alone. A positive trend in predicting

B-call presence was most likely a result of more blue whales being in the southern California area during summer and fall. However, as mentioned, season alone did not fit as well as SST and therefore, an unknown function of SST may be influential for B-call production. Since B-calls are known reproductive displays, it is hypothesized that this influence of SST on B-calls may indicate good habitat or good territory that the whales are defending for the purposes of increasing reproductive fitness. However, the hypothesis requires more investigation.

Although we found that both blue and humpback whale reproductive calls were modelled by season and depth, the interactions between season and depth indicate different habitat use patterns for each species. They exhibit different habitat use despite the hypothesized similarity in function of the call type. Blue whale B-calls occurred in shallower depths. Humpback whale song is best modelled by season and deeper depths during the winter and spring, which is driven by the calling that occurs offshore during the times of year humpback whales are known to sing in the Northern Hemisphere. The lack of oceanographic connection to singing may indicate that song is not related to conditions that would lead to enhanced productivity and prey resources. Improving the model for predicting humpback whales requires additional information beyond the simple environmental variables used here.

3.4.7 Data limitations

The statistical analysis of these data was complicated for several reasons. 1) The collected environmental data represent point samples for potentially large areas over which the whale vocalized. 2) There may be temporal correlation and/or spatial correlation, and both may be complicated. 3) The data are irregularly spaced and each station was not sampled at regular time intervals. 4) There was heterogeneity over seasons. 5) There may have been an interannual trend from 2004-2012 that may be non-linear. 6) The acoustic detection ranges for each station changed depending on bathymetry, and weather.

Understanding which environmental factors drive whale distribution is critical for the development of effective management measures, but investigations at appropriate spatial and temporal scales need to occur in order for viable habitat-use patterns to emerge. Because direct observations of whales may be difficult during certain parts of the year, acoustics is a well-suited method for detecting non-zero occurrence of calling whales. Nevertheless, the passive acoustic techniques used in this study faced some issues provided below.

Detection range

While detection ranges for visual effort occur at less than ~10 km (Clark and Fristrup, 1997), passive acoustic methods allow for a larger detection range. Despite the usefulness of acoustic methods, especially for detection of individual callers during inclement weather and thereby increasing the non-zero probability of acoustic detections during the winter and spring, there remain limitations in the use of passive acoustic techniques to investigate habitat-induced distribution of acoustically active whales. First, the call types used in this study are likely omni-directional and may be detected from up to 10's of kilometers away. Of the four call types used in this study, blue whale B-calls and fin whale 20 Hz pulses are potentially the calls that could be detected from the furthest distance. Blue whale B-calls have been located up to 10's of kilometers away (McDonald et al., 2001) but under ideal propagation circumstances, may be detected hundreds of kilometers away (Stafford et al., 1998). Typically the hydrophones were launched to occupy either half the water column in shallow environments or up to 333m depth in the deep water environments. The relatively near-surface depths of the sonobuoy hydrophones and the downward refracting sound-speed profile of the shelf and deep waters likely limit the acoustic detection range in this study to tens of kilometers.

Our inclusion of a weighted detection range co-variate was intended to account for the variability in detection area for each call type due to sound transmission properties of the water column and other propagation characteristics at each sampling station. While the weighted detection range variable was insigificant for most models, it was included in the best-fit model for predicting B-call occurrence and showed, unsurprisingly, high acoustic detection with an increase in the detection range index. The approach taken in this chapter and the inclusion of the variable for detecting B-calls exemplifies a preliminary attempt to normalize call detections over a known area. If possible, extensive propagation modelling should be done for each acoustic recording station in order to normalize the call detections by area (Sirovic et al., 2015).

Potential effects of noise

Each call type is also subject to variation in call reception due variation in noise levels due to local and distant shipping. Site C, which has been a sampled location in other published studies (Sirovic et al., 2015; McKenna, 2011) is exposed to one of the highest average low-frequency sound levels (e.g., 86 dB re $1\text{Pa}^2/\text{Hz}$ at 40 Hz with maximum levels at 117 dB) when compared to a sample of other sites in the Southern California Bight. Only 25% of measured sound levels at this site was below 80 dB re $1\text{Pa}^2/\text{Hz}$ at 40 Hz 4 (McKenna, 2011). Although not in a shipping lane, the site is exposed to both local ships passing through to the LA/Long Beach Port and distant ships. Therefore, this site is subject to unpredictable variability in noise which can bias call counts (e.g. as shown in (Helble, 2013)).

Scale considerations

There is uncertainty about the spatial and temporal scales at which environmental features may be associated with baleen whale acoustic activity. Investigating distribution at mismatched resolutions may result in misleading predictions (DoniolValcroze et al., 2007). Acoustic detections representing a large area underline the reality that an acoustic detection does not provide exact knowledge of the location of the calling whale. The relationship between the sonobuoy locations and environmental parameters, therefore, does not necessarily reflect the exact relationship between the whales and the environment therein it lies, which potentially explains the poor predictive power of our models.

Mismatched scales may lead to the underdetection or overestimation of the heterogeneity of the habitat as well as the distribution of the animals. Our study shows the central results of our models do not change as we adjust the spatial scales over which we sample. The models at the three investigated spatial scales retain the importance of season and depth as important predictors of all call types. However, the marginal influences of SST and MLD hold true for the habitat models incorporating spatial sampling at the smallest scale. A possible explanation for why oceanographic variables diminish in importance as we increase in spatial scale is that the heterogenetity of the environment may not be sufficiently captured on such large scales. Despite the evidence that spatial variability of an oceanographic feature, such as ocean color, operates on decorrelation length scales of $\sim$150 km (or approximately 2-3 stations) at the latitudes of the CCE study region (Doney et al., 2003), the variability of the highly productive southern California region may not apply in the global models presented by Doney et al. [2003] and mesoscale and submesoscale processes may dominate.

To adequately address the concerns about appropriate temporal and spatial scales, tighter coupling of whales and their environment should occur. Whether detection of whales is done acoustically or visually, future work linking acoustic detections and environmental factors should make certain the tight coupling of species-environment occurrence. Small-scale linkages can be attempted from the acoustic record if localization of calling whales is possible. Or, for passive acoustic methods from long-term recorders, one can restrict call detections to include high SNR calls, translating to a smaller, known detection radius. The improved knowledge on associated habitat may improve predictive power of these acoustic habitat models. Whales tagged with recorders and environmental sensors also provide a viable option when investigating fine-scale habitat use.

Interannual variation

The observed interannual variation from 2001 to 2003 (Oleson et al., 2007c) and Chapter 2 suggested that the specific timing of arrival and migration of individuals fluctuated from year to year. The surveys showed a degree of interannual variability in this region which were addressed by building mixed effects models with year-specific random effects used to explicitly model between-year variation in the data. I modeled this random effect to account for interannual variation without specific expectations for the trajectory of the trend. I was instead interested in testing whether including year as a random effect was significant and adequate to capture the between-year variation. Therefore, I tested the random effects variance components equal to zero and found that including a random effect was necessary. However, future work would be needed in order to answer specific questions about interannual long-term trends and the environmental predictors that influence them.

The climate-induced effects from phenomena like El Nino/La Nina has the potential to influence cetacean distribution and occurrence. However, over the course of the study period from 2004-2012, the described transitions during La Nina conditions in 2007 and from La Nina to El Nino in 2009 have been dampened in the southern California region while heightened in other subregions (McClatchie et al., 2009; Bjorkstedt et al., 2011). Therefore the treatment of year as a random effect is sufficient during the phenomenon-starved time period of this study. However, subsequent years have been influenced by the arrival of anomalously hot water temperatures, the shift towards strong El Nino conditions, and the prevalence of the warm-water Blob. Such major changes might require different approaches to analyses of the data to account for strong, interannual variability.

3.5 Conclusions

This study distilled information from quarterly surveys occurring over 9 years with the purposes of determining which, if any, environmental predictors influence the distribution of calling baleen whales. These surveys provide a 2-week snapshop at quarterly conditions within a dynamic oceanic ecosystem.

There are few studies with consistent year-round effort of near-continuous temporal coverage and wide spatial coverage which are necessary for studying the ecology of wide-ranging, migratory baleen whales. The analytical framework used in this study highlighted the spatio-temporal patterns of call types of blue, fin, and humpback whales and has potential application for other species. The influence of a seasonal factor and depth on whale acoustic occurrence was robust on all spatial scales while investigations on the smallest spatial scale revealed marginal influence of SST on blue whales and MLD on fin whales. It is important to understand the relationship between these whale species and the dynamic, upwelling-dominated CCE region, as climatic changes will likely occur and habitat range expansion and differentiation for these species will inevitably follow. Consequently, the success of identifying relevant variables and critical habitat can be used in development of management strategies for these mobile top predators (Dalla Rosa et al., 2012; Redfern et al., 2013).

3.6 Acknowledgments

The authors gratefully acknowledge the efforts of all those involved in the collection of these data, especially SWAL lab engineers and numerous field volunteers from 2004-2012 as well as the scientific and operational crew of the various vessels of CalCOFI cruises past. We gratefully acknowledge the funding support of Frank Stone, Ernie Young, and Linda Petitpas at the Chief of Naval Operations, division N45, and Curt Collins at the Naval Postgraduate School.

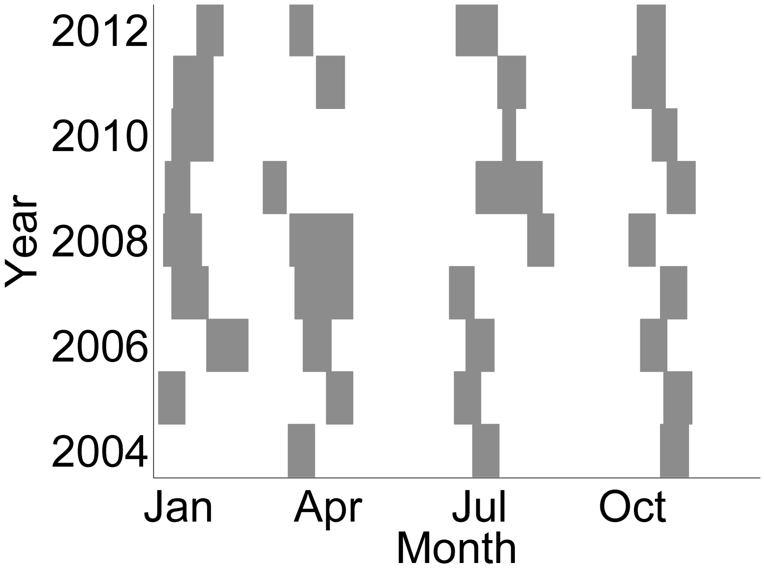

Figure 3.1: Dates of CalCOFI cruises from spring 2004- fall 2012.

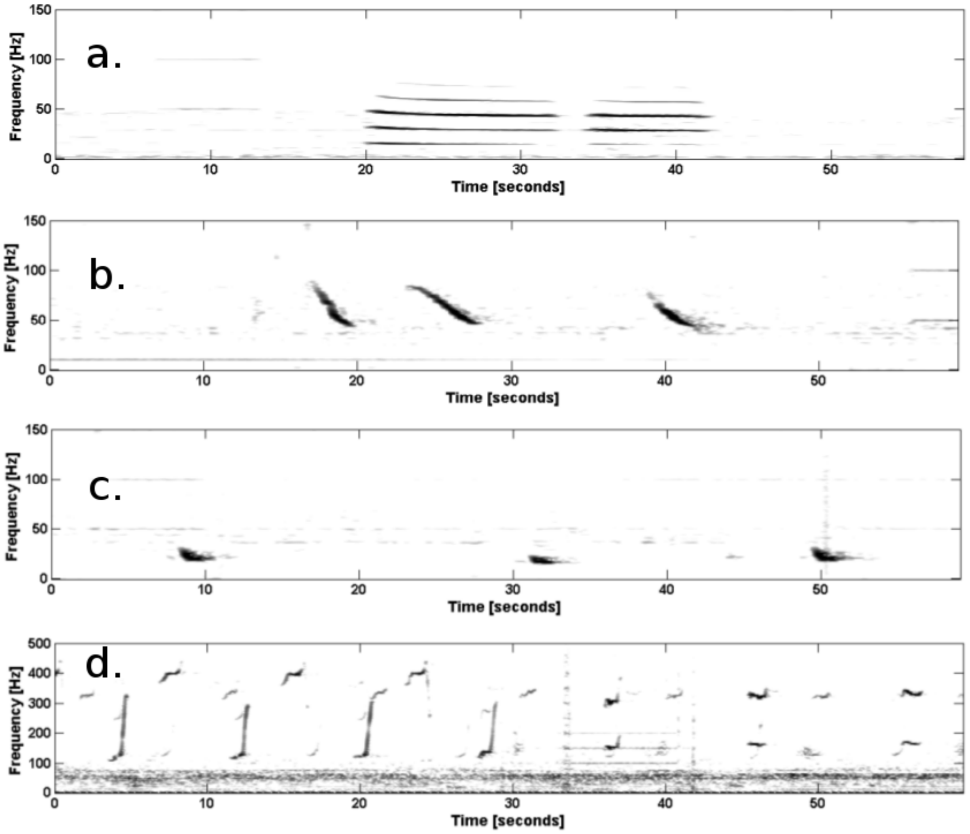

Figure 3.2: Spectrogram of (a) tonal blue whale B-calls with a series of harmonically-related components (the third harmonic is used for detection due to its high SNR) (b) downswept blue whale D-calls, which exhibit more variability in frequency range and duration than B-calls (c) fin whale 20 Hz pulses and (d) humpback whale song. Spectrograms were constructed to display signals in 1 Hz bins with 90% temporal overlap.

