

GEOGRAPHICALLY DISTINCT B CALL VARIANTS IN THE NORTHEAST  
PACIFIC BLUE WHALE POPULATION

A Thesis

by

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Submitted to the Office of Graduate and Professional Studies of  
Texas A&M University  
in partial fulfillment of the requirements for the degree of

MASTER OF SCIENCE

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December 2020

Major Subject: Marine Biology

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## ABSTRACT

Passive acoustic monitoring is an effective tool for delineating population structure of blue whales (*Balaenoptera musculus*). Globally, there are at least nine regionally distinct blue whale songs, with two to three distinct groups within the North Pacific Ocean: The Northeast Pacific (NEP), Central-Western Pacific, and putative Japanese populations. Investigation of the fine-scale frequency characteristics of the NEP blue whale song B unit was conducted from passive acoustic data collected between 2010 and 2013. Data were collected at two low latitude, putative breeding sites at Palmyra Atoll and the Hawaiian Islands, and three higher latitude, feeding locations: off Southern California, off Washington state, and in the Gulf of Alaska. Frequency measurements were extracted along the entire contour of the third harmonic of B calls using a custom feature extraction tool in MATLAB. Data from these different geographic regions were compared to investigate possible fine-scale song separation within the NEP, and regionally distinct differences were observed. Calls recorded in the Gulf of Alaska presented a noticeable downshift in frequency that begins just past the midway point of the contour. This downshift was absent in calls recorded from Southern California, and calls recorded in Washington displayed intermediate characteristics of these two sites. Furthermore, frequency differences were observed between the three feeding grounds, with calls recorded from the Gulf of Alaska displaying the highest frequency on average, followed by Washington, followed by Southern California. Contours from Palmyra Atoll showed striking resemblances to those in Southern California, and contours from Hawaii

showed similarities to those of the Gulf of Alaska. Cluster Analysis further supported these results, by indicating that there are at least two unique B call groupings across these five sites, and contours from Washington and Hawaii were consistently grouped together while contours from Hawaii and Gulf of Alaska were consistently grouped together. These results provide the first evidence of vocally distinct subpopulations within the NEP, or that these animals are demonstrating vocal plasticity in a regionally-specific manner.

## DEDICATION

I would like to dedicate this thesis first and foremost to my family, who fostered my passion and love for marine biology, and constantly supported me throughout my pursuits. I would also like to dedicate this to the Oregon State Louis Stokes Alliance for Participation (LSAMP) program, without whom I may not have made it to where I am today.

Lastly, I would like to dedicate this to all the young students of color, struggling with the reality of being an underrepresented minority in a STEM field. Never give up.

## ACKNOWLEDGEMENTS

I would like to thank my committee chair, Dr. Ana Širović, as well as my committee members, Dr. Christopher Marshall and Dr. Randall Davis for their mentorship throughout the course of this project.

I would also like to thank Dr. Blair Sterba-Boatwright for his help with my statistical analyses. And of course, I'd like to thank my lab-mates, instructors and colleagues at Texas A&M University at Galveston for making my time here an informative and inclusive learning experience. Finally, I would like to especially acknowledge Dr. Jeppe Have Rasmussen for developing several custom MATLAB-based interfaces, which made the cleaning and preparation of my data much more efficient.

## CONTRIBUTORS AND FUNDING SOURCES

### **Contributors**

This work was supervised by a thesis committee consisting of Professor Ana Širović, Dr. Christopher Marshall and Dr. Randall Davis of the Department of Marine Biology. Dr. Jeppe Have Rasmussen contributed several custom-built MATLAB based interfaces, designed to make data cleaning more streamlined. HARP deployment and collection of the data analyzed in this project was conducted by the Scripps Whale Acoustics Lab. Development and maintenance of the Aloha Cabled Observatory (ACO) was made possible thanks to contributions from, among several others, the University of Hawaii, the Applied Physics Laboratory of the University of Washington, the Monterey Bay Aquarium Research Institute, and the Woods Hole Oceanographic Institute. All other work conducted for this thesis was completed by myself independently.

### **Funding Sources**

Graduate study was supported by a 2-Year Competitive Graduate Fellowship from Texas A&M University at Galveston. Funding for instrument deployment and retrieval was supported by US Navy Fleet Environmental Monitoring Program (Chip Johnson), Chief of Naval Operations N45 (Dr. Frank Stone and Ernie Young). Palmyra data was collected in cooperation with The Nature Conservancy, Palmyra Atoll Research Consortium, and US Fish and Wildlife Service. Development and deployment of the

Aloha Cabled Observatory was supported by grants from the National Science Foundation (NSF).

## NOMENCLATURE

ACO	Aloha Cabled Observatory
CWP	Central Western Pacific
HARP	High Frequency Acoustic Recording Package
NEP	Northeast Pacific



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## 1. INTRODUCTION

Blue whales (*Balaenoptera musculus*) are charismatic endangered species with widely distributed populations across the globe. Like all other balaenopterids, blue whales are obligate suspension feeders, that feed on small planktonic organisms (Goldbogen et al., 2011). Reaching a maximum length of approximately 30 meters, they are the largest animals to ever exist, which made them a prime target for the commercial whaling industry (Sears and Calambokidis, 2002). During the peak years of commercial whaling, over 360,000 individuals were harvested globally and although the majority of these animals were taken from the Southern Ocean, nearly all regions saw a dramatic decline in their population numbers (Clapham and Baker, 2018). Consequently, blue whales were granted worldwide protection from commercial whaling in 1966 by the International Whaling Commission. Shortly after, in 1970, they were listed as Endangered by the Endangered Species Conservation Act, the precursor to the Endangered Species Act, in the United States. Since receiving protections, efforts have been made to determine their populations' status, and what impacts from whaling still remain. Most recent population estimates are between 5,000 and 15,000 individuals remaining globally (Cooke, 2018), of which approximately 2,000 belong to the Northeast Pacific (NEP) population (Monnahan and Branch, 2015). However, due to the pelagic nature of these animals, estimating recovery rates and understanding population structure is challenging.

Ship-based surveys are a traditional approach to answering population-level questions. However, these surveys are limited to daylight hours and good sea-state conditions. Passive acoustic methodologies on the other hand, are operational under a greater variety of conditions and may be an efficient tool for understanding population structure, as has been proposed for blue whales (McDonald et al., 2006). In addition, deploying long-duration passive acoustic monitoring equipment across multiple locations, allows for a long-term investigation of the distribution, seasonality, and/or changes in abundance of these vocal marine mammals (Širović et al., 2004; Oleson et al., 2007; Širović et al., 2007; Širović et al., 2015).

### **1.1. Blue Whale Acoustics**

Baleen whales produce two types of species-specific sounds: songs and social calls. Both the songs and social calls produced by blue whales are generally high-amplitude (approximately 175-190 dB *re*: 1  $\mu$ Pa @ 1m) and low-frequency (10-110-Hz) signals (McDonald et al., 2001). While songs are mostly hypothesized to play a role in reproduction, the social sounds of blue whales appear to function in short-distance communication with conspecifics, as they are only produced by whales within close proximity to other whales (Oleson et al., 2007).

There are at least nine regionally distinct blue whale songs (McDonald et al., 2006). In the Northeast Pacific (NEP), their song is composed of two distinct units (Rivers, 1997; Lewis and Širović, 2018). The first unit is dubbed the A call, which is comprised of a

long series (about 20 s) of pulsed signals (Figure 1) (Rivers, 1997; McDonald et al., 2001). The second unit is a tonal B call which is a long-duration (10+ s) call with a slightly down swept contour (Figure 1 & 2)(Rivers, 1997; McDonald et al., 2001). B calls generally have their greatest spectral energy in the third harmonic, which has shown a consistent linear decline at a rate of about 0.4 Hz per year, dating back to the 1960s (McDonald et al., 2009). Repetitive sequences of AB calls have only been documented from solitary traveling males, and this apparent sex-distinction in calling behavior has been used as an indicator they likely serve a reproductive purpose (Oleson et al., 2007).