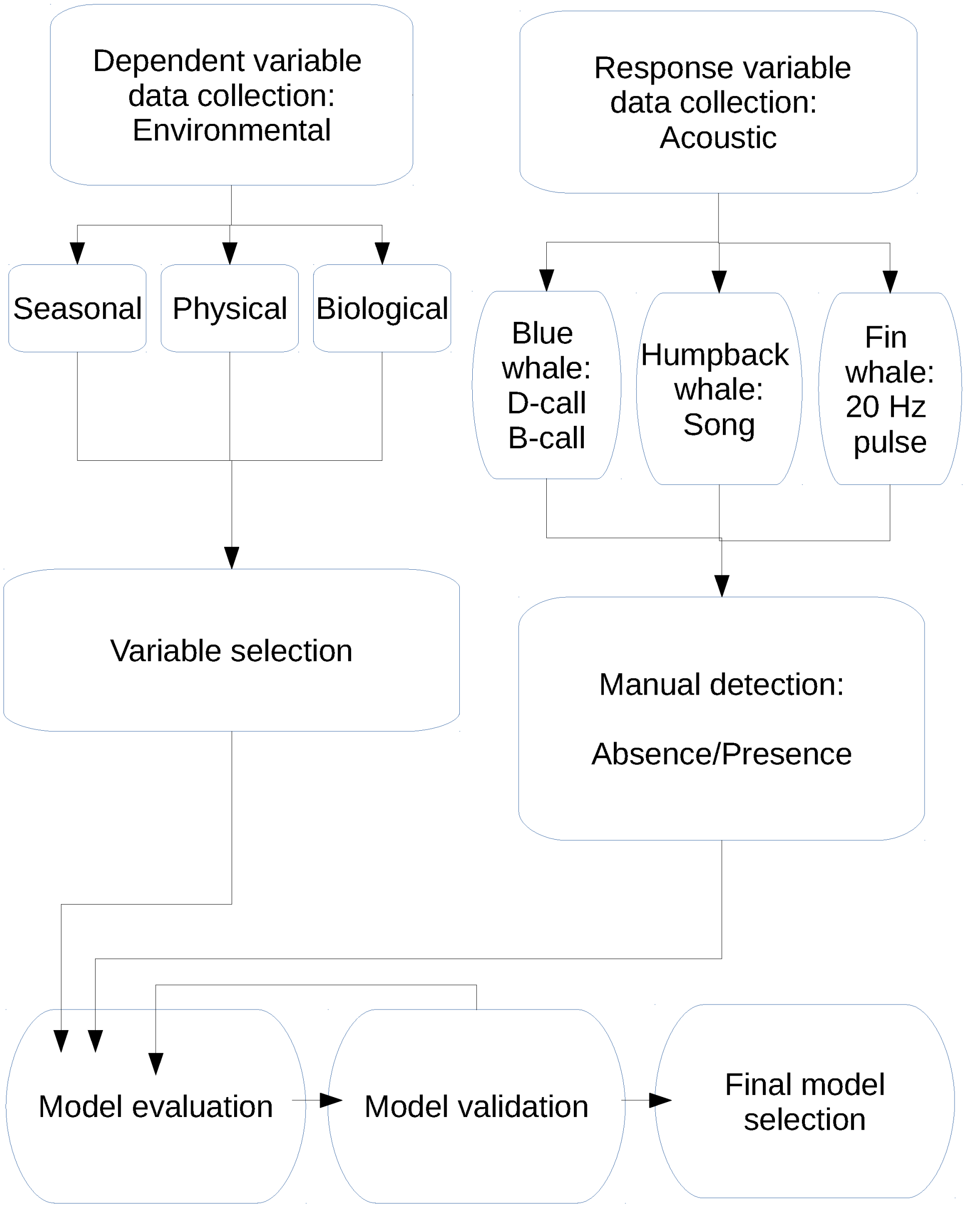

Figure 3.3: Modelling flowchart which shows the various steps of data preparation and analysis leading to the final selected models which best explain whale acoustic presence in the southern California region.

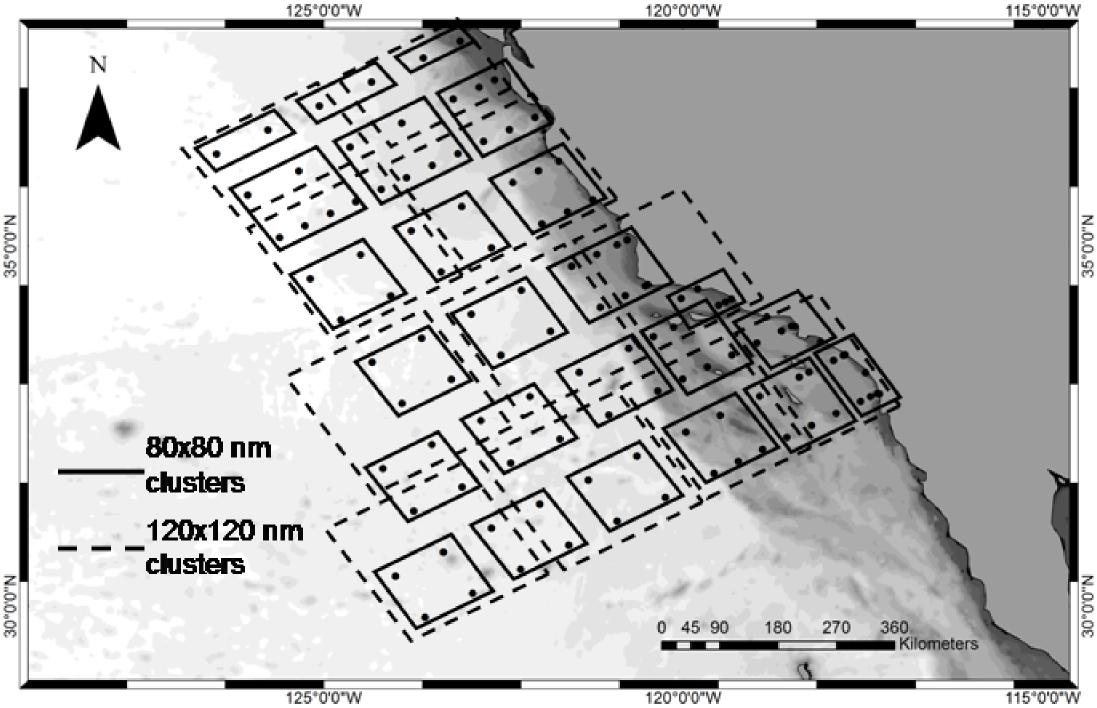

Figure 3.4: Locations of CalCOFI sampling stations and the clusters used in binning acoustic detections and associated environmental parameters. The grid was separated into three spatial scales: 1) single station locations 2) clusters of stations within 80 x 80 nmi area and 3) clusters of stations within 120 x 120 nmi area.

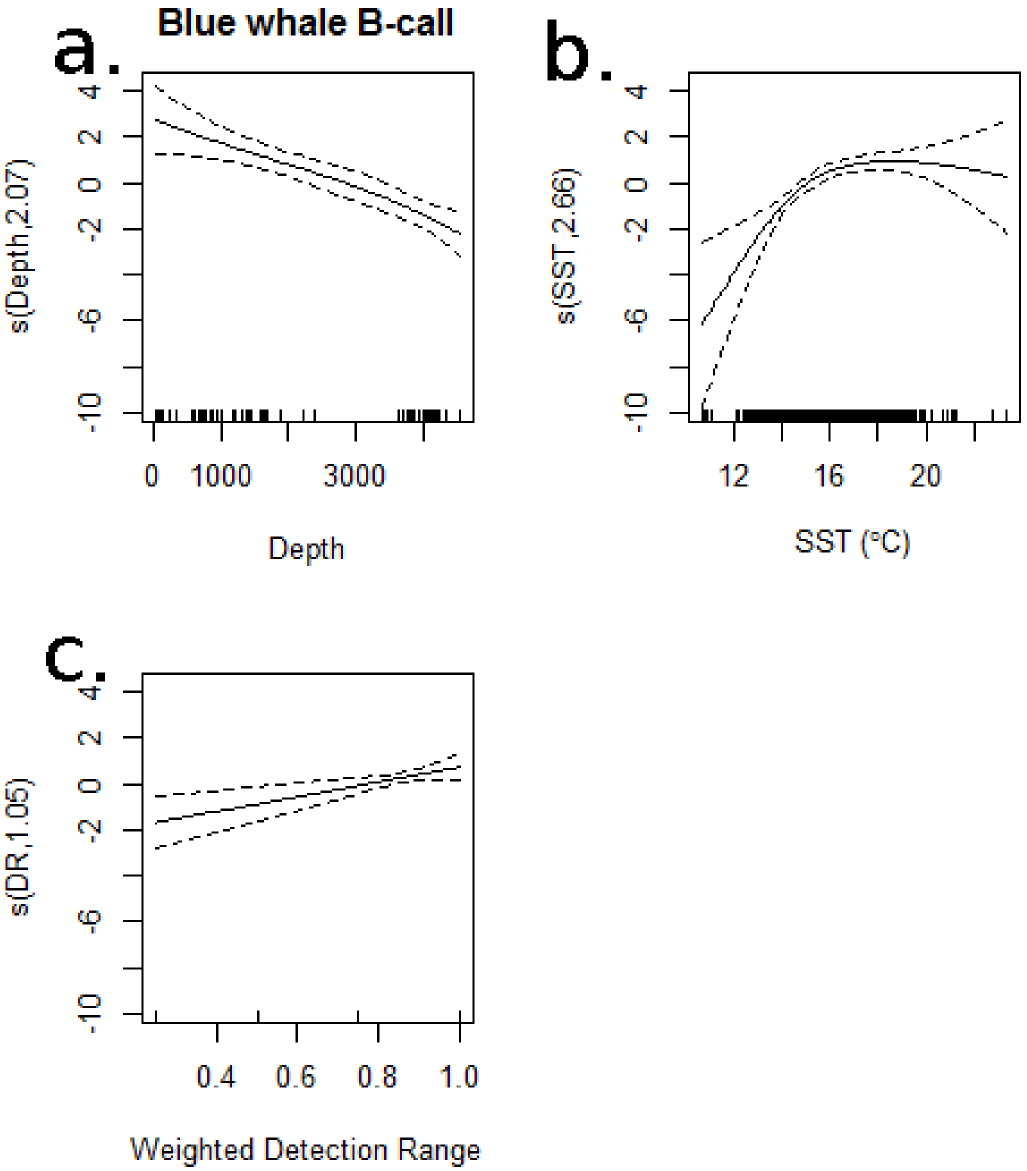

Figure 3.5: Partial contribution of variables to the modelled response from best selected binary generalized additive mixed model of presence/absence of blue whale B-calls in two-hour recording efforts at CalCOFI stations across 9 years of sampling. (a) Estimated relationship between the response variable and depth. (b) Estimated relationship with the response variable and sea surface temperature. (c) Estimated relationship with the response variable and weighted detection range. The dotted lines represent the 95% confidence intervals. The rug plot shows the actual data values of the predictor variables.

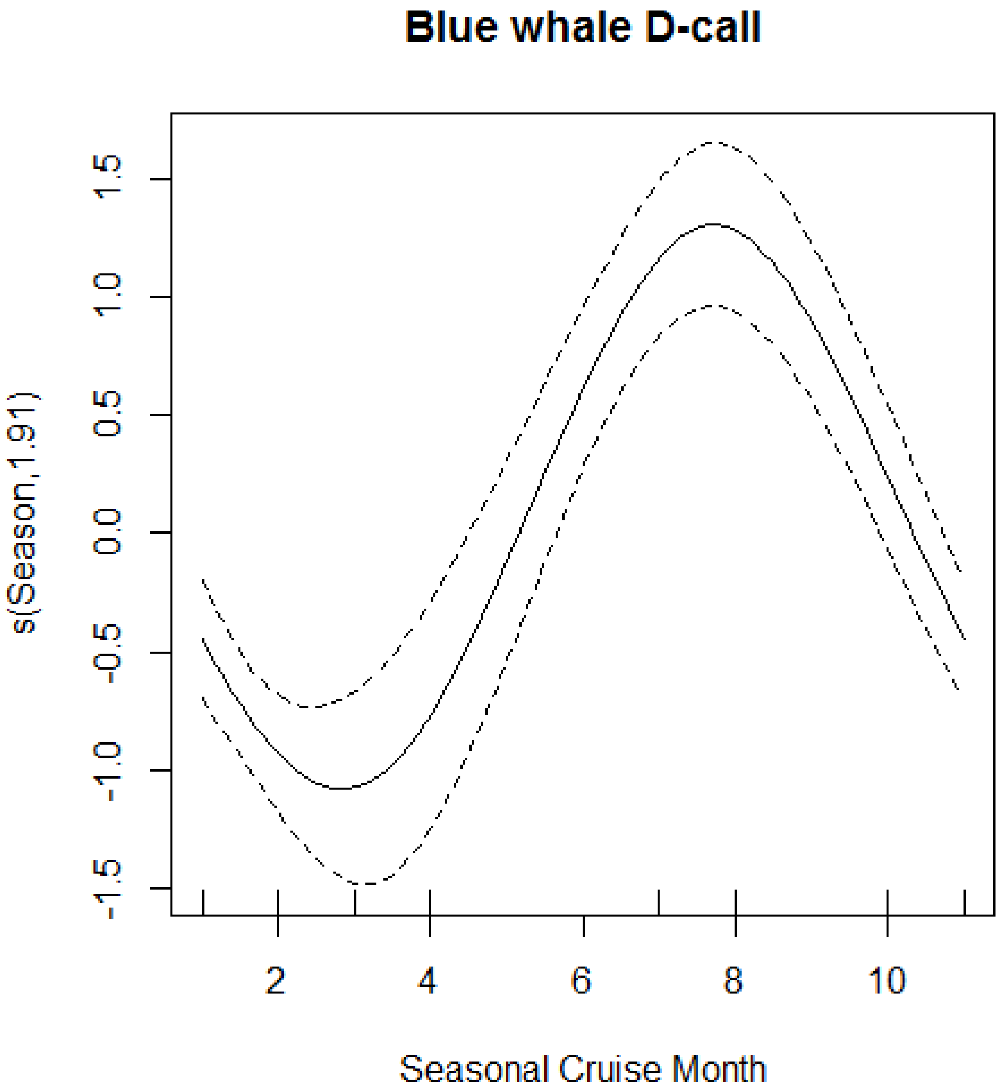

Figure 3.6: Partial contribution of variables to the modelled response from best selected binary generalized additive mixed model of presence/absence of blue whale D-calls in two-hour recording efforts at CalCOFI stations across 9 years of sampling. Estimated relationship between the response variable and month of the cruise. The dotted lines represent the 95% confidence intervals. The rug plot shows the actual data values of the predictor variables.

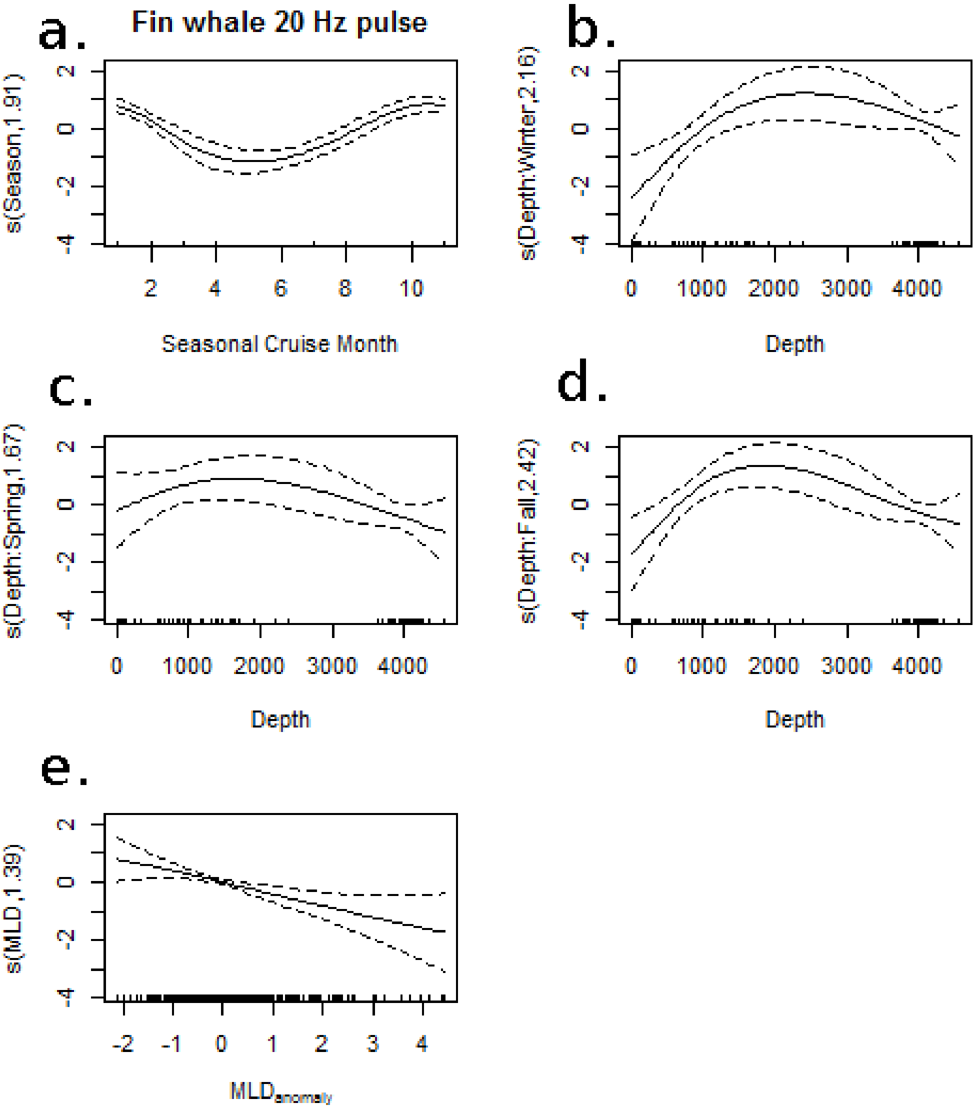

Figure 3.7: Partial contribution of variables to the modelled response from best selected binary generalized additive mixed model of presence/absence of fin whale 20-Hz pulses in two-hour recording efforts at CalCOFI stations across 9 years of sampling. (a) Estimated relationship between the response variable and month of the cruise. (b) Estimated relationship with the response variable and depth for winter detections. (c) Estimated relationship with the response variable and depth for sring detections. (d) Estimated relationship with the response variable and depth for fall detections. (e) Estimated relationship with the response variable and mixed layer depth seasonal anomaly. The dotted lines represent the 95% confidence intervals. The rug plot shows the actual data values of the predictor variables.

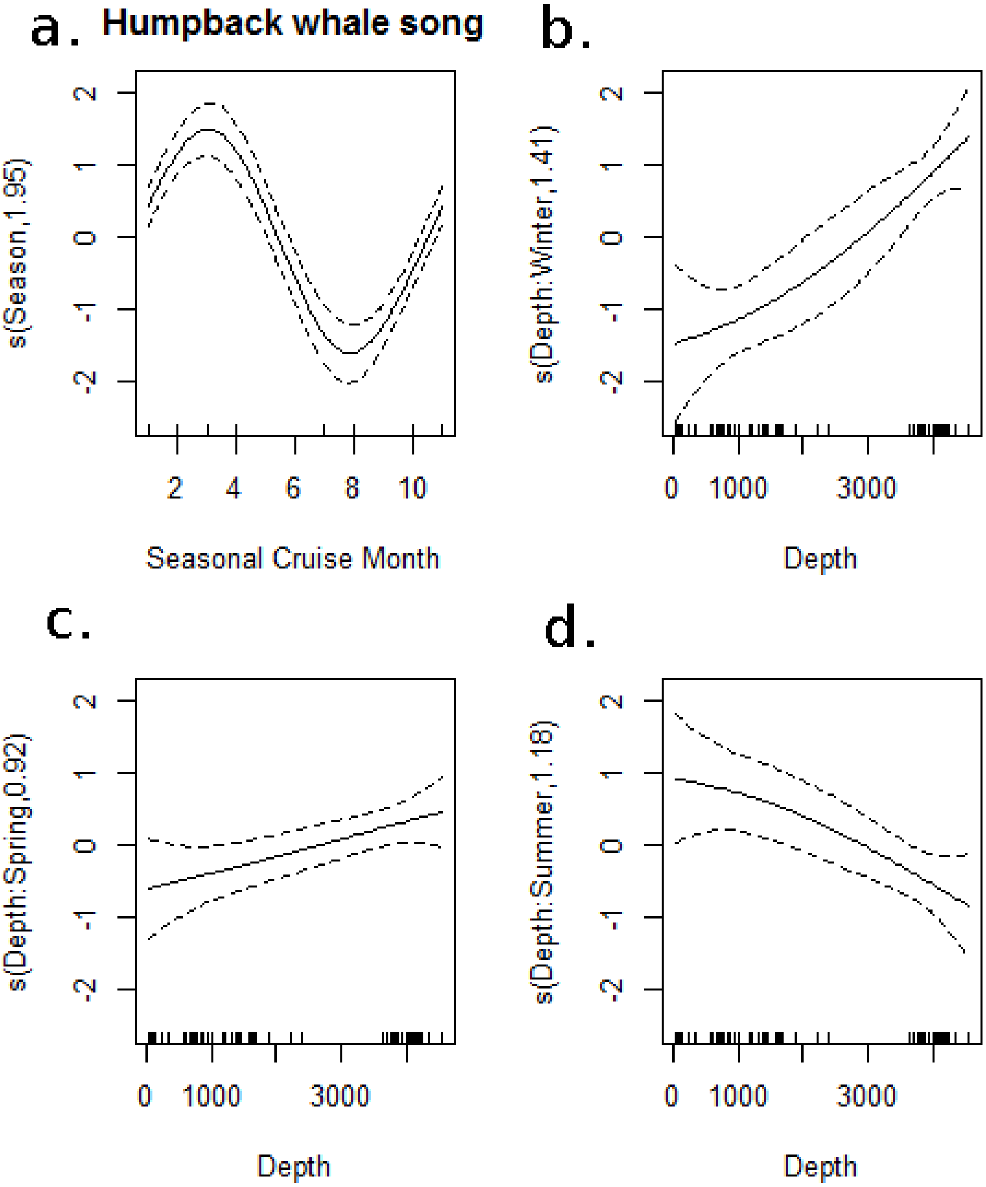

Figure 3.8: Partial contribution of variables to the modelled response from best selected binary generalized additive mixed model of presence/absence of humpback whale song in two-hour recording efforts at CalCOFI stations across 9 years of sampling. The model was a binary generalized additive mixed model. (a) Estimated relationship between the response variable and month of the cruise. (b) Estimated relationship with the response variable and depth for winter detections. (c) Estimated relationship with the response variable and depth for spring detections. (d) Estimated relationship between the response variable and depth for summer detections. The dotted lines represent the 95% confidence intervals. The rug plot shows the actual data values of the predictor variables.

Table 3.1: Final variables for model input. psu = practical salinity units; m= meters; nm = nautical miles; mg=milligrams, m^3 = cubic meter volume

Name	Category	Notes	Units
Depth	Bathymetric		m
Slope	Bathymetric	Range: 0-90	°
Temperature	Oceanographic	SST; at surface (seasonal anomaly)	°C
Thermocline	Oceanographic	Magnitude of thermocline	–
Salinity	Oceanographic	at surface	psu
Mixed Layer Depth	Oceanographic	Depth of thermocline (seasonal anomaly)	m
Chlorophyll	Biological	at surface (seasonal anomaly) (seasonal anomaly)	mg/m^3
Season	Temporal	Cruise month	–
Detection Range	–	Weighted acoustic property	–
Year	–	Random effect	–

Table 3.2: Subset of GAMM results and goodness of fit values for the presence of blue whale B-call, Dcall, humpback whale song, and fin whale pulse. The final selected model is in bold ; Deviance explained for nested models are provided for individual model terms. MLD = mixed layer depth. SST = sea surface temperature. All models included a random effect for year (not shown).

Call Type	Model terms		Deviance explained
D-call	**Season**		**.11**
B-call	SST		.05
	Depth		.06
	Detection Range		.06
	SST	**Depth** **Detection Range**	**.17**
Song	Season		.14
	Depth:Season		.10
	Season	**Depth:Season**	**.23**
20 Hz pulse	Season		.10
	Depth:Season		.08
	$\mathrm{MLD}_{\mathrm{anomaly}}$		.03
	Season	**Depth:Season** $\mathbf{MLD}_{\mathbf{anomaly}}$	**.19**

Table 3.3: Best GAMM models selected for acoustic presence of blue whale, fin whale, and humpback whale call types across three spatial scales. Goodness of fit is given as adjusted r-squared values. MLD = Mixed layer depth. SST=sea surface temperature. All models included a random effect for year (not shown).

Call type Spatial scale	Model terms		n	Adjusted R-sq.
B-call				
Small scale	SST	Depth Detection Range	525	.17
Medium scale	SST	Depth	325	.18
Large scale	SST	Depth	207	.27
D-call				
Small scale	Season		525	.11
Medium scale	Season		325	.16
Large scale	Season		207	.22
Song				
Small scale	Season	Depth:Season	525	.23
Medium scale	Season	Depth:Season	325	.16
Large scale	Season	Depth:Season	207	.18
20 Hz pulse				
Small scale	Season	Depth:Season $\text{MLD}_{\text{anomaly}}$	525	.19
Medium scale	Season	Depth:Season	325	.15
Large scale	Season	Depth:Season	207	.18

Chapter 4

Depth-dependent and time-variable influences on baleen whale calling in the southern California region

4.1 Introduction

Use of synoptic, remotely-sensed oceanographic variables is common in habitat modelling studies (Becker, 2007; Baumgartner and Mate, 2005; Burtenshaw et al., 2004). However, these variables typically represent conditions at the surface of the ocean. There is evidence that subsurface features influence baleen whale distribution (Dransfield et al., 2014). For example, subsurface water column properties and prey information reveal fine-scale movements of right whales (*Eubalaena glacialis*) in relation to prey items (Baumgartner and Mate, 2003). Blue whale density has been inferred from absolute dynamic topography (ADT), which derives information from the entire water column as opposed to just surface water properties (Pardo et al., 2015). While there is a paucity in studies relating depth-stratified water column properties to whale distribution, the increased availability of subsurface water properties from increased sampling effort has allowed for further investigation of the importance of depth-dependent environmental variables to whales.

In addition to subsurface information, increased oceanographic sampling from mooring platforms has provided high-resolution time series of oceanographic variables such as temperature, salinity, and chlorophyll. Previous studies have used metrics of variation and gradient over space as a proxy for frontal activity (Becker, 2007; Baumgartner and Mate, 2003). The variation and persistence of oceanographic variables over time and space has been used as a potential explanatory driver of distribution of top predators (Suryan et al., 2012).

Sound production and propagation is critical to cetacean life history and survival (Richardson et al., 1995). Because sound is conducted well in water, sound has been identified as a primary sensory modality for biological communication in the ocean (Tyack, 2000). The ability to record these sounds in a near-continuous fashion has allowed for investigations of habitat use year-round (Soldevilla, 2008; Merkens, 2013). The main objective of this chapter is to integrate co-occurring high resolution acoustic and environmental data sets and investigate the extent to which certain depth-dependent and temporally variable properties of oceanographic factors are relevant to baleen whale acoustic occurrence on a southern California feeding ground.

4.1.1 Seasonality of baleen whale vocalizations

From visual and acoustic evidence, blue (*Balaenoptera musculus*) and humpback whales (*Megaptera novaeangliae*) are known to migrate to and from the southern California region. Blue whale vocalizations have been studied extensively in the SCB for several years (Oleson et al., 2007a). They are known to produce at least three call types in the eastern North Pacific (Oleson et al., 2007a; McDonald et al., 2006; Thompson et al., 1996; Rivers, 1997): A-, B-, and D-calls. A- and B-calls (∼10-20 second duration) are pulsed or tonal in character, respectively, and occur in repeated sequences. They are only produced by males, and therefore serve a reproductive function (Oleson et al., 2007b). D-calls (down-sweep from 90-25 Hz, ∼1-4 second duration) are highly variable in frequency and temporal characteristics, are recorded from both males and females, and are produced in a foraging context (Oleson et al., 2007b). Upon arrival of blue whales in the southern CCE, D-calls are recorded from April to November while B-calls are recorded from June to January (Oleson et al., 2007a).