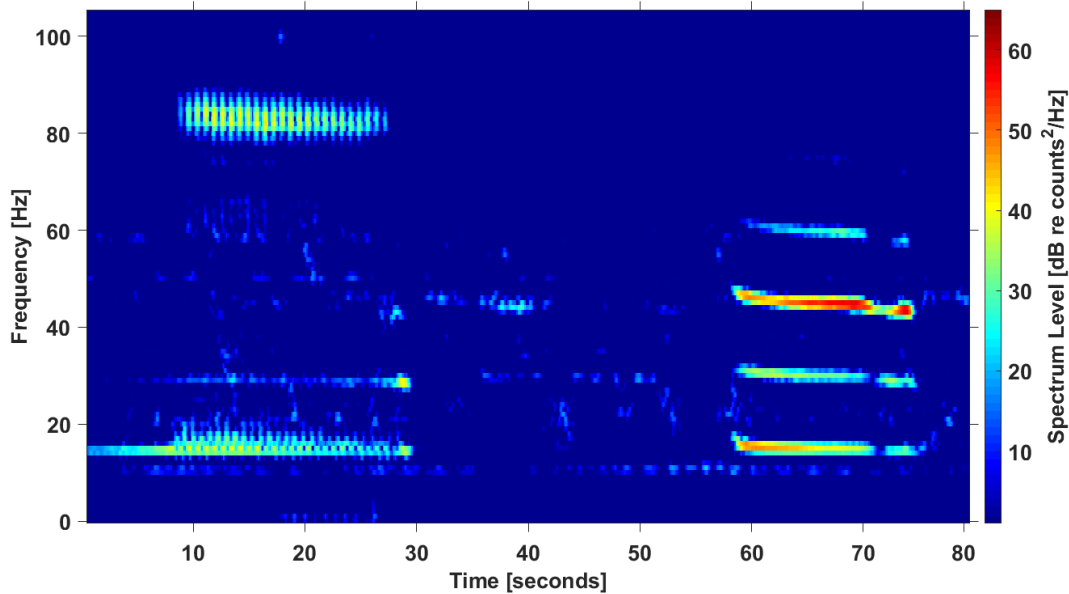


Figure 1: Example spectrogram of the NEP blue whale song recorded in Southern California (2,000-point Fast Fourier Transform, FFT, 90% overlap, Hann window) in 2010. On the left is the pulsed A call, followed by the tonal B call on the right.



NEP blue whales also produce non-song related signals including singular A/B calls and D calls. Singular A and B calls are structurally similar to the AB song units as described previously, however they do not occur in repetitive phrases. While these singular calls are also only known to be produced by males, they contrast AB songs in that they have only been recorded by males in close proximity to other whales, suggesting they may play a role in short-distance communication as well as reproduction (Oleson et al., 2007). D calls on the other hand have been recorded from both males and females, and were documented in between foraging bouts, often times from animals that are paired or in close proximity to other whales (Oleson et al., 2007). Structurally, D calls are more variable in nature, but can generally be described as approximately two second-long signals, that have a down-swept contour ranging from around 80Hz to 40Hz (Oleson et al., 2007).

## **1.2. Northeast Pacific Blue Whale Migrations**

NEP blue whale acoustic data supports a tentative migratory route between warm water, winter breeding grounds and cooler, nutrient rich waters for feeding. In the putative breeding grounds of the Eastern Tropical Pacific, B call detections peak between January and May, during the Northern Hemisphere winter and spring. Then, B call presence in this area declines between June and November, during the Northern Hemisphere summer and fall (Stafford et al., 1999). Furthermore, in the Gulf of California, another putative breeding ground, songs and AB singular calls also occur at their highest rates in the winter, between December and February, after which the detection rate decreases

until March (Paniagua-Mendoza et al., 2017). The presence of NEP blue whale B calls in the Central Pacific has not been examined in detail previously.

In the cooler and more productive waters of Southern California, B call rates peak in the summer and fall, between August and November (Širović et al., 2015). In the Gulf of Alaska, visual observations of blue whales have been exceptionally rare since the cessation of whaling (Stafford, 2003; Calambokidis et al., 2009). However, acoustic evidence supports a summer/fall peak in calling behavior here as well, with peak B call occurrence falling between September and October, and indicates a potential return to pre-whaling migratory behaviors (Calambokidis et al., 2009; Širović et al., 2016). The totality of these studies strongly supports the seasonal movement of the NEP blue whales between warmer waters during winter and spring months, and cooler, more productive high latitude waters during the summer and fall months.

A preliminary study investigating the variations of NEP blue whale B calls at different foraging regions found fine-scale frequency differences in calls recorded in Southern California, Washington and in the Gulf of Alaska (Figure 2)(Širović et al., 2016). One difference was in the average call frequency (approximately 48 Hz calls in the Gulf of Alaska, 46.5 Hz in Southern California, and 47 Hz in Washington in 2012; Figure 3). The other was a in the down-step in frequency towards the end of the call; the calls recorded in the Gulf of Alaska had a down-step in frequency, whereas the calls recorded

in Southern California did not. The calls off Washington displayed intermediate characteristics.

These results indicate that there might be additional population structure among blue whales within the North Pacific (Širović et al., 2016). Therefore, in this thesis I investigate the fine-scale frequency characteristics of NEP blue whale B calls recorded at both the high and low latitude locations, using an archive of passive acoustic data collected from 2010 until 2013.

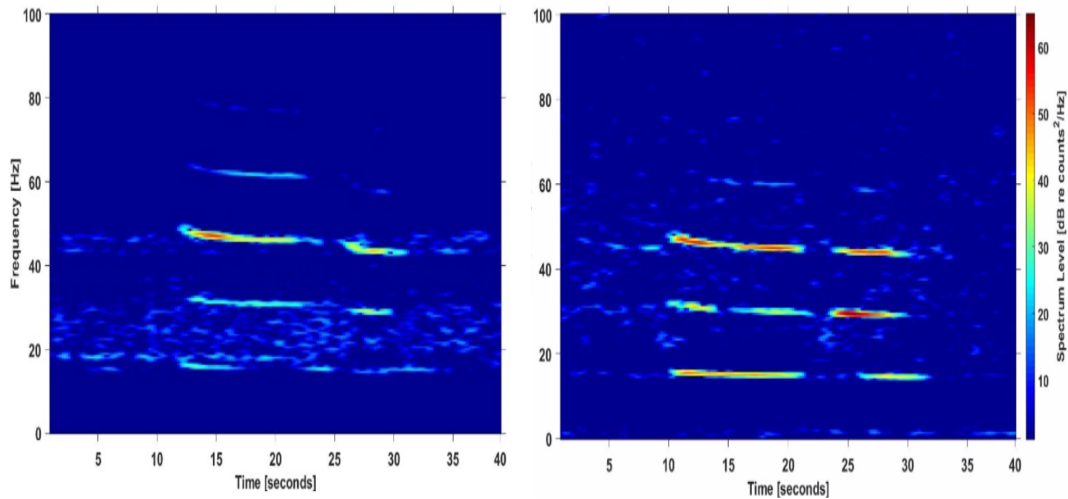


Figure 2: Example spectrograms of blue whale B calls recorded in the Gulf of Alaska (left) and Southern California (right) (4,000-point FFT, 90% overlap, Hann window). Note an apparent down-step in frequency in the Gulf of Alaska B call (beginning at ~25s), and its absence in the Southern California B call.

## 2. OBJECTIVES AND HYPOTHESES

### 2.1. Objectives

My goal was to investigate NEP blue whale population structure by exploring the variability in the fine-scale frequency characteristics of their distinctive B call. Calls recorded along both the west coast of North America (high latitude locations), and in the Central Pacific Ocean (low latitude locations) were used for this study. Specifically, the two objectives of the study were:

- 1) To determine if differences in the fine-scale frequency features of NEP blue whale B calls can be found at both high and low latitude sites across the North Pacific.
- 2) To evaluate the interannual persistence of regionally distinct differences in blue whale B call features across the North Pacific Ocean.

### 2.2. Hypotheses

- 1) There is a difference in average B call contours from Southern California and the Gulf of Alaska, with B calls from Washington exhibiting intermediate traits.
- 2) Average fine-scale frequency contours measured from Palmyra Atoll data are different from those measured from the Hawaiian Islands data.
- 3) Average fine-scale frequency contours measured from sites at lower latitudes will show matching characteristics to at least one site at higher latitudes.

- 4) Average fine-scale frequency contours at all sites will show a linear annual decrease in third harmonic frequency, consistent with the trend observed by McDonald et. al (2009).
- 5) Notwithstanding the predicted linear decrease in fundamental frequency, general contour shape and structure of blue whale B calls will remain consistent from year to year at each site.

### 3. METHODS

I used passive acoustic data collected at five sites between 2010 and 2013 for analysis of blue whale song features. Three of these sites, Southern California, Washington, and the Gulf of Alaska, are known feeding grounds located off the west coast of North America (Calambokidis et al., 2009) and the remaining two sites, Palmyra Atoll and the Hawaiian Islands, are tentative breeding grounds in the Central Pacific (Figure 3). Data were collected at two locations within the Gulf of Alaska. Using data from two sites within the Gulf enabled me to increase both sample size and the number of years with data.

Because blue whale song occurs seasonally, and their seasons at their feeding grounds span two traditional calendar years, data discussed in this study will be presented in terms of two-year increments which describe the season in which they were collected. For example, any data collected from a site between August, 2011 and January, 2012, will be presented as the 2011-2012 season for that site.



### **3.1. Passive Acoustic Data Collection**

Passive acoustic data were collected using two systems. High Frequency Acoustic Recording Packages (HARPs) were used to collect data from Southern California, Washington, Gulf of Alaska and Palmyra Atoll. These are bottom-moored acoustic recording systems that contain a hydrophone which is typically suspended 10m off the seafloor, an acoustic release system for instrument retrieval, data loggers for data acquisition, and batteries enabling long-duration of recording (Wiggins & Hildebrand, 2007). All HARPs sampled at a rate of 200 kHz with the exception of one deployment in Southern California which sampled at a rate of 320 kHz. Collected data were decimated by a factor of 100 (from 200kHz to 2 kHz and from 320 kHz to 3.2 kHz), leading to an effective bandwidth of 10-1000 Hz and 10-1600 Hz, respectively. All sites had continuous sampling, except one deployment in the Gulf of Alaska which used a duty cycle of 10 min of sampling every 12 minutes. Long-term spectral averages (LTSAs) were calculated from down-sampled data by calculating 5 s averaged spectra with a frequency resolution of 1 Hz. Data from Hawaii were collected via University of Hawaii's ALOHA Cabled Observatory (ACO), a deep-sea multi-purpose observatory that has continuously collected passive acoustic data since 2011. ACO data were collected at a sample rate of 24kHz, and were decimated by a factor of 12, which produced data with a Nyquist frequency of 1kHz.

Blue whale calls can propagate over long ranges that exceed 100 km (Stafford et al., 1998; Širović et al., 2007). Acoustic detection area for these low frequency calls is



dependent on the bathymetry of each deployment site (Širović et al., 2015). The use of two deployment sites in the Gulf of Alaska allowed for coverage of signals across much of the deep waters of the Gulf. Deployments in Washington occurred in deep water just off the continental shelf, and therefore detected offshore signals. HARPs in Southern California were deployed in a basin within the Southern California Bight and therefore received signals originating from within that basin. In the Central Pacific, recorders were placed on the north facing slope of Palmyra atoll, and 100 km north of Oahu in the abyssal plain. Therefore, they received signals originating to the north from their nearest respective body of land or underwater ridge.

### **3.2. Call Sampling**

NEP blue whale B calls were manually located and sampled from long-term acoustic data collected between 2010 and 2013. These years were selected due to the degree of overlap in available recordings across the five regions, which allowed for comparisons across sites within individual years (Tables 1 & 2). Data from all sites, with the exception of Hawaii, were manually reviewed using LTSAs with a window-size of 1-hour, and days were selected for sampling based on the abundance of B calls with a strong signal-to-noise ratios. Hawaii had data available from 2011 to 2013. However, these data were stored in a format that was not conducive to the formation of LTSAs, which made manual scrutiny of the data, via inspection of individual spectrograms, much less efficient. Therefore, data were sampled from expected months of peak occurrence during two breeding seasons, 2011-2012 and 2012-2013.

To the maximum extent practicable, I conducted contour extraction from at least five days per month at each site. In an attempt to avoid over-representing any single animal in the study, back-to-back days were not sampled whenever possible, and all calls sampled within one day were averaged and the average was used in all subsequent analyses. The following contour extraction procedure was followed for B calls with high signal-to-noise ratios that occurred on selected days.

Table 1: Sampling effort conducted for each site. Months Sampled indicates months during which data were scrutinized to find high quality B calls. # Days Sampled represents number of days during which contour extraction occurred and # of Contours is a total number of contours extracted during that month.

Site	Season	Months Sampled	# Days Sampled	# of Contours
Gulf of Alaska	2011-2012	Aug-Nov	15	82
	2012-2013	Sep-Nov	15	128
	2013-2014	Sep-Nov	14	181
	Total		44	391
Washington	2011-2012	Dec-Jan	10	134
	2012-2013	Sep-Feb	26	330
	Total		36	464
Southern California	2010-2011	Jul-Nov	22	215
	2011-2012	Jul-Jan	27	292
	2012-2013	Aug-Dec	25	300
	2013-2014	Jul-Dec	29	395
	Total		103	1,202
Hawaii	2011-2012	Dec	2	54
	2012-2013	Jan	2	36
	Total		4	90
Palmyra Atoll	2010-2011	Jun-Dec	36	102
Grand Total			223	2,249

Table 2: Recording times at the six deployment locations. Boxes shaded grey represent months in which data were available. Boxes with no fill indicate months in which no data were collected at that location.

[illegible]

### **3.3. Contour Extraction**

I extracted the frequency contour of each selected call using the following protocol. First, a spectrogram for the call of interest was plotted in the MATLAB-based software Triton version 1.81. B calls from Southern California had particularly strong signal strengths, and therefore spectrograms from this site could be created with a 0.25 Hz frequency resolution. Data from all other sites were created with a 0.5 Hz frequency resolution. The resulting time resolution in the contour measurements were 0.4 s for Southern California and 0.2 s for all other sites. Next, using custom MATLAB software, I outlined the boundaries of each call, and the following features were automatically extracted from within the box: absolute time at the start of measurement, and along each time-step – peak amplitude, frequency at peak amplitude, and relative time of that step along the length of the call (Figure 4). Extracted contours thus consisted of a frequency measurement every 0.4 or 0.2 s along the duration of a call, and the corresponding amplitude values for those frequency measurements.