Male humpback whales sing long, complex, repetitive song (Payne and McVay, 1971), inferring a reproductive function, while both males and females make social non-song sounds (Dunlop et al., 2008). The structure and function of their vocalizations, especially song, have been well studied, but the only reports of year-round acoustic presence include a winter and early spring presence in low latitudes (Watkins et al., 2000), bimodal (October, April) peaks in acoustic presence off central California (Helble, 2013), and opportunistic singing detection during migration (Norris et al., 1999).

4.1.2 Research objectives

My overall research objective was to investigate environmental variables sampled at various depths in the water column and evaluate their significance in explaining the calling abundance of baleen whales in the southern California region. I compared multiple models incorporating temperature at surface, 40 meters depth, and a stratification index, to determine the strongest explanatory variables for each call type.

I investigated a derived variable which served as a proxy for temporal variablity and evaluated their importance in explaining the distribution and occurrence of baleen whale acoustic abundance. I compared multiple models incorporating a temperature variability index to test for the importance of this variable.

4.2 Methods

4.2.1 Study area and data collection

Data were collected from an environmental mooring located at Site C approximately 50 km off Point Conception at 34.3 ° latitude, -120.8 ° longitude at a depth of approximately 800m. The data were collected using a passive acoustic recorder (HARP) from 2010 to 2014. Corresponding environmental data from the mooring maintained by the SIO Ocean Time Series Group included a suite of interdiscplinary oceanographic (CTD) and biological sensors (FLNTUS; Figure 4.1).

Detector analyses for HARP recordings

Passive acoustic data were analyzed using a combination of automatic and manual detection methods for blue, fin, and humpback whale call types (Figure 4.4).

The Generalized Power-Law (GPL) detector, originally designed for humpback whale vocalizations (Helble et al., 2012), was modified to allow for the detection of the highly variable blue whale D-call, constraining the parameters to fit the downswept nature of the call. The GPL detector was run over four years of acoustic record from 2010 to 2014. A groundtruthing process was implemented to determine the true positive (recall) rate for the detector. I randomly selected a subsample of 24 hours for each deployment for manual detection and confirmation. The D-call recall rate was between 67% and 85% for the 10 HARP deployments (Table 4.2). Because of the generalized nature of the detector and ubiquitous self-noise from the recorder, D-call detections yielded an order of magnitude more false detections than true detections. Therefore, the detections were verified by a human analyst to exclude false detections, thereby reducing the false alarm rate to zero.

Blue whale B-calls were automatically detected using spectrogram cross-correlation (Mellinger and Clark, 2000). Spectrogram correlation for B-calls is a viable option due to the relatively stereotypical frequency and temporal characteristic of the the call. A kernel, or reference function, was developed from approximately 30 hand-picked B-calls with each call separated by at least 24 hours to ensure independence of calls for each deployment. This kernel was determined from the peak frequency of the third harmonic of the B-calls measured automatically at five time periods within the call (0, 1.5, 3, 4.5, 10 seconds) using customized MATLAB-based software. The deployment-specific template was run on a subset of data (containing at least 200 hand-picked calls) at various threshold values in order to obtain the optimum threshold value that minimizes false detections, minimizes missed calls, while maximizing true detections. The optimal threshold was manually chosen to minimize the tradeoff between precision and recall (Table 4.2). For this study, multiple detector templates and detection thresholds were determined by a human analyst for each deployment in order to account for the shift in frequency content of the call and changes in deployment hardware. The automatic detector was run on all audio files using the appropriate kernel and threshold. Detections from February to May were always verified by a human analyst due to the scarcity of calls during these months. False detections were deleted from the record for these months. All detections times and threshold scores were stored in the Tethys metadata database (Roch et al., 2013).

Manual acoustic analyses of HARP recordings

A human analyst reviewed Long Term Spectral Averages (LTSAs) for all HARP deployments decimated by a factor of 100 from deployments sampled at either 200 or 320 kHz. LTSAs were annotated with hourly presence of song activity lasting at least one theme (Payne and McVay, 1971) or longer. LTSAs were constructed and acoustic annotations were logged using custom software Triton version 1.81. When necessary, close inspection of call spectrograms confirmed detection annotations. To calculate the spectrograms, 2,000 or 3,200 point fast Fourier transforms (FFTs) were calculated with 90% overlap and a Hamming window.

Environmental variable collection and derivation

The environmental measurements obtained from the CCE-2 environmental mooring included sea surface temperature (SST), temperature at 40 meters (T_{40}), and the difference between the two readings, which I called a stratification index. The larger the value of the stratification index, the larger the difference between SST and T_{40}, which provided information about the uniformity of the water layer between surface and 40m and the potential for mixing to occur. Because of the strong seasonal forcing in all the temperature readings, I calculated seasonal anomalies of each time series.

The temperature variability index was calculated as the absolute value of the difference between temperature readings in sequential two-day time windows at 40 meters depth. I preliminarily explored various time windows over which to average before gradient calculations. Initially, I explored windows longer than 24 hours to avoid potential bias from diurnal patterns. In the end, I chose two-day average windows based on previously calculated decorrelation time scales in the nearshore CCE region, which were found to be $\sim$2 days for both SST and chlorophyll values (Abbott and Letelier, 1998).

4.2.2 Assessment of temporal properties of time series

Analyses of the highly-resolved time series environmental data resulted in, at maximum, a data point per every hour. The temporal autocorrelation of call detections and the environmental measurements becomes problematic when trying to model the effects of environmental variables on individual callers. Each call detection does not necessarily represent one independent individual and most likely has an influence on the probability of detection of the next call. In lieu of incorporating an autocorrelation structure into my models, I investigated appropriate time scales over which to bin acoustic and environmental data to avoid the potential redundancy of information leading to temporal autocorrelation.

To determine the appropriate temporal scale for each call type, I calculated the integrated time scale (ITS) over which autocorrelation of the response variable was minimized and binned the environmental variables accordingly. A 51 hour (2.2 days) binning period was determined to minimize autocorrelation for blue whale D-calls, The ITS for B-calls was 14 days and for humpback song 7 days.

4.2.3 Modelling framework

Baleen whale call abundance (in the metric of call counts per unit time) was modelled with environmental variables listed in Table 4.1. Habitat models were constructed for depth-, time-dependent multiple model comparisons. All data were temporally aligned to compare the presence of blue and humpback whale calls with environmental variables, a generalized additive mixed modelling (GAMM) framework was used to identify the most significant habitat variables that explain the calling presence of these whales in the southern California region. GAMMs allow for investigation into the relationships between whale detections and environmental factors via a non-linear framework (Hastie and Tibshirani, 1990). Generalized additive models include fixed effects and represent an extension of the generalized linear model (GLM), but do not constrain the relationship between y and x to be linear or of any particular function. GAMMs allow for additional model terms to represent the random effects. These models can be represented by:

$$GAM : g(E(Y)) = X_m\beta + f_1(x_1) + f_2(x_2) + ... + f_m(x_m) \tag{4.1}$$

$$GAMM : g(E(Y)) = X_m\beta + f_1(x_1) + f_2(x_2) + ... + f_m(x_m) + X_m\alpha \tag{4.2}$$

where E(Y) are the estimates of the non-normal response variable (e.g.

baleen whale acoustic detections) and g is the link function with a given distribution function. The link function addresses the non-normally distributed response data. $X_m\beta$ represents an intercept parameter, $X_i\alpha$ represents a random term, and the f_m smoothing functions can be parametric or non-parametric (e.g. functions comprised of smoothing splines or LOESS smoothing functions).

Discrete count data are often approximated with a Poisson distribution (McCullagh and Nelder, 1989). However, when modeling counts for our study, I chose to use the negative binomial (nb) family which allows for further flexibility in characterizing the relationship between the variance and the mean of a response variable. By considering the nb family, I characterized the variance of the response variable as a quadratic function of the mean which is automatically estimated by mgcv (Ver Hoef and Boveng, 2007). This option is available through the mgcv R package (version R 3.1.2) (Wood, 2006) and was found to be a more appropriate fit than the Poisson (or quasipoisson) distribution family based on preliminary inspection of model residuals.

A cyclic cubic regression smooth was applied to the Julian Day temporal variable, which allows for the last day of the year to be smoothly connected with the first. The other functions were constructed with cubic regression smoothing splines with shrinkage, which allows for third order polynomials to be fit on segments of data and allows for the smoothness selection to approach zero term completely. Each spline was applied with a maximum of 3 degrees of freedom in order to prevent overfitting and an overly complex model which may be difficult to interpret ecologically (Forney, 2000; Ferguson et al., 2006). An added modelling parameter Gamma was set to 1.4 to allow for an additional check on overfitting (Wood, 2006).

For all iterations of the models, year was treated as a random effect.

4.2.4 Model selection

Models were initially fit to a single variable, Julian Day, to assess the seasonality of the call counts. One by one, the variables listed in Table 4.1 were added as a term to the seasonal models. Because I was interested in comparing the performance of models with temperatures at different depths, I did not build models with more than two fixed terms. Models were compared using the Aikake Information Criterion (AIC) values calculated for each model fit, with AIC defined as:

$$AIC = -2(log(likelihood)) + 2K \tag{4.3}$$

where K represents the number of parameters included in the model fit.

Models with the lowest AIC values were chosen as the final model. Likelihood ratio tests were used to assess significance of model terms. I provide plots of model fits run on the 4-year data set.

4.3 Results

In ∼30,000 hours of recordings, over 250,000 B-calls and over 20,000 D-calls were detected, and 3,500 positive hourly records in which at least one humpback song theme was detected.

There was a seasonal separation in the occurrence of blue whale B-calls and D-calls, and humpback whale song throughout 2010 to 2014 at Site C (Figure 4.5). Blue whale D-calls were detected predominantly from April to November, which a peak in late June. B-calls were detected from June to January, with a peak in September. Humpback song was detected from September of one year to May of the following year with peaks in early November and late March. More detailed analyses on this acoustic record can be found in Chapter 2.

SST peaked in late summer and warm values prevailed through the fall. T_{40} also showed seasonality but to a less degree than the seasonality displayed at sea surface (Figure 4.2). The stratification index (Figure 4.2) was higher during the summer and fall months. The temperature variability index showed high values in mid 2010, late 2011, mid 2012, and late 2013.

4.3.1 Model Results

For blue whale B-calls, the models including different temperature variables did not improve the model consisting of just Julian Day. For blue whale D-calls, adding stratification as a term improved the model with just Julian Day by 7% deviance explained. For humpback whale song, the T_{40} was selected as the best model (Table 4.3) with a 5% improvement in deviance explained. Julian Day was a strong explanatory variable in models for all call types accounting for 31% to 57% of the variance. There was a near-linear relationship between blue whale D-call abundance and stratification. There was a negative relationship between humpback whale song and T_{40} (Figure 4.6).

For all call types, the temperature variability index was not selected as a significant term in the best-fit models. Wald significance tests rejected the index as a significant term (Table 4.4).

4.4 Discussion

4.4.1 Multi-model comparison between temperatures at different depths

While Julian Day was a strong explanatory model across all call types, temperature at depth and stratification were generally better models when compared with SST. SST was generally the worst for explaining yearlong acoustic activity. Stratification and T_{40} were more meaningful for humpback whale song and blue whale D-calls, respectively, which could mean that temperatures sampled at deeper depths contain some information that better explains call counts throughout the year.

The reason why information at depth may play a role may be related to prey. Keiper et al.(2005) recorded higher sighting rates of marine mammals during times of upwelling relaxation, which led to stronger stratification. They hypothesized that the strength of stratification in spring surveys contributed to stabilization and aggregation of prey. If whales are cued by stratification, they may be picking up on a factor that determines the distribution of their prey. Subsurface water column information was important for predicting abundance of fish species with different vertical habitat preferences (Manderson et al., 2011). Whether whales might be reponding to depth-dependent metrics directly or indirectly via the prey that are affected by subsurface properties, it is important to consider conditions below the surface to further test possible mechanistic or explanatory models for the production of certain call types.

In a previous study, adequate sampling coverage of the water column allowed for the tight correlation between the depth of right whale feeding dives and the depth at which there was maximum abundance of prey (Baumgartner and Mate, 2003).

Blue whale density was found to be driven by absolute dynamic topogrpaphy and thought to be well-characterized by a variable which derives information from the entire water column as opposed to just surface water properties (Pardo et al., 2015). These studies corroborate our findings that water column or at least subsurface properties provide an alternative, and sometimes improved factor for enhancing explanatory power for cetacean occurrrence.

4.4.2 Temperature variability index

These models did not improve in fit when using a variable that accounts for temporal heterogeneity and I rejected the hypothesis that the temperature variability index is a signifcant factor for predicting any of the call types. Past studies have highlighted the importance of a gradient or variance factor (representing frontal systems, persistence, or hotspot indices) for marine top predators (Becker et al., 2010; Baumgartner and Mate, 2003; Suryan et al., 2012). Specifically, in a study using seabirds as a top predator model, using a variance metric instead of a standard measurement of SST or chlorophyll improved seabird habitat models substantially (Suryan et al., 2012), explaining up to 90% of the variance. In my approach, the time variability index did not contain spatial context, and knowing the importance of bathymetric depth as a predictor variable for the models in Chapter 3, it is possible that the unexplored drivers are spatial and bathymetric, could be based on social context, or caused by internal, physiological drivers.