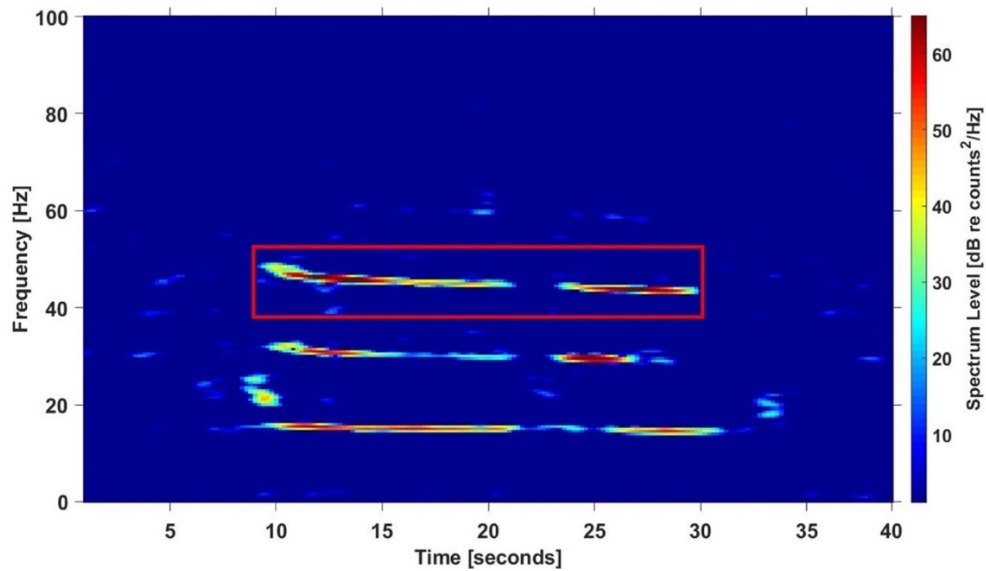


Figure 4: Example spectrogram of blue whale B call recorded in Southern California in 2010 (4,000-point FFT, 90% overlap, Hann window). The red box indicates the marked call for the contour extraction. Frequencies were extracted every 0.4 or 0.2 seconds (site-dependent) along the maximum amplitude contour within the box. Low amplitude sections such as that representing the gap in the call (at approximately 20-23 seconds) were removed from subsequent analysis.

### 3.4. Data Cleaning

Upon completion of contour extraction for each site, features extracted from each call were reviewed for their signal strength using a custom-built MATLAB based program. Within each site for each year, an amplitude threshold roughly equivalent to the background noise level was empirically determined. Frequency contours were plotted one at a time (frequency on the y-axis, timesteps on the x-axis) and frequency measurements along the contour with a corresponding amplitude value below the desired threshold were removed. If, after the removal of these data points, a contour was still largely complete, taking special consideration not to lose the beginning features of the

call, it was saved for later analyses. If too much of the contour was deemed to be missing, the entire contour was removed from the dataset.

### **3.5. Contour Averaging**

Once all the calls from a given site were measured and cleaned, daily average contours were calculated to avoid over-representing any individual animal in this study. In addition, monthly site-average contours and annual site-average contours were generated and plotted for visual comparison of B call structure across sites and years.

### **3.6. Analyses**

To determine if these data corroborate the 0.4 Hz annual decrease in the third harmonic frequency observed by McDonald et al. (2009), I fit linear models to these data using simple linear regression using the *lm()* command in RStudio (version 3.5.1) (R Development Core Team, 2018). To do this, a single frequency measurement was extracted from all of daily averaged contours at the point six seconds after the time of peak frequency. These data were then used to look for frequency shifts across months and years. This specific time-step was selected because it falls within the region where the slope of the B call contour is the least steep. Therefore, selecting a point within this region ensured consistency in the measurements in spite of any minor variabilities in call duration that may be present in the data. Per my hypotheses, contours from each site were treated as if they came from unique grouping of animals, and therefore regressions were run on data from each site independently. This allowed me to observe whether the

animals at each respective site have shifted their frequency at different rates. Data from Palmyra and Hawaii were not included in regression analyses due to the sparsity of data from these sites.

To verify the results of the regressions, diagnostic plots were created for each site's dataset, to test for the assumptions of linear regression. Residual versus fitted plots were created to ensure that a linear model was, in fact, the correct model to fit to the data, and to ensure that there were no issues with homoscedasticity. I used normal Q-Q plots to ensure all datasets had a normal distribution of their residuals. And finally, I checked for presence of influential data points via Cook's distance plots (Quinn and Keough, 2002).

Next, tests were conducted to see whether B call contours could be grouped by site according to their contour structure and frequency characteristics. The first step in these analyses was to quantify contour structure. This was done by extracting 10 representative measurements from each of my daily averaged contours. These measurements included the peak frequency, as well as frequency measurements in 3 second intervals following the peak frequency, up to 15 seconds after the peak. Also included was a measurement of the slope between the 2 second mark and 4 second mark of each contour and finally, to quantify the downstep in frequency, the difference in frequency between a point just prior to and just after the downstep in frequency was calculated.

Once all contours were quantified and compiled into a single dataset, cluster analyses were conducted using both k-means clustering and Kruskal's non-metric multidimensional scaling. These were completed using the *kmeans* command in the *stats* package and the *isoMDS* command in the *MASS* package in RStudio, respectively. K-means clustering requires that the number of clusters (k) be stated prior to analysis. Three independent methods were used to determine what k-value should be used, and results using all recommended values are reported. The three methods of selection were the gap statistic (Tibshirani et al., 2000), K-means partitioning using a range of values of k (Calinski and Harabasz, 1974), and selection of k in k-means clustering based on Pham et al. (2004). These tests were conducted, respectively, using *clusGap* in the *cluster* package, *cascadeKM* in the *vegan* package and *kselection* in the *kselection* package.



#### 4. RESULTS

At least two regionally distinct B call variants were found across all sites – one dominant in Southern California with a similar variant recorded off Palmyra and the other in the Gulf of Alaska with similar calls found off Hawaii (Figure 5). There were two characteristics that differentiated them from one another, frequency and the presence (or absence) of a notable downstep in frequency that began approximately 10-12s from the start of the call. On average, B calls from the Gulf of Alaska were produced at a higher frequency than those recorded from both Washington and Southern California (Figure 5). The downstep in frequency was much more prominent in calls recorded from the Gulf of Alaska than it was at the other two feeding grounds, where this step was more or less non-existent. While calls from Washington consistently displayed intermediate characteristics between the other two feeding sites, they were more similar to B calls from Southern California both visually (Figure 5) and statistically (Figures 6-7). Contours from both putative breeding grounds in the Central Pacific displayed similar characteristics to B call variants observed in the NEP foraging grounds. Data from Palmyra Atoll yielded mean B call contours that strongly resembled B calls of the Southern California variant, whereas contours measured from Hawaii displayed a very prominent downstep in frequency, and as such bore strong resemblance to the Gulf of Alaska B call variant (Figure 5). The matches in contour structure between breeding and feeding grounds were further supported with cluster analysis (Figures 6-7) and multidimensional scaling (Figure 8).

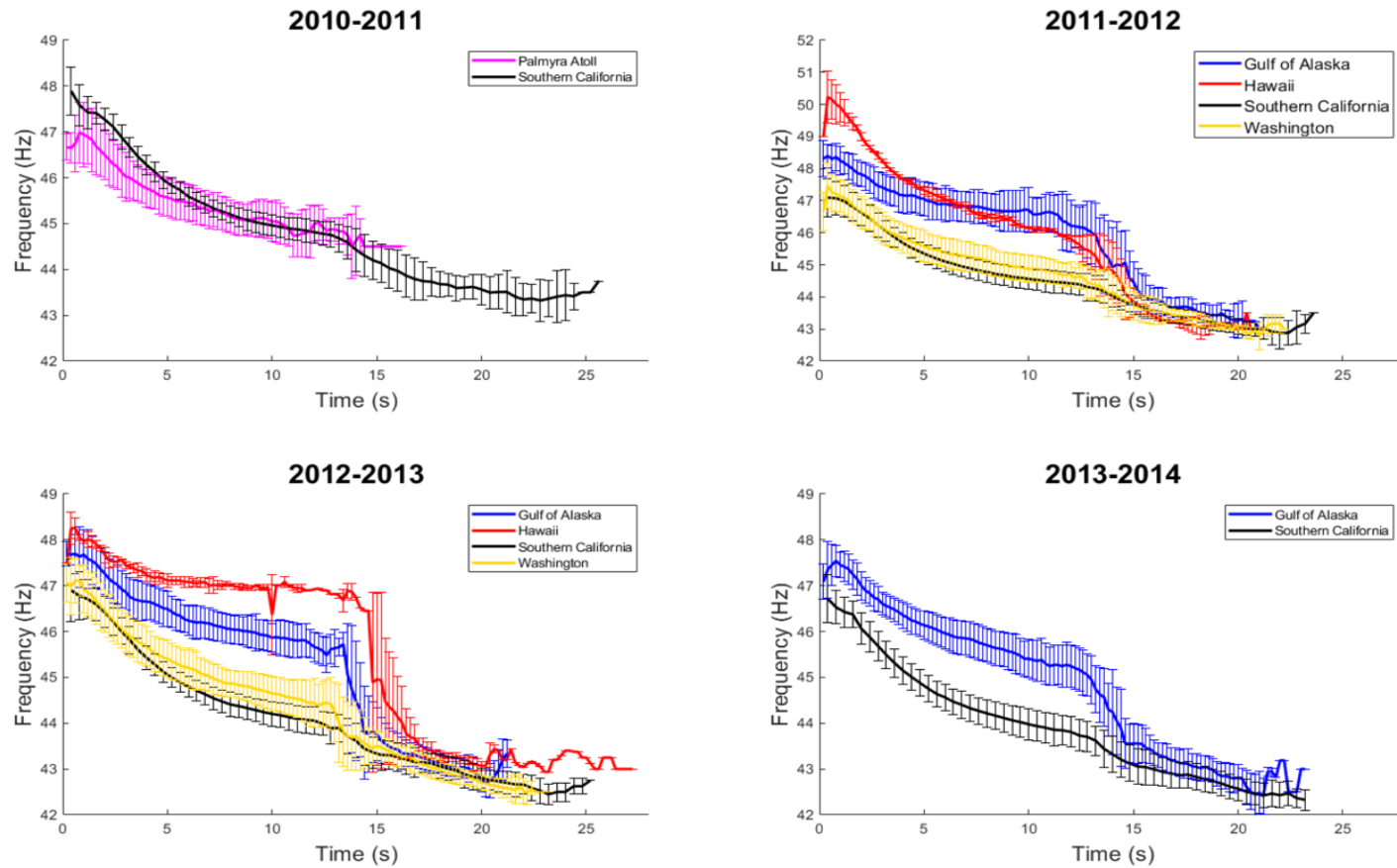


Figure 5: Average NEP B call contours measured from all five sites for each analyzed season. Error bars represent the standard deviation of all daily averaged measurements that were used to generate the seasonal average value for each timestep

#### **4.1. Clustering of contours from different sites**

All three independent methods for determining the number of clusters suggested using two clusters for the 2011-2012 data, and therefore, this was the number of clusters selected for that analysis. One of the resulting clusters contained all Gulf of Alaska contours, all Hawaii contours, and 2 out of 10 Washington contours (Figure 6). The other cluster had all Southern California contours and 8 out of 10 contours from Washington (Figure 6).

Tests for determining the appropriate number of clusters for 2012-2013 data indicated that either two or three clusters should be used. Thus, I ran analyses using both values. Using the assumption of two clusters, 100% of contours from Washington and Southern California were clustered together along with one contour from the Gulf of Alaska (Figure 7A). The majority of contours from the Gulf of Alaska (13/14) and both contours from Hawaii were sorted into the second group (Figure 7A). When three clusters were assumed, all three feeding sites were mostly correctly placed into their own groups, with only a small degree of overlap (Figure 7B). The strongest overlap occurred between Southern California and Washington. In one group, 5/25 contours from Washington were clustered with 21/25 contours from Southern California. The remaining contours from each of these two sites were placed together in a second group, meaning that ultimately, all contours from Washington and Southern California were sorted together, across two groups. The third group contained only contours from the Gulf of Alaska and

Hawaii. This pattern of grouping is consistent with the analysis of two clusters as well as the site-averaged contour plots for 2012-2013.

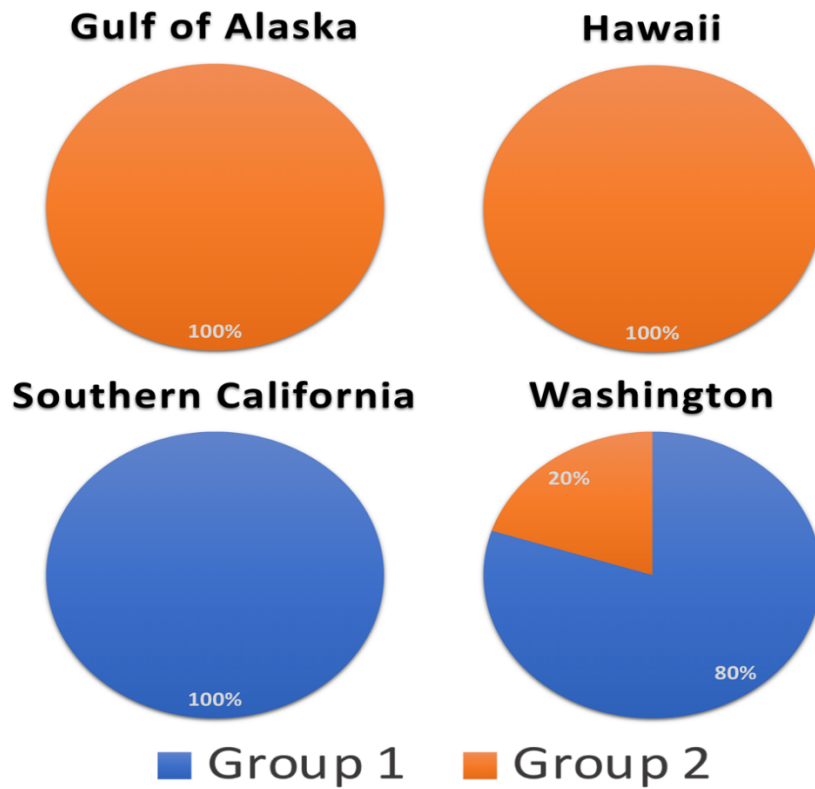


Figure 6: Results of cluster analysis for 2 clusters for the 2011-2012 season. Each pie represents a site, and colors indicate what proportion of contours were grouped into group 1 (blue) or group 2 (orange).