Co-occurrence with fronts continues to be a popular choice of covariate due to the hypothesized mechanism fronts serve for top predators. Johnston et al. (2005) explored fin and minke whale co-occurrence with an island wake habitat and established that visual sightings were highest during flood tides. Whales are thought to be attracted to these features due to prey entrainment in the lower-current velocity areas of the wake. In a completely different oceanic zone, blue, humpback, and fin whales were heavily influenced by thermal fronts (DoniolValcroze et al., 2007). The influence of oceanographic fronts was also shown in the northern CCE where SST and distance to the alongshore upwelling front were the most important variables during late spring for humpback whales (Tynan et al., 2005). Since we did not find a strong correlation between acoustic activity and the variability index, the question remains how this temperature variability index relates to frontal systems, if at all.

Regardless of what the temperature variability index represents, it is important to continue to look for metrics that accurately represent a proxy for frontal systems. Ocean fronts have been illustrated as the major mechanism which drives nutrient and biomass accumulation (Woodson and Litvin, 2015), which inevitably affects top predators in the CCE. These models were built using parameters collected at a single HARP location, subject to seasonal and diurnal changes which reflect the dynamic, fluid nature of the ocean environment. The changes in environment measured at this single location represent changes over time as different water masses move in and out of the area, as tidal dynamics move past the mooring, or as internal waves pass through. However, because the temperature variability index represented a point sample in time, it is difficult to say how well the temperature time series and the derived variability index represent the larger distance (potentially 10s of km away) over which each call type could be detected. Such a large detection range represented by a single sample ignores the heterogeneity in the detection area and decreases the certainty by which we can characterize the relationship between whale acoustics and fronts.

4.4.3 Data Limitations

Autocorrelation considerations

All call types were modelled using different time bins over which acoustic detections and associated environment parameters were averaged. The integrated time scale that minimizes autocorrelation was shorter for D-calls, a foraging call, than for B-calls and humpback whale song, both reproductive calls. Due to the nature of song being repetitive and meant for reproductive display, the high integrated time scale for reproductive type calls is unsurprising. The approach taken here to minimize autocorrelation involved pre-model data manipulation. Other approaches in future work may involve integrating autocorrelation-specific structures into the model framework itself.

Propagation of call types

The different acoustic properties of each call type affect the spatial extent to which the calls were detectable. I investigated these differences by estimating the transmission loss of a sound source using simple geometrical spreading law (Urick, 1983).

Assuming spherical spreading, the maximum range over which the detected calls can occur can be calculated by accounting for source level (SL) and received level (RL). The source level for D-calls is 160 dB re 1 μ Pa (Berchok et al., 2006; Thode et al., 2000; Melcon et al., 2012), for B-calls $\sim$180 dB re 1 μ Pa (McDonald et al., 2001; Thode et al., 2000), and humpback whale song units were estimated to have SL $\sim$160 dB re 1 μ Pa (Au et al., 2006). I calculated average noise levels over corresponding single Hz bands overlapping each call type ($\sim$80 dB re 1 μ Pa at 20 Hz and 50 Hz and $\sim$65 dB re 1 μ Pa at 200 Hz), then back-calculated the maximum range at which the faintest call can be detected for Site C: $\sim$3 km for blue whale D-calls, $\sim$30 km for blue whale B-calls, and $\sim$ 18 km for humpback whale song. To justify whether a point source of environment measurement can correspond to a whale detection from $\sim$3 to 30 km away, I considered the literature for decorrelation length scales and found that for latitudes at which the southern California Current ecosystem resides, length scales for ocean color occur at $\sim$150 km (Doney et al., 2003). Since the theoretical detection ranges are less than 150 km, the point sample should be sufficient to represent the area of the associated call detections. However, this assumption seems inappropriate for the CCE due to the micro- and mesoscale oceanography that characterizes the area. Future studies should test for the association of the environmental point sample to the location of the calling whale.

4.5 Conclusions

In this study, I used the co-occurrence of a continuous year-round acoustic time series with a depth-resolved dataset from an ocean-observing mooring platform, and investigated the effects of seasonality on the acoustic detections. I laid out a framework to start to understand the underlying ecological relationship between temperature and whales. I also asked specific questions about the value of information from the water column and tested whether subsurface properties may be more predictive for whale acoustic activity.

Due to the data limitations of pairing an acoustic signal to a single point sample, future studies should ensure tight spatial coupling of sound production and measured environmental parameters. Past studies using tagging technology have been able to determine depths at which right whales forage and how that relates to ecologically significant oceanographic features for prey aggregation (Baumgartner and Mate, 2003). To obtain such data, fine-scale studies involving tags and a highly-coupled sampling scheme are needed.

4.6 Acknowledgments

Thank you to Ally Rice who validated and implemented the B-call detector used in this study. Thank you to Tyler Helble who developed the GPL detector used for D-call detection. Thank you to Hey-Jin Kim and Mark Ohman who helped with the post-processing of the CCE-2 mooring data. The authors gratefully acknowledge the efforts of all those involved in the collection of these data, especially SWAL lab engineers and numerous field volunteers from 2010-2014 as well as the SIO Ocean Time Series group, especially Hey-Jin Kim. We gratefully acknowledge the funding support of Frank Stone, Ernie Young, and Linda Petitpas at the Chief of Naval Operations, division N45, and Curt Collins at the Naval Post Graduate School.

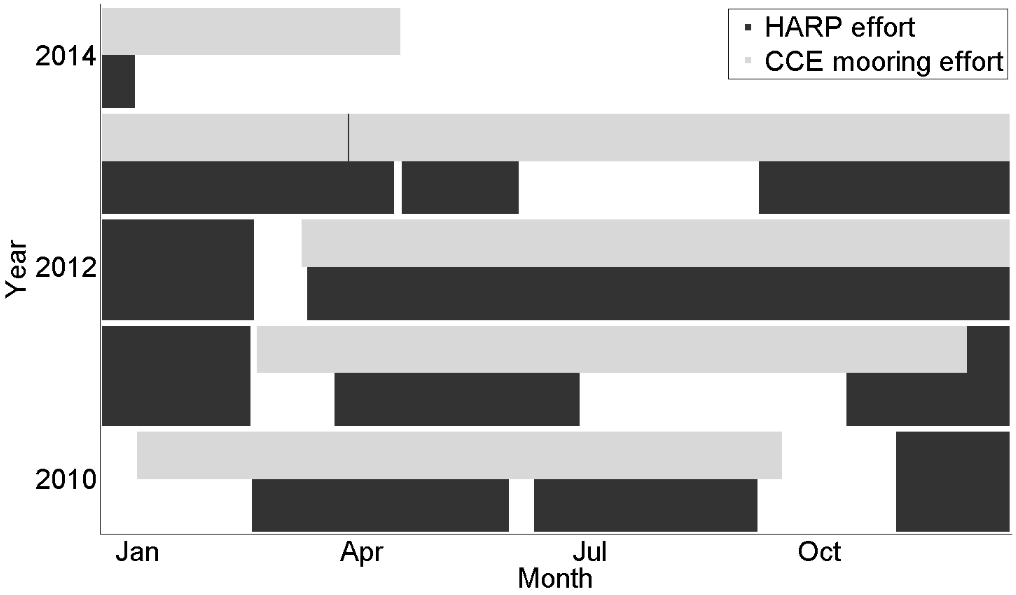

Figure 4.1: Dates of High Frequency Recording Package(HARP) recording effort and SIO Ocean Time Series Group (CCE-2) environment mooring sampling effort.

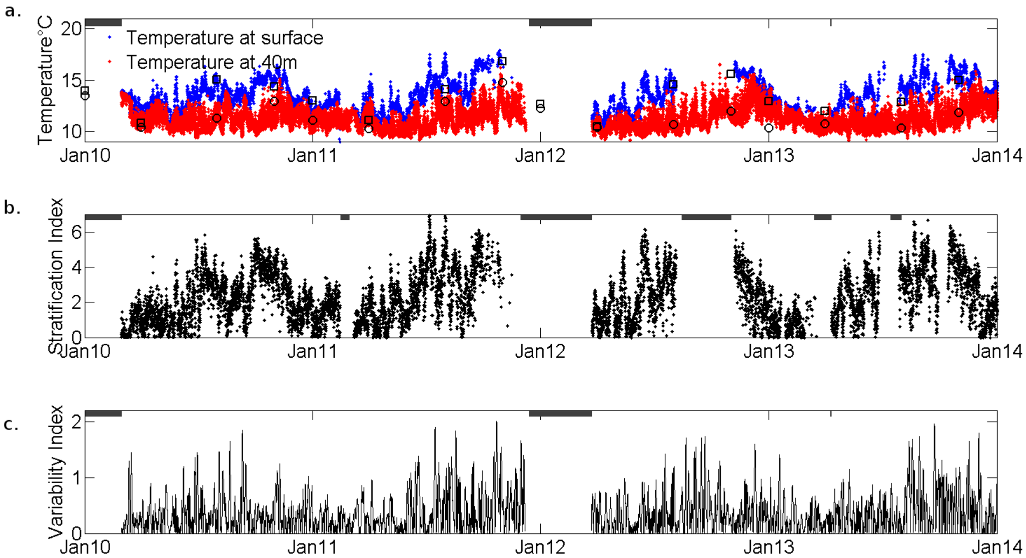

Figure 4.2: (a) Time series of sea surface temperature (SST; blue), temperature at 40m (T_{40}; red), (b) the difference between SST and T_{40} (stratification index) and (c) the T_{40} temperature variability index. Symbols overlaying the temperature time series (a) represent in-situ values collected from the CalCOFI station 80/55 which is the closest station to the environmental mooring. Squares correspond to SST and circles correspond to T_{40}

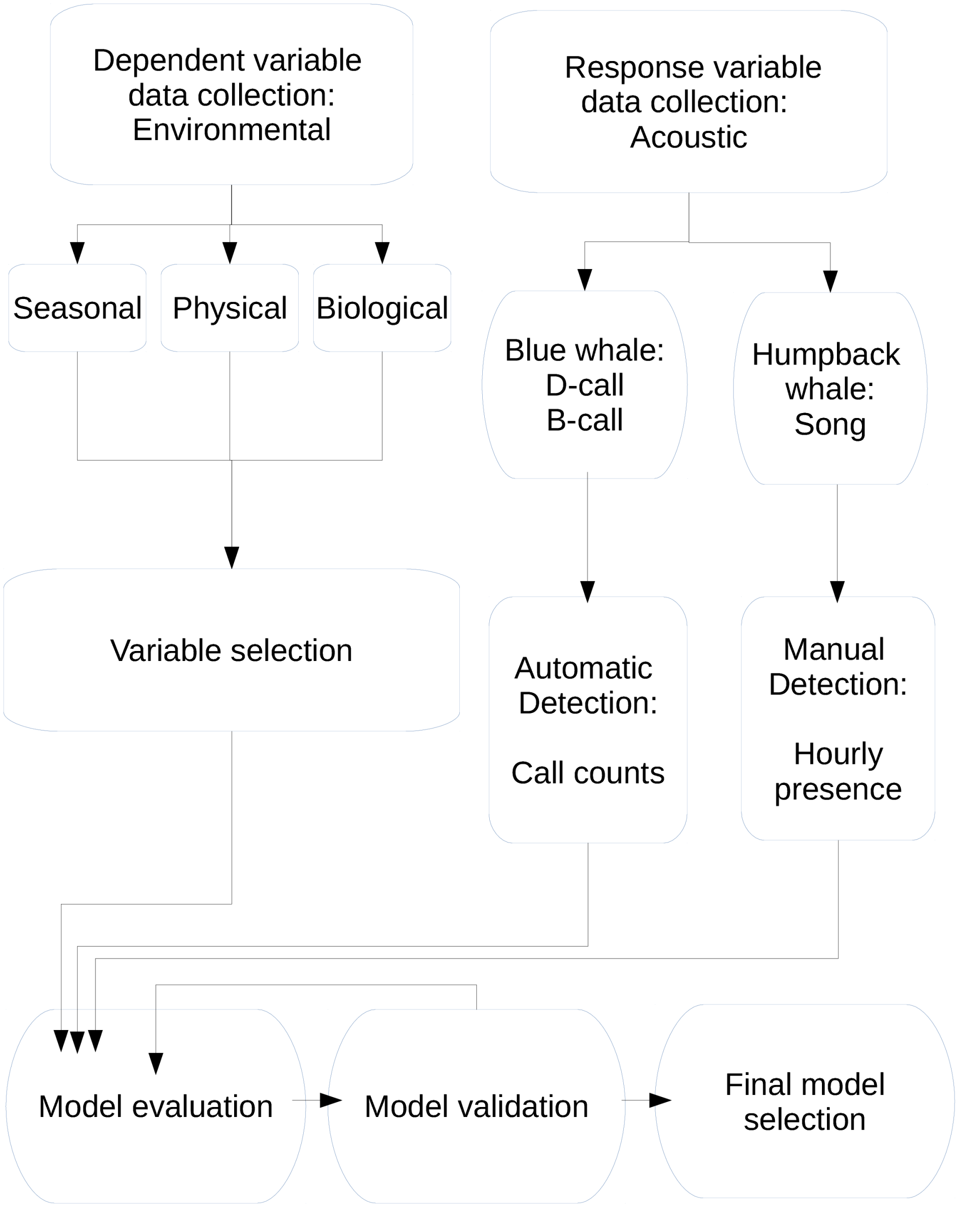

Figure 4.3: Modelling flowchart which shows the various steps of data preparation and analysis leading to the final selected model which best explains whale acoustic calling abundance in the southern California region.