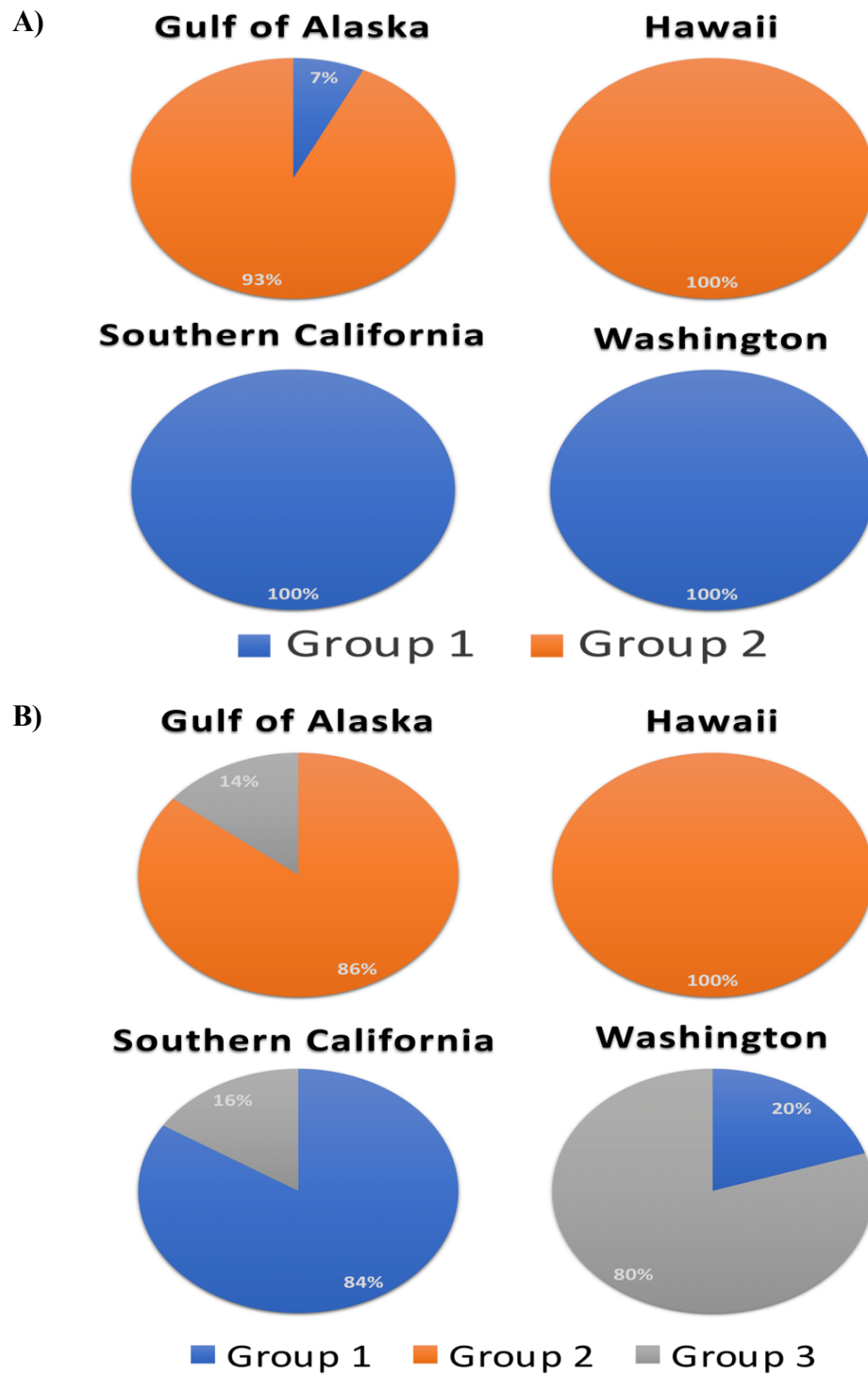


Figure 7: Results of cluster analysis results for the 2012-2013 season using (A) 2 and (B) 3 clusters. Each pie represents a site, and colors indicate what proportion of contours were grouped into group 1 (blue), group 2 (orange) and group 3 (grey).

In the multidimensional scaling plots, at least two distinct groupings are apparent, one including data from the Gulf of Alaska and Hawaii, and the other including data from Southern California and Washington, with very little overlap between the two groups (Figure 8). Furthermore, the stress values were 6.8 for 2011-2012 and 6.9 for 2012-2013 data, which indicates that the representation of the true distances between data points, when plotted into two-dimensional space, can be classified as “good” (Dugard et al., 2010). These results further support the clustering into two unique groupings of B call variants in these data.

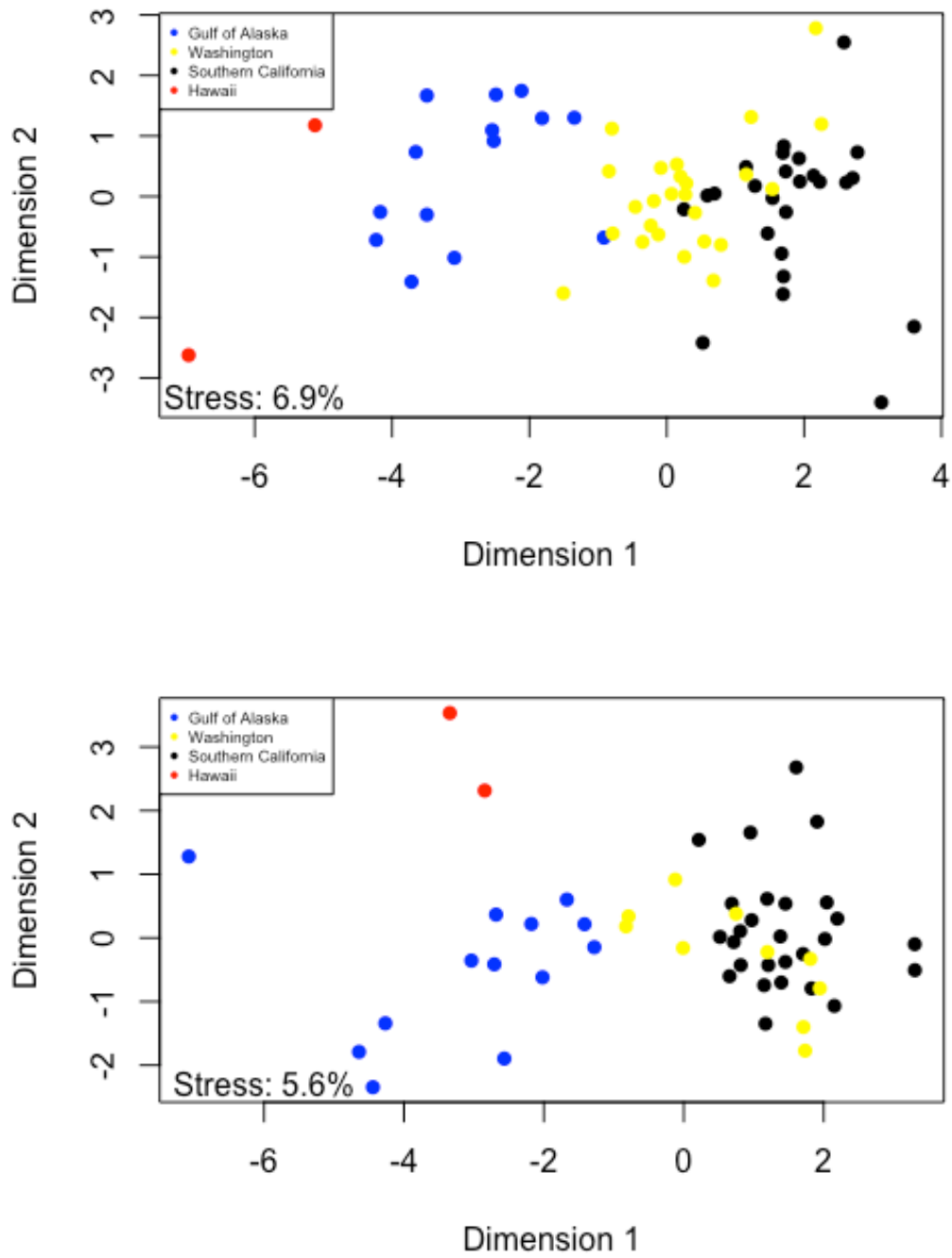


Figure 8: Results of Kruskal's non-metric multidimensional scaling analyses performed on quantified contours from the 2011-2012 (top panel) and 2012-2013 seasons (bottom panel).

## 4.2. Frequency shift

Diagnostic plots created for these datasets indicated the assumptions of simple linear regression were mostly supported across the data. Residual versus fitted plots revealed that there were no issues with homoscedasticity and that a linear model is the correct model for all sites (spline p-values all  $>0.05$ ). The residuals from the Gulf of Alaska and Washington data were normally distributed (Shapiro-Wilk test,  $p = 0.74$  &  $0.89$ , respectively). The Southern California displayed only minor issues with normality but these are considered relatively unimportant (Sterba-Boatwright, personal communication). No sites contained measurements with a Cook's distance  $>1$ , meaning there were no influential points amongst my datasets.

B calls from both the Gulf of Alaska and Southern California showed a significant linear decline in third-harmonic frequency (Figure 9). In the Gulf of Alaska, third-harmonic frequency declined at a rate of  $0.48$  Hz/year, with a 95% confidence interval of  $0.63 - 0.34$  ( $R^2 = 0.51$ ,  $p = 3.51 \times 10^{-08}$ ). In Southern California, frequency declined at a rate of  $0.32$  Hz/year, with a 95% confidence interval of  $0.37 - 0.27$  ( $R^2 = 0.63$ ,  $p < 2.2 \times 10^{-16}$ ). Over the two seasons in which data were available for Washington, B calls showed an insignificant decline in the third-harmonic frequency ( $R^2 = 0.03$ ,  $p = 0.15$ ).



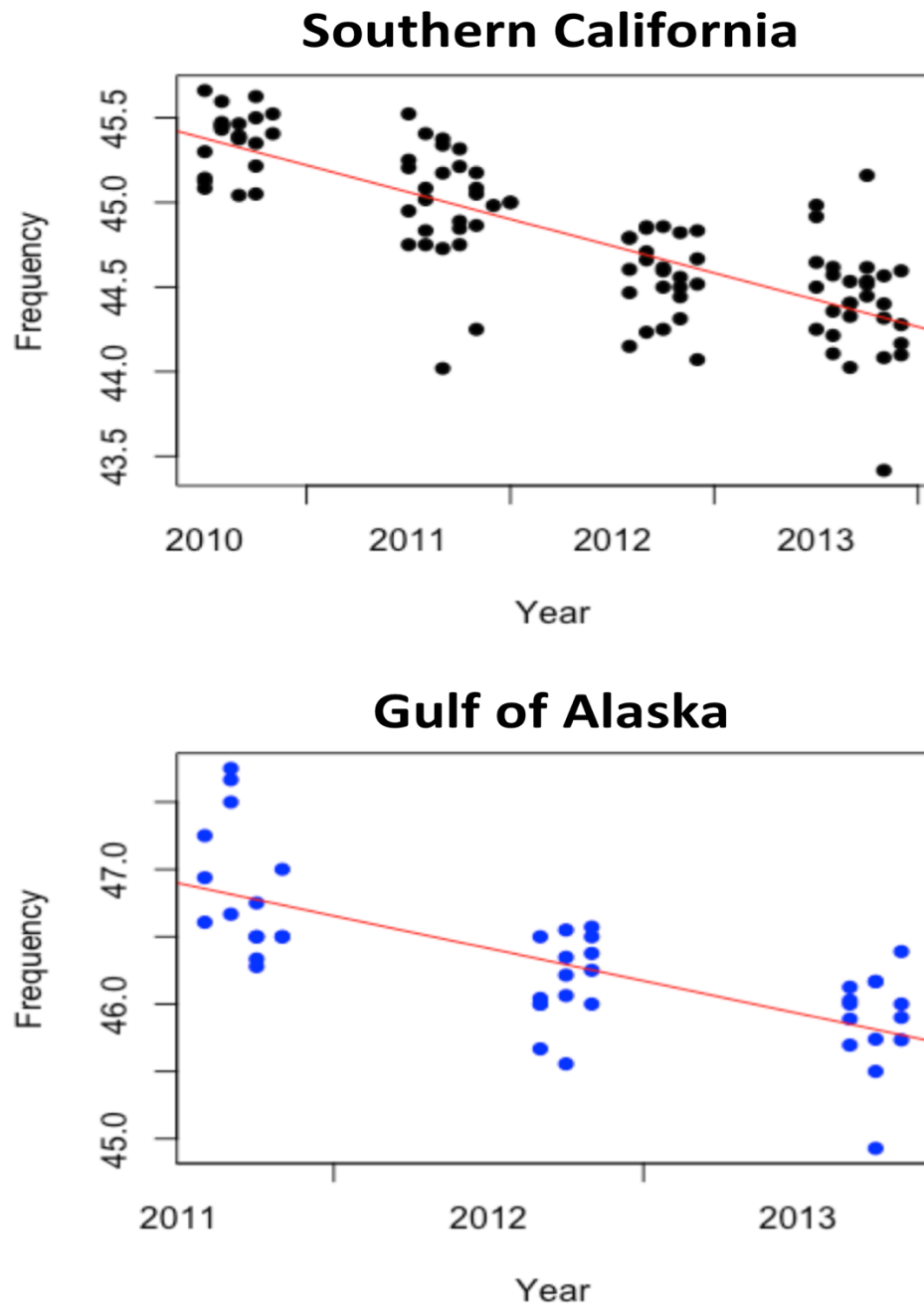


Figure 9: B call frequency measurements at the point 6 s after the maximum frequency, extracted from daily averaged contours from Southern California (top panel) and the Gulf of Alaska (bottom panel). The red line is the trendline from regression analysis.

## 5. DISCUSSION / LIMITATIONS

### 5.1. Discussion / Limitations

In this thesis, I describe two distinct B call variants within the Northeast Pacific population of blue whales. Because these distinct variants have not been previously described, I will label them the NEP B1 call and the NEP B2 call. The B1 call is produced by animals in the waters off Southern California and Washington, and has tentatively been matched to B calls produced near Palmyra Atoll in the Central Pacific. Contours of the B1 variant display little to no downstep in frequency, and are produced at a lower frequency when compared to the second variant. B2 call variants are produced by animals in the Gulf of Alaska, and have been grouped with B calls recorded north of Oahu, Hawaii. The contours of B2 calls have a very steep and noticeable downstep in frequency that occurs roughly between 12 and 15 seconds into the call. Furthermore, B2 calls are produced at a higher frequency than B1 calls within a given year.

Blue whale song has been proposed as a tool for delineating their population structure worldwide (McDonald et al., 2006). Following that logic, the apparent geographic separation of these two call variants opens the possibility of two distinct groupings of animals within the Northeast Pacific population. Off Southern California and near Palmyra Atoll, B1 was the only B call variant observed. In the Gulf of Alaska and Hawaii, B2 was the only B call variant observed. Larger-scale variation in blue whale song has been shown to reflect their population structure around the globe (McDonald et

al., 2006; Torres-Florez et al., 2014; Barlow et al., 2018; Pastene et al., 2019). It is possible that the fine-scale differences observed may reflect population-level differences, both geographically and reproductively, that have not been explored previously. While the separation between California and Gulf of Alaska is clear, in the waters off Washington the situation may be more complex. While contours in Washington were dominated by the B1 variant, average contours from that region consistently displayed intermediate characteristics of both variants, which may be the result of geographic overlap between the two call-types, and thus two populations.

If the logic holds that differences in song structure are indicative of population-level differences, then it is possible that the degree of difference in song structure could also be a measure of the degree of divergence between the population. For example, Antarctic and pygmy blue whales each produce their own unique song-types which are quite distinct from one-another visually (McDonald et al., 2006; Gavrilov et al., 2011), and these two groups are distinguishable from each other genetically (Sremba et al., 2012). Conversely, two song types off the coast of Chile, SEP1 and SEP2, which are more similar in spectral shapes have been attributed to a group of blue whales which are genetically homogenous (Torres-Florez et al., 2014; Pastene et al., 2019). Given that song serves a reproductive purpose for these animals (Oleson et al., 2007), it is possible that differences in song structure are indicative of early-stage population-level divergence that is not yet measurable in genetic analyses.