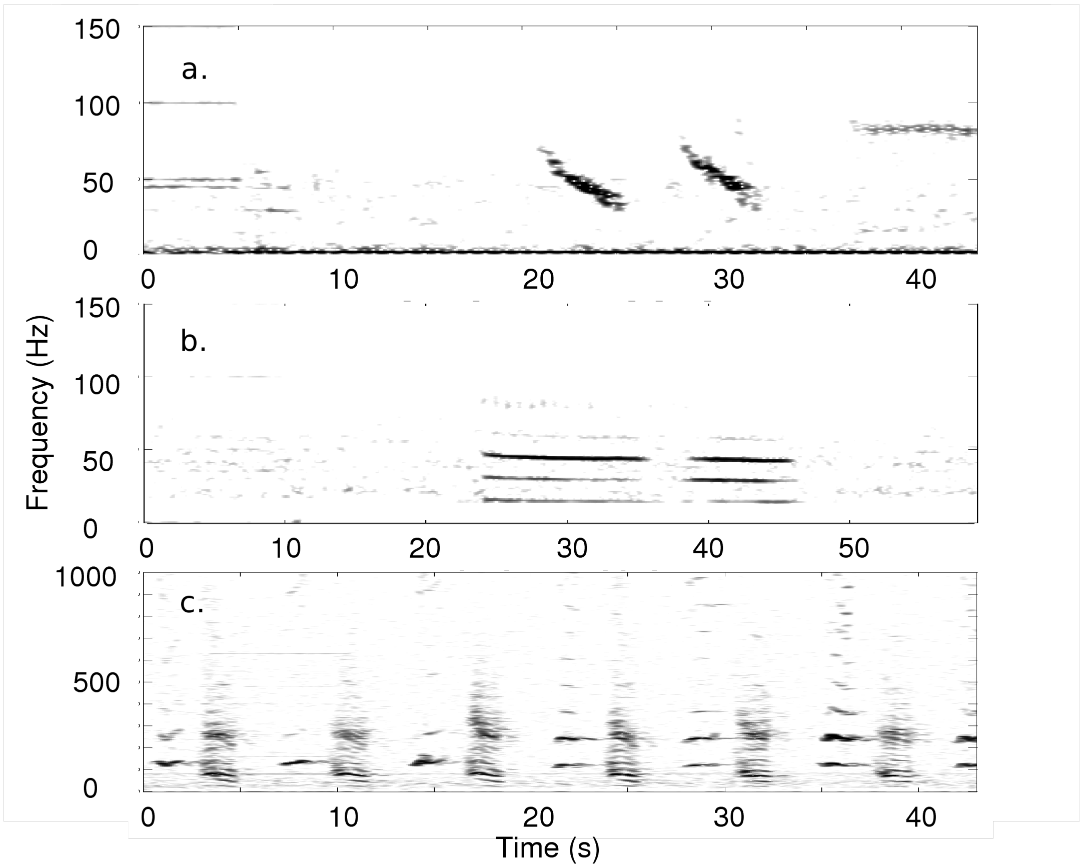

Figure 4.4: Spectrogram of baleen whale call types used in this study: (a) downswept blue whale D-calls, which exhibit variability in frequency range and duration b) tonal blue whale B-calls with a series of harmonically-related components (the third harmonic is used for detection due to its high SNR) and (c) humpback whale song. Spectrograms were constructed to display signals in 1 Hz bins with 90% temporal overlap.

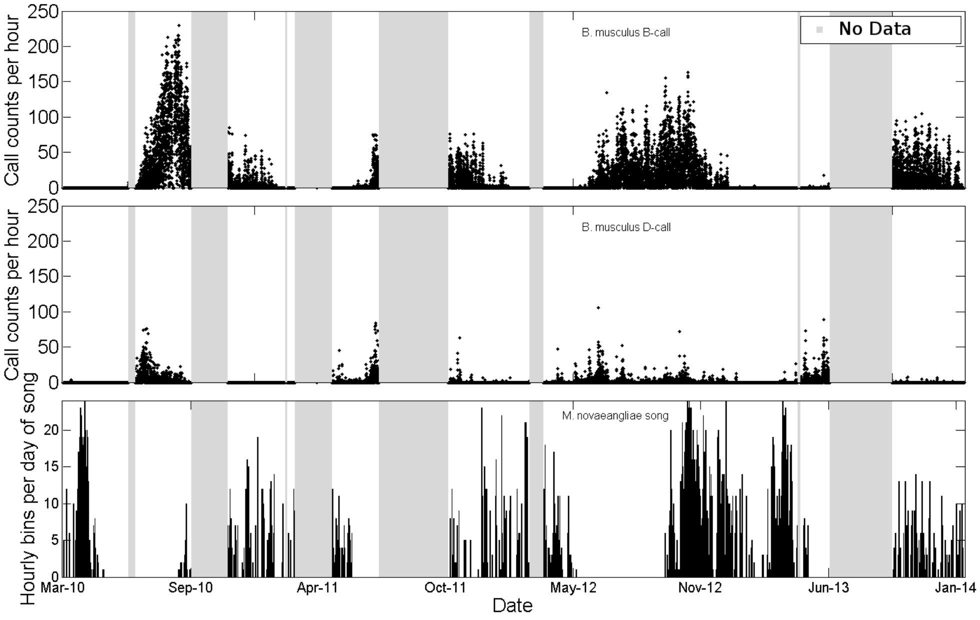

Figure 4.5: Hourly call rates for blue whale B-calls, D-calls, and humpback whale hourly song presence. Gray areas represent time periods with no data.

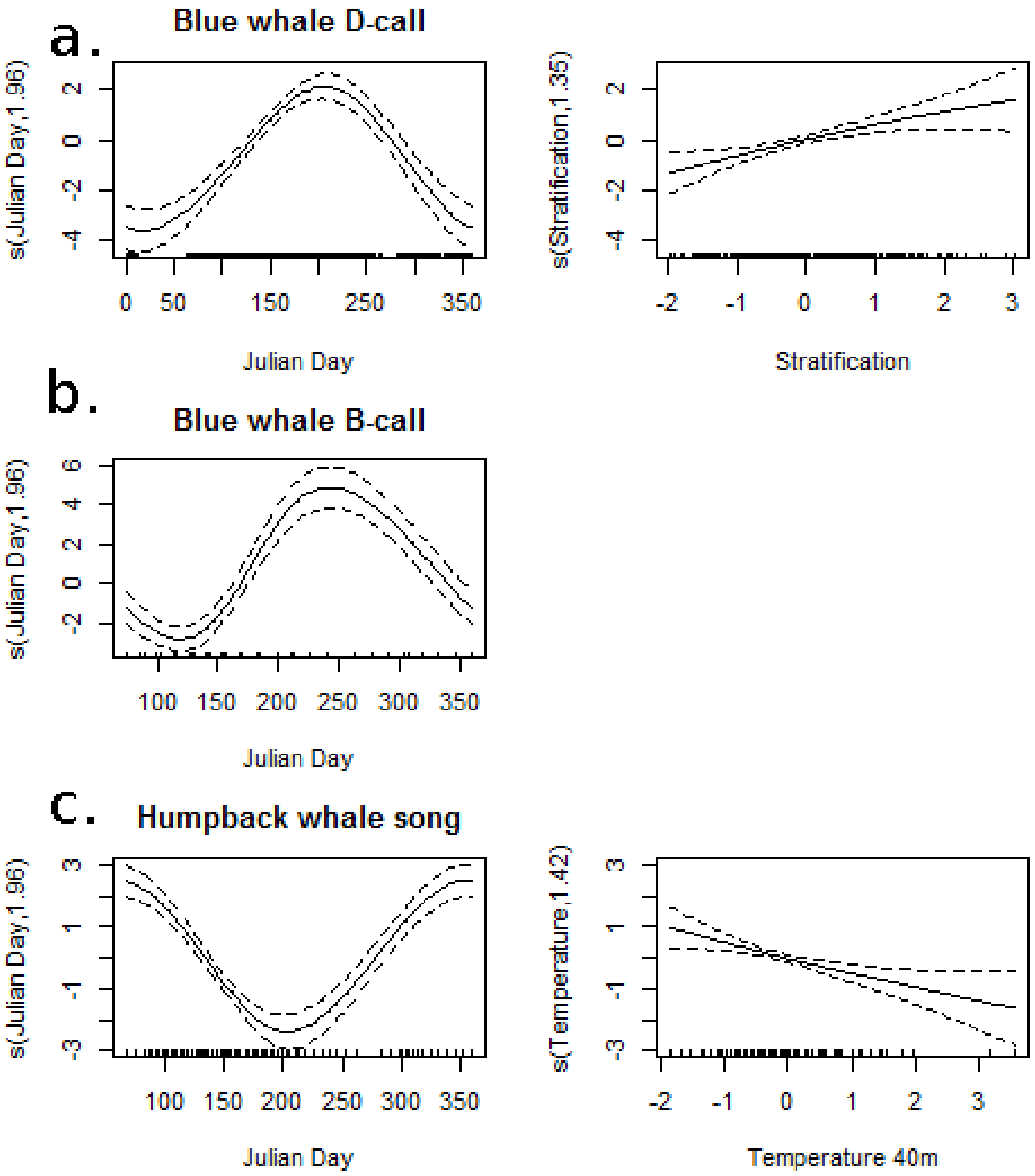

Figure 4.6: Partial contribution of explanatory variables to modelled response from best selected Generalized Additive Mixed Models for call counts of (a) blue whale D-calls (b) blue whale B-calls and (c) humpback whale song presence from 2010-2014 at Site C, ~50 km from Pt. Conception. Each panel shows the estimated relationship between the response variable and Julian Day and (if applicable), temperature or stratification index. The dotted lines represent the 95% confidence intervals. The rug plot shows the actual data values of the predictor variables.

Table 4.1: Final variables used for model input. m= meters; C = Celsius

Name	Depth of sensor	Notes	Units
SST	surface	Calculated as seasonal anomaly	°C
T_{40}	40m	Calculated as seasonal anomaly	°C
Stratification	surface, 40m	Difference between surface and 40m Calculated as seasonal anomaly	°C
temperature variability index	40m	Measures variability of temperature	–
Date	–	Julian Day	–
Year	–	Modelled as random effect	

Table 4.2: Precision (fraction of true positives over true positives and false positives) and recall (fraction of true positives over true positives and false negatives) rates for each HARP deployment for B-call and D-call detection efforts. *A detection kernel used from a previous deployment. **No true detections present and recall rate could not be calculated.

HARP			
	B-call		**D-call**
	Precision	Recall	Recall
CINMS 12	.86*	.83*	.71
CINMS 13	.86	.87	.67
CINMS 15	.93	.95	**
CINMS 16	.81	.84	.72
CINMS 17	.94	.93	**
CINMS 18	.89	.84	.67
CINMS 19	.88	.88	.67
CINMS 20	.97	.95	**
CINMS 21	.88	.64	.85
CINMS 22	.92	.82	**

Table 4.3: Truncated list of GAMM model parameters and associated AIC scores. Each temperature-related predictor represents the seasonal anomaly. The selected model for each call type is shown in bold. m= meters

Blue whale D-call				
Fixed Effects	Random Effect	AIC	%Deviance	n
Julian	Year	1781	31	284
Julian + SST	Year	1764	34	284
Julian + T_{40}	Year	1780	32	284
Julian + Stratification	**Year**	**1754**	**38**	284
Blue whale B-call				
Fixed Effects	Random Effect	AIC	%Deviance	n
Julian	**Year**	**341**	**57**	32
Julian + SST	Year	341	57	32
Julian + T_{40}	Year	341	57	32
Julian + Stratification	Year	341	57	32
Humpback whale song				
Fixed Effects	Random Effect	AIC	%Deviance	n
Julian	Year	271	50	81
Julian + SST	Year	271	50	81
Julian + T_{40}	**Year**	**265**	**55**	81
Julian + Stratification	Year	270	50	81

Table 4.4: Results of Wald tests of the significance of Julian Day and Temperature Variability Index in a fitted GAMM model for each call type (edf=effective degrees of freedom)

Term	*edf*	*F-statistic*	*p-value*
Blue whale D-call			
Julian day	1.96	57.76	p $<$ 0.001***
Temperature Variability Index	.01	0.93	0.92
Blue whale B-call			
Julian day	1.96	44.53	p $<$ 0.001***
Temperature Variability Index	$<$ 0.001	0.002	1.00
Humpback whale song			
Julian day	1.96	34.22	p $<$ 0.001***
Temperature Variability Index	$<$ 0.001	0.26	1.00

Chapter 5

Seasonal patterns of humpback whale (*Megaptera novaeangliae*) testosterone hormone levels

5.1 Introduction

The study of endocrine hormones has accelerated knowledge of marine mammal physiology, health, and reproduction (Hunt et al., 2013). Although blood is most commonly used in hormone-related research (e.g., in humans and captive animals), few studies use blood serum for baleen whale research with the exception of postmortem samples (Kjeld et al., 1992, 2003, 2004; Mogoe et al., 2000; Watanabe et al., 2004; Fukui et al., 1996). Cetacean researchers have typically used other matrices - feces (Hunt et al., 2006; Rolland et al., 2005), respiratory samples (Hogg et al., 2009), cerumen (Trumble et al., 2013), baleen (Hunt et al., 2014), and blubber (Mansour et al., 2002; Kellar et al., 2013b) - to study baleen whale endocrinology. Novel applications of techniques used in measuring reproductive hormones in the blubber of free-ranging cetaceans has allowed for analyses of samples collected over wide spatial and time scales, thus providing information about population-wide reproductive status. For example, studies of progesterone concentrations in female odontocetes (Kellar et al., 2006; Trego et al., 2013) and testosterone concentrations in male delphinids (Kellar et al., 2009) have shown significant differences in hormone concentrations between pregnant and nonpregnant females and mature and immature males. Similarly, (Mansour et al., 2002) and (Kellar et al., 2013a) were able to quantify significant progesterone values in pregnant minke and bowhead whales, respectively. There are no published studies of blubber testosterone concentrations in male baleen whales to date.

A historic study from the commercial whaling era showed that Southern Hemisphere humpback whales (*Megaptera novaeangliae*) had a seasonal peak in testes size from July to October that corresponded to the austral breeding season (Chittleborough, 1955). Testes size in whales of the corresponding austral feeding season was reported to be one-third smaller and lacked spermatozoa. It is not known whether testosterone concentrations mirror these seasonal changes in testes size. To investigate seasonality in hormone concentrations, we measured blubber testosterone concentrations in 35 opportunistic biopsy samples from male North Pacific humpback whales over several seasons in different habitats (Figure 5.1). We tested the expectation that the highest concentration of testosterone occurred during their breeding season, the lowest concentrations during their feeding season, and intermediate values during the fall shoulder season. We also investigated the change in testosterone concentration throughout the year.

5.2 Methods

To cover several seasons, we selected blubber biopsy samples from a large archive of tissue samples collected by Cascadia Research Collective as part of the SPLASH - Structure of Populations, Levels of Abundance, and Status of Humpbacks - project of 2004-2006 (Calambokidis, 2008; Barlow et al., 2011). Twelve blubber samples were selected for analysis: four samples from the winter breeding season (January - March) collected off Central America, four samples from the summer feeding season (May - September) and four samples from the fall shoulder season (October - November), collected off Washington and California. Past photo-identification and genetics have demonstrated the migration of humpback whales between Central America wintering areas and summer feeding areas off the US West Coast (Baker et al., 2013). An additional 23 samples from a summer field season conducted in Monterey Bay in 2011 were also analyzed. To investigate individual variation, we selected biopsies that were collected from the same individual based on photo-identification in different locations and times of the year. In the archive, we were able to find three individuals who were each sampled twice during different seasons for a total of six samples.

The hormonal extraction and measurement methods were modified from those described in (Kellar et al., 2006). Frozen tissues samples with at least 150 mg of blubber were subsampled and prepped for hormone extraction. Samples were homogenized in 1,400 L 100% ethanol using an automated, multi-tube Omni Bead Ruptor (Omni International, Kennesaw, GA) and processed for six 45-second periods in 2mL reinforced lysing tubes with 0.70 mm garnet beads (Omni International, Kennesaw, GA). The homogenates were individually mixed and transferred through three wash steps of 500 L 100% ethanol. Two mL of ethanol:acetone (4:1) were added to the homogenate, then mixed and centrifuged. Supernatants were aspirated and evaporated. Volumes of acetonitrile and hexane were added and thoroughly vortexed, centrifuged, and evaporated, resulting in a final residue. Samples were then applied to the enzyme immunoassay (EIA) kit ADI-901-065 (Enzo Life Sciences, Farmingdale, NY) with a standard curve range between 1.95 and 2,000 pg/mL. The reported interassay coefficient of variation (CV) ranged from 0.093 to 0.146 and intra-assay CV ranged from 0.078 to 0.108 for the two assays run on 35 samples. Extraction efficiency was determined by spiking select subsamples from 0 to 5 ng according to (Kellar et al., 2009). The resulting extraction efficiency rate was estimated as the percentage of testosterone recovered in the final quantification after correcting for the intrinsic amount measured in the nonspiked samples. The averaged extraction efficiency across all extractions was 96%.

5.2.1 Statistical analyses

Due to the small sample size in our study, randomization tests (Efron and Tibshirani, 1993) were performed on the samples, testing the expectation that summer concentrations are different from winter and fall concentrations. Additionally, a third-order polynomial regression was conducted to investigate how testosterone concentrations change over time. The value of 365 was added to Julian day only for winter samples in order to have the winter values occur directly after the fall values and thereby excluding the large gap in samples during spring.

5.3 Results

Male humpback whale testosterone concentrations were fit with a third-order polynomial regression, with Julian calendar day as a significant predictor ($r_2 = 0.672$; $P < .001$; Figure 5.2). Randomization tests of testosterone concentrations calculated from permutated samples (with replacement, 1,000 times) revealed significantly lower summer values than the winter breeding and fall shoulder seasons (Table 5.3). Moreover, fall and winter concentrations represented the highest values of testosterone within this study with no difference between the two seasons.

5.4 Discussion

These significantly greater concentrations of testosterone in North Pacific humpback whale blubber during the winter breeding season correspond with Chittleboroughs [1955] findings of a seasonal peak in testes size during the austral breeding season. Taken in context with terrestrial studies of testosterones known role in testis development and spermatogenesis (Dixson and Anderson, 2004), the co-occurrence of peak testis size and testosterone concentration supports the existence of a positive feedback loop within the pituitary-gonadal axis as seen in other marine mammalian taxa (Atkinson, 1997).

Increased mean testosterone concentrations in blubber observed during the shoulder fall season were greater than the expected. The expectation of intermediate testosterone values was based on (Kjeld et al., 1992, 2003, 2004), who showed steady increasing blood testosterone concentration in fin (*Balaenoptera physalus*), minke (*Balaenoptera acutorostrata*), and sei (*Balaenoptera borealis*) whales as the season progressed from summer to fall. Elevated fall testosterone values support the idea that the physiological conditioning for reproductive behavior occurs prior to the breeding season and outside of the geographical breeding regions, likely as preparation for the coming breeding season.

Of note, the three individuals who were each sampled two times were sampled in different seasons (Figure 5.2). One individual showed an increase in hormone values from summer to fall within the same year. Another individual showed a decrease in testosterone concentration from fall of 2004 to the summer of 2005. For the third individual, sbmpling from fall to winter showed a slight decrease in testosterone concentration, although this decrease was within the 95% confidence interval of the testosterone EIAs intra-assay variation estimate of 0.108 ng/g. The results from these three multi-sampled individuals emphasize intra-individual variation while also reflecting the overall sample populations seasonal trend.

Age-class is particularly important to note due to the significant differences in testosterone concentrations between immature and mature males seen in killer whales (Robeck and Monfort, 2006). Of the presumed 32 individual whales sampled in this study, 11 whales were not photographically identifiable. Of the 21 whales that were given a photo-identification number, eight were confirmed to be fully mature adults at the time of biopsy, determined from previous photo-id records spanning eight years. The whales that were not confirmed to be fully mature were at least juvenile, if not fully mature, males. No samples were taken from calves.

Despite the detectable seasonal trend, there are many factors which may contribute to the variability seen in this study. In addition to the aforementioned age-class and development stage of the individual males, other sources of variability include the location of the biopsy on the body of the animal as well as the depth of the blubber biopsy sample. (Kellar et al., 2009) was able to investigate the relationship between biopsy depth, body site, and testosterone in odontocetes. They found no significant effect of biopsy depth on testosterone concentration. Additionally, they found significantly lower values of testosterone only in the dorsal fin and caudal tail regions. However, these analyses were done on bycaught odontocetes and have yet to be investigated for larger baleen whales. As biopsy effort increases and biopsy archives grow in size, researchers can select for samples which minimize these sources of variability. Thus, alternative analyses can be performed on larger samples sizes tban what was possible for this study.

Our results have shown that the minimally-invasive collection of biopsies can yield and detect testosterone concentrations from blubber that generally reflect what we expect from humpback whale seasonal reproductive physiology. We have also shown that elevated testosterone concentrations during the fall season while animals are still on their high latitude feeding areas are unexpected but support the notion that reproductive conditioning starts months before peak breeding time. In light of previous findings that singing, another conferred reproductive behavior, is not limited to breeding grounds (Norris et al., 1999; Vu et al., 2012; Clark and Clapham, 2004), and shows a seasonality that resembles that of seasonal hormone concentration in two different ocean basins (Ch.2; Vu et al. (2012)) the hormonal patterns reported in this study may hold implications about breeding, singing behavior, or migration that we have yet to understand.

5.5 Acknowledgments

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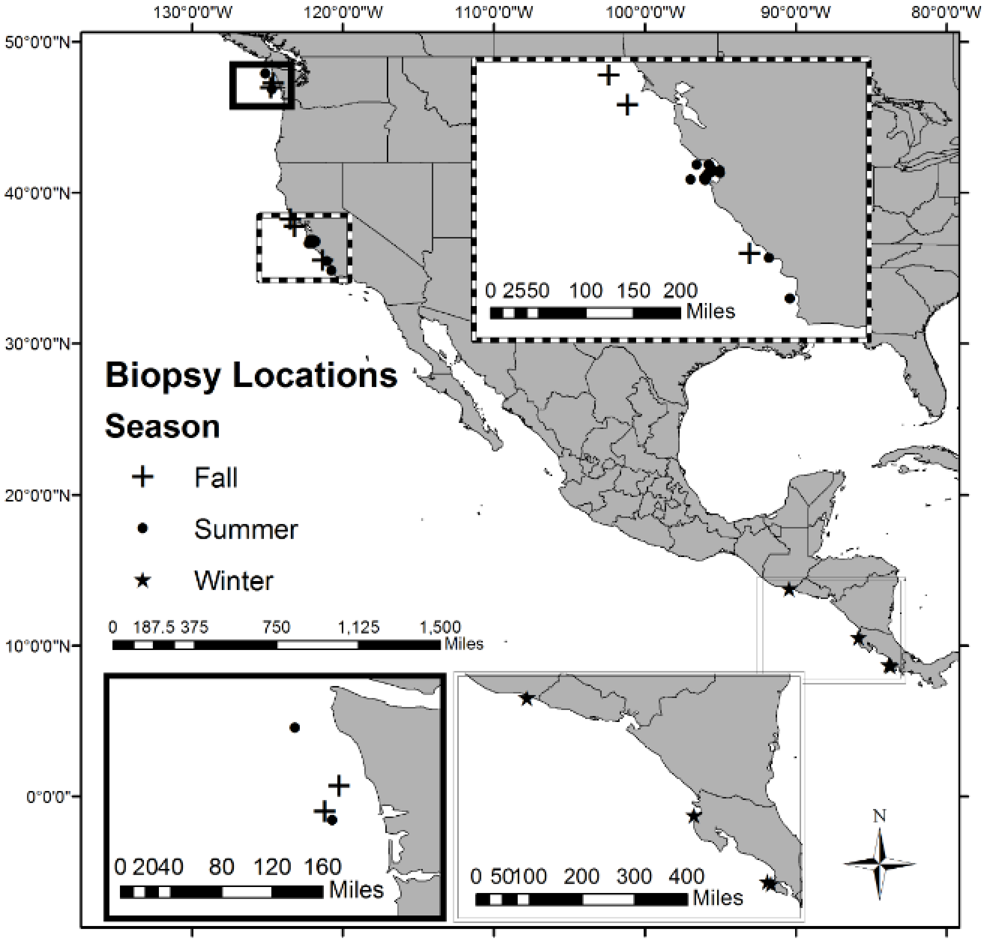


Figure 5.1: Humpback whale (*Megaptera novaeangliae*) biopsy sample locations during the winter, summer, and fall seasons from 2004 to 2011.

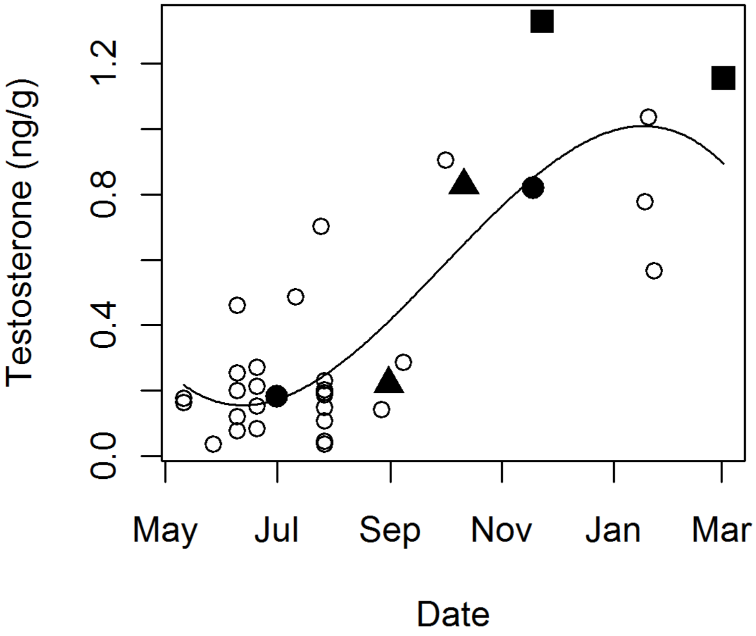
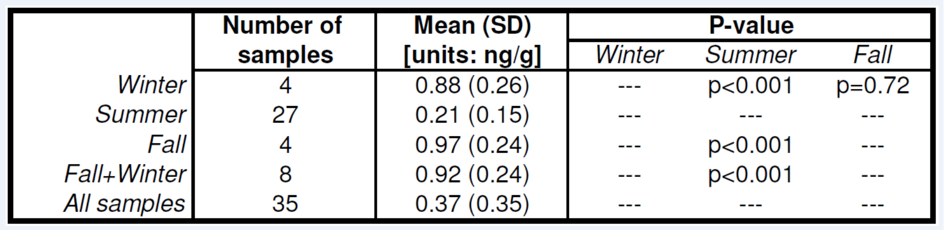


Figure 5.2: Testosterone extraction concentrations (ng/g) versus time of year of biopsy collection (Julian day). The three matching symbols refer to three individuals who were each sampled twice during different seasons of the year. The curve represents the polynomial fit: Testosterone = .0000163x3 + 0.00133x2 0.0305x + 2.29 where x represents the Julian calendar day. The value of 365 was added to the winter Julian day samples to have the winter values occur directly after the fall values and thereby excluding the large gap in samples during spring.



	Number of samples	Mean (SD) [units: ng/g]	P-value		
			Winter	*Summer*	*Fall*
Winter	4	0.88 (0.26)	---	p<0.001	p=0.72
Summer	27	0.21 (0.15)	---	---	---
Fall	4	0.97 (0.24)	---	p<0.001	---
Fall+Winter	8	0.92 (0.24)	---	p<0.001	---
All samples	35	0.37 (0.35)	---	---	---

Figure 5.3: P-values from randomization tests of humpback whale blubber testosterone concentrations over three seasons. Summer concentration values were significantly different from fall, winter, and pooled fall and winter samples. Fall and winter concentrations were not significantly different from each other.

Chapter 6

Conclusions

In this dissertation I described the general patterns of acoustic presence for three baleen whale species in the southern California Current ecosystem using data collected on passive acoustic recorders. I determined how call types varied seasonally and evaluated how these patterns are tied to behavioral context, internal physiological conditions, and external environmental conditions. Unlike previous studies which were seasonally biased due to logistical constraints, I analyzed the spatio-temporal distribution of calling presence found at over 75 stations occurring over four seasons in a nine-year period in order to describe the role environmental and seasonal factors play in the regional southern California ecosystem. I also examined cross-seasonal changes in endocrine-related physiology or at least those changes detectable in the blubber layer of cetaceans. In this concluding chapter, I suggest future research directions within the context of the main results of this dissertation, which will expand our understanding of the ecological and other determinants of whale distribution on feeding grounds.

6.1 Seasonality in the CCE and its role in the distribution of baleen whale acoustic presence

The general seasonal and geographic patterns of acoustic presence presented in this dissertation are supported by previous studies (Oleson et al., 2007c; Helble, 2013; Sirovic et al., 2012; Forney and Barlow, 1998; Campbell et al., 2015; Douglas et al., 2014). The seasonal occurrence reflects the mobility exhibited by a long-ranging, migratory Balaenopterid family. The acoustic presence of blue whales matches their seasonality in the region based on visual detection. They are heard when they are seen in southern California although calling intensity increases towards the end of their seasonal tenure. Humpback whales visual and acoustic coupling, however, does not match. Humpback whales are not singing as much when they are seen in higher proportion onshore in the summer months. Instead, they are singing briefly when they first arrive, cease singing throughout the summer months, and start singing again in the fall. Furthermore, offshore singing is attributed to travelling animals that are probably migrating to and from feeding and breeding grounds during the winter and early spring months. Fin whales are known to occur year-round in the region, but are heard calling more in the fall and winter months rather than during their visually-based peaks in summer and fall. Due to the mismatch in calling and visual detection rates across seasons, it is inferred that calling rates on an individual-level increase as reproductive season approaches. Humpback and fin whale individual-level calling increases during the winter months. Blue whale individual-level singing increases during fall. Increase in calling rates over time indicates cue rates for density estimation based on passive acoustics need to be appropriately qualified with temporal or behavioral context.

In Chapter 3, I demonstrated strong seasonal influence on baleen whale acoustic presence. Sea surface temperature (SST) was an important driver and, in the case of blue whales, was a probable proxy for seasonality. Because of the possible interactions between SST and season, basic environmental observations in habitat models can obfuscate the role that physical environmental habitat factors play in determining baleen whale distributions (as inferred from acoustic presence). While seasonality was the largest influence for baleen whale calling, much unexplained variance remains and further investigation is needed to fill this gap.

Cetacean-habitat investigations have been a well-explored topic, especially for predictive purposes. However, investigation of habitat-specific determinants often do not explore explanatory, descriptive, or mechanistic questions and therefore have undefined ecological underpinnings (Palacios et al., 2013). Sophisticated predictive models, while powerful, often fail to explain complicated relationships between predictors and responses due to increasing complexity and potential interactions. I presented explanatory models in this dissertation to serve as foundation for future predictive models. A predictive ecological model should be an approximation to true underlying ecological mechanisms (Burnham and Anderson, 1998). Therefore, alongside the powerful predictive habitat models, future studies should seek to build elegant and robust models designed to under the true underlying ecological mechanisms driving rorqual distribution.

Furthermore, when there is evidence for overwhelming influence of reproductive context, an alternative non-ecological, or hybrid model should be considered. For this dissertation, an endocrinological factor was investigated in Chapter 5. By quantifying a reproductive hormone, we showed that seasonal singing patterns matched the seasonal patterns observed in testosterone concentrations in humpback whale blubber and suggests a seasonal physiological conditioning that dictates calling behavior. However, the same issue applies here - that the seasonality of hormone concentration only resembles and correlates with the seasonality of the whale acoustic presence. Causality is still uninvestigated, untested, and unknown.

In the end, I believe that the timing of whale migration, length of residence of whales on feeding grounds, the spatial pattern therein, and peak in abundance and occurrence of call types likely depend on the combination of the funcional significance of each call type, behavioral context, and external environmental factors. This dissertation addressed each influence independently. Future work should be dedicated to procuring more relevant ecological data and consider all factors simultaneously.

6.2 Future steps: Follow the food

At large scales ($>$ 1000 km), the distribution of baleen whales broadly matches that of zooplankton biomass and primary production in the world ocean. That is, primary production is supported by higher levels of nutrients in coastal areas and upwelling zones, which support zooplankton growth and a seasonal co-occurrence of baleen whales. Biomass - that of whales, zooplankton, and primary production - is lower offshore where nutrients are scarce.

The timing of whale migration to these high production regions, therefore, is hypothesized to be controlled by bottom-up processes that structure and control zooplankton distributions. Due to the sampling constraints of this study in which the quarterly CalCOFI cruises occurred slightly before or after the first arrival of blue whales, and in which the data gaps occurred in the four-year HARP record in early spring, I could not test that hypothesis thoroughly in this dissertation.

However, at the mesoscale (100-1000 km) and submesoscale (1-100 km), zooplankton distributions, primary production, and the physical properties controlling both, are highly variable in space and time. While the mechanisms which shape baleen whale distribution (and zooplankton distributions, for that matter) at these scales are unclear, primary production at these scales is determined by nutrient availability linked to coastal, wind-driven upwelling. By measuring the properties of oceanic physical processes leading to primary production, one may be able to link these patterns with the distribution of top consumers, albeit removed by degrees of separation along the food chain. Auspiciously, for baleen whales, this food chain is relatively short due to their diets comprising of mainly secondary producers. The link between secondary production and seabirds in the CCE has been well-documented (Sydeman et al., 2010; Santora et al., 2011). The justification of linking physical properties and primary production to predators atop longer food chains (e.g., odontocetes) would be more difficult. Nevertheless, the variance explained by physical measurements such as temperature and mixed layer depth was low - no higher than 20% in this work. Predator (e.g., dolphins) and prey (e.g. fish) respond to environment variables similarly even if direct inclusion of a prey index does not necessarily improve model prediction (Torres et al., 2008). Therefore, future investigation should focus on the direct link to baleen whales in the food web: their prey.

6.2.1 Prey preferences

Blue whales off California have been shown to feed exclusively on krill species (Fiedler et al., 1998) namely *E. Pacifica* and *T. spinifera*, while fin whales and humpback whales have more general diets which include krill, copepods, and small schooling fish such as sardine, mackeral, herring, sandlance, and anchovies (Clapham et al., 1997; Flinn et al., 2002; Mizroch et al., 1984). Munger et al. [2009] correlated baleen whale visual detections with the prey data best available at the time: displacement volume of biomass in the water column. These macrozooplankton sampling methods, however, were not specifically geared toward measuring krill abundance. Therefore, despite a broad correlation of prey biomass and visual detections of whales, the macrozooplankton samples did not explain distributions unconditionally.

The relatively higher presence of fin whales and humpback whales in the winter and spring months off southern California might be linked to the less selective and more varied diet of these species versus blue whales. Humpback whales seem to switch their prey preference due to climatological drivers (PDO; Fleming et al., in press). The plasticity in prey preference has yet to be shown for blue whales. The seasonality of *E. pacifica* from the 1950's time series of the CalCOFI monthly cruises (Brinton, 1976) show high abundance of carbon biomass during the summer months (Figure 6.1) which supports the strong seasonal presence and marked arrival of blue whales in the region during this time. Whether the varied diets of fin and humpback whales may be linked to the seasonality of the other prey targets has not been investigated but would elucidate the strength by which prey availability determines year-round presence of fin and humpback whales.

The extent to which these prey items are available on breeding grounds, outside of the southern CCE, may also influence migration timing and acoustic behavior during feeding ground occupancy. Oleson et al. (2007c) hypothesized that the delay in song production on the southern California feeding grounds may be indicative of the time necessary for male blue whales to obtain adequate food resources following scant feeding on the southern breeding grounds. Summer singing increases can therefore coincide with more males having consumed sufficient prey and thus allocate more time to singing. If this hypothesis applies, we would expect to see years with little abundance of krill associated with either a delayed ramp up of song or an overall reduction in song. Since humpback and fin whales are known to be more generalized in their feeding preferences, their singing behavior can be less affected by fluctuations in a single prey species.

6.2.2 Hypothesis-based inquiry

The results presented in this dissertation relied extensively on environmental data collected by instrument packages and sampling protocols that were predetermined prior to my research due to an interdisciplinary approach to the CCE-2 mooring design and the long, historical legacy of CalCOFI. Environmental and biological data collection optimized for the study of cetacean distribution would require substantial effort to tightly couple distribution of euphausiids and other prey targets and calling cetaceans. Although the CCE mooring and CalCOFI data contain zooplankton measures, it was not in the scope of this dissertation to conduct analyses of prey samples or active acoustic measurements of prey.

Potential hypotheses that could be tested in future studies include: that cetacean call types are associated with prey abundance, patchiness, or both; that social and foraging cetacean acoustic calling behavior is moderated by prey availability; that cetacean reproductive acoustic displays may be related to the quality of habitat as represented by the availability feeding resources.

In Chapter 4, I found that temporal variability in temperature did not co-vary with changes in call counts of blue whales or humpback whales. The investigation of a temperature variability index was inspired by previous studies which shown strong connections between whale distribution and gradients (Baumgartner and Mate, 2003), fronts (Moore et al., 2002b; Tynan et al., 2005), or a persistence/hotspot index (Suryan et al., 2012). Fronts, or areas of quick change in properties, have been shown to be areas of increased biological production and accumulation (Powell and Ohman, 2015). However, the temperature variability index used in this dissertation was probably not representative of what may be considered a true front. This may be due to the lack of of horizontal spatial resolution in the index. Because zooplankton distributions at any given time are the result of an integration of many processes (e.g., advection, reproduction, growth, predation, and vertical migration) occurring over a period of weeks to months, it is not surprising that a rough temperature variability index could not be proven to be explanatory for whale calls. Further proof that fronts and their potential as the mechanism of bioaccumulation would require dedicated sampling of a different metric.

Although this dissertation incorporated the most available, complete dataset with the best temporal resolution over a substantial spatial scale, it is only at best seen as several two-week long snapshops four times a year. We still lack the true mechanistic understanding above and beyond explanatory or predictive power of simple variables such as SST and mixed layer depth. The question that follows is whether increasing the number of cruises, the number of data points, will allow us to predict baleen whale distribution based on environmental factors or will we need to reconsider which information to collect? With networked platforms of increased acoustic, visual, and environmental sampling, we may begin to ask and answer such overarching questions.

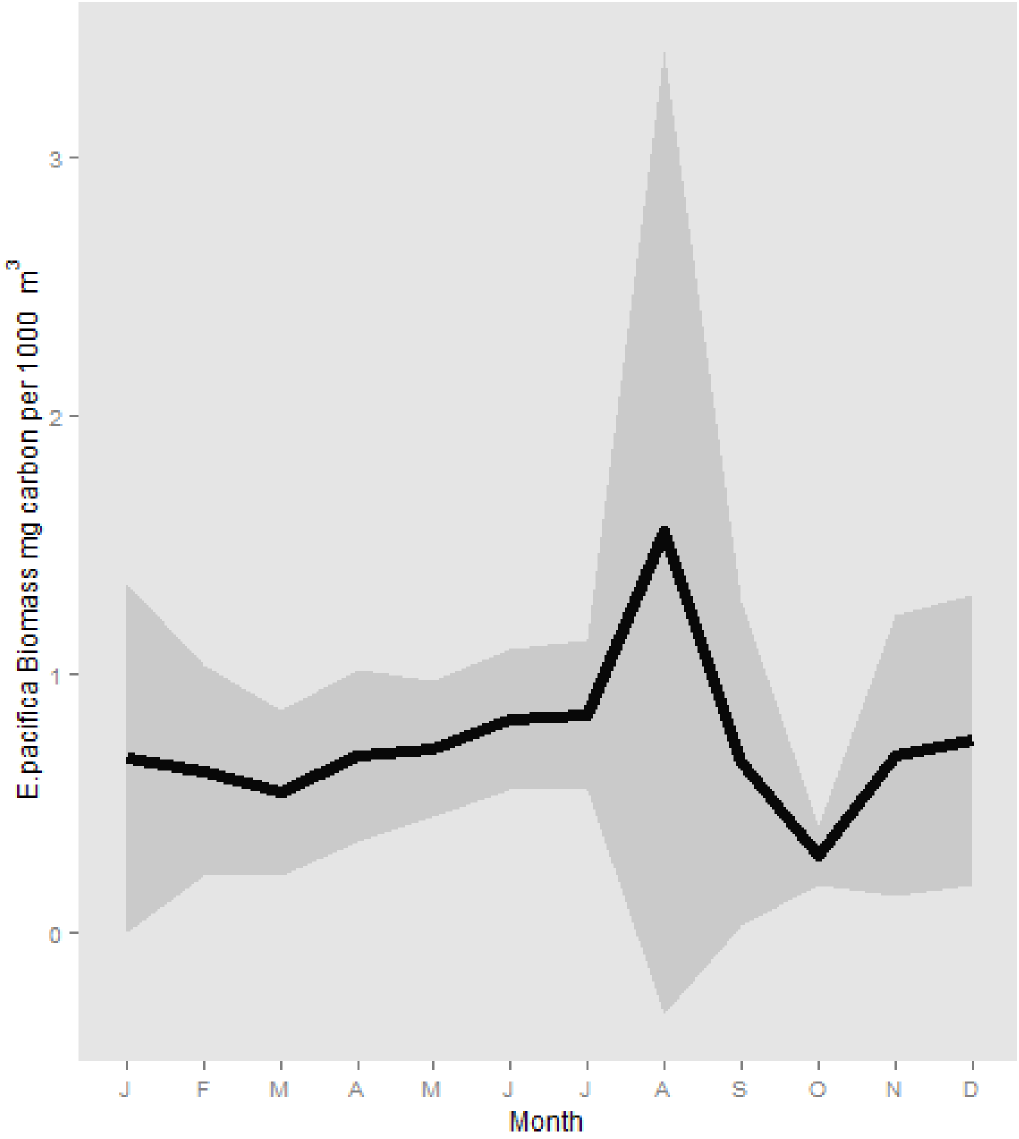


Figure 6.1: Seasonality of *Euphausia pacifica* biomass dominated by individuals in the adult class in the southern onshore lines of the CalCOFI (California Cooperative Oceanic Fisheries Investigations) grid from monthly cruises from 1950-1959. Gray area represent the 95% confidence intervals.

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