In regards to the NEP population, it is important to consider what pressures may lead to population divergence. Their population numbers rose steadily after the cessation of commercial whaling, but have been at a plateau for several decades, which has led some to believe that the population has approached its carrying capacity (Calambokidis and Barlow, 2004; Calambokidis et al., 2015; Campbell et al., 2015; Monnahan et al., 2015). The emergence of blue whales in the Gulf of Alaska is a relatively new occurrence could be an indication that these animals have returned to a historic, pre-whaling foraging region (Stafford, 2003). As blue whales may use memory to direct their movements to productive foraging grounds year after year (Abrahms et al., 2019), it is possible that a small subgroup of animals from the NEP population has extended its range to include the productive waters of the Gulf of Alaska, subsequently adjusting the structure of their mating call in response to site-specific pressures.

The B2 variant was observed in both the Gulf of Alaska and Hawaii, two regions in which the NEP and Central and Western Pacific (CWP) blue whale populations are known to overlap in both time and space (Stafford, 2003). CWP blue whales produce a low-frequency, tonal reproductive call that has little variation in frequency across the duration of the call (McDonald et al., 2006). It is possible that, because these populations overlap, the sharp downstep in frequency observed in the B2 variant could be an attempt by the NEP males to differentiate themselves from the more monotone calls of the CWP males. The fundamental frequency of CWP blue whale calls ranges between 17-19 Hz, which is only a few Hz higher than the fundamental frequency of the NEP blue whale

calls (~15Hz). The temporal and spatial overlap with another group of animals that produce reproductive calls that are not only similar in structure, but frequency as well, may have driven NEP blue whales to differentiate their calls from the CWP calls in these regions. A preference for more complex signals is found elsewhere in animal kingdom, as female swamp sparrows (*Melospiza georgiana*), for example, show preferential selection towards males that produce complex songs with a higher degree of proficiency (Ballentine, 2004). Therefore, it is possible that the increased complexity of NEP B2 calls in the Gulf of Alaska and Hawaii is a competitive response to the presence of males from another sub-population.

Ideally, my hypothesis on population sub-structure should be tested using both satellite tags and genetic sequencing. It would be interesting to compare genetic samples of animals in the Gulf of Alaska, with the animals in Washington and Southern California, to see if any degree of divergence is evident within the NEP population, and if so, along what geographical boundaries has this divergence occurred. However, if this population is in the early stages of divergence, separation may not yet be observable genetically. Long-duration satellite tags could provide further verification of movements into the Central Pacific. To date, no tags have been deployed on animals in the Gulf of Alaska. While that would be a very challenging task, doing so would provide insights on the potential migratory route into the Central Pacific, or other regions of the Eastern Tropical Pacific. However, because the eastern and central populations overlap in the Gulf of Alaska (Stafford, 2003), identifying whether the tagged animal is from the CWP

or NEP population would be a challenge, and would require the use of real-time acoustic data as well. An alternative solution to this challenge would be to conduct tagging in the fall, which would lead to a higher chance of tagging NEP blue whales (Rice et al., in prep) but this may be even more challenging to accomplish due to weather.

Over 150 satellite tags have been deployed on blue whales in the NEP, most with initial attachment off the coast of Southern California, but none of the published data contain examples of animals moving as far southwest as Palmyra Atoll or Hawaii (Mate et al., 1999; Bailey et al., 2009; Irvine et al., 2014). Yet, acoustic data from this study still support the presence of NEP blue whales in the Central Pacific. This discrepancy is not entirely surprising considering the relatively low number of detected calls and likely long propagation ranges at these lower latitude locations. In addition, variability in the migratory behaviors of individual animals within this population could further account for the discrepancies between passive acoustic and satellite tag data. Differential migration occurs when, within a single population, there are differences in migratory behavior between either sexes or between older and younger individuals (Dingle and Drake, 2007). This concept is not unheard of in the marine environment. Eastern North Pacific grey whales (*Eschrichtius robustus* Lilljeborg) stagger their migrations by sex, age and reproductive condition (Rice and Wolman, 1971). Similar observations have been made for humpback whales (*Megaptera novaeangliae*) in the Northern Central Pacific, and adult male northern elephant seals (*Mirounga angustirostris*) which migrate further north during their feeding season than females and juvenile animals, a behavior

which is thought to confer benefits to pubescent males (Stewart, 1997; Craig et al., 2003). Similarly, differential migration could confer currently unknown benefits to juvenile blue whales, such as the avoidance of competition or aggression from larger animals in the breeding grounds. It is therefore possible that only a small proportion of the population, such as animals that have not reached reproductive maturity for example, move out to the Central Pacific, and that satellite tag studies have, as of yet, not been sufficient to capture one of these individuals, or they have not included enough life-history data to discern any fine-scale sex or age-dependent migratory patterns. While, at this point, little is known about blue whale dynamics on their breeding grounds, the idea of differential migration warrants further investigation.

From the management perspective, the possible existence of two distinct groups within the NEP population could have large implications. NOAA currently recognizes a single group in the Northeast Pacific that extends from the Gulf of Alaska to the Eastern Tropical Pacific, but does not mention animals that may occur in U.S. Exclusive Economic Zones in the Central Pacific (NOAA, 2019). In a recent assessment on North Pacific blue whales for the International Whaling Commission, Monnahan et al. (2014) split North Pacific blue whale catch records by population based on the presence of two geographically distinct song-types that exist within the region, the CWP and the NEP song. Historically high catch-rate of blue whales in the Gulf of Alaska when compared to Southern California (Monnahan et al., 2014) indicate that this region used to be an important blue whale habitat. The results of my study indicate that catch and recovery

assessments might need to be further evaluated by dividing catch records between regions where the B1 variant is present, and regions where the B2 variant is present, to evaluate separate recovery states if there are two potential groups in the region. If there are or historically were in fact two unique groups in this area, then it is possible that one was disproportionally affected and has been slower to recover from the impacts of whaling. Alternatively, if the Gulf of Alaska population was extirpated, recent range expansion from the population off California and Washington could have seeded a new sub-group.

B calls measured in this study also displayed a consistent decrease in third harmonic frequency, as measured by the frequency at the point six seconds after the peak frequency. This is largely consistent with previous observations of a decline in blue whale B call frequency (McDonald et al., 2009; Gavrilov et al., 2012; Širović, 2016; Leroy et al., 2018). The rate of decrease was different across locations. Calls recorded from the Gulf of Alaska (B2 variants) declined at a slightly higher annual rate than the calls recorded from Southern California (B1 variants). The decline rate was smallest off Washington.

Several theories have been proposed to explain the decrease in frequency of blue whale songs which include a steady decrease in depth at which calls are produced, sexual selection, Doppler shift, and response to the change in abundance post-whaling (McDonald et al., 2009; Gavrilov et al., 2012; Miller et al., 2014). At this point in time,



no single theory is widely accepted. One theory however, that may explain why the rate of change observed in this study was different from site to site, is that the animals lower their frequency in response to anthropogenic noise (Leroy et al., 2018; Malige et al., 2020). If that is the case, then the different rates of decline observed in this study could be an example of site-specific responses to anthropogenic noise.

Malige et al. (2020) found that the rate of decline, as percent of call frequency, in blue whale songs was substantially higher in the North Pacific than in the Indian Ocean. The results of my study are generally comparable to the rates observed in the NEP (0.91%), and also show a similar pattern in which sites with higher levels of anthropogenic noise yield a higher rate of decrease in frequency. In the Gulf of Alaska, shipping noise contributed substantially to noise levels below 100 Hz, with levels around 85 dB re 1  $\mu\text{Pa}^2/\text{Hz}$  at a bands between 30-100 Hz (Debich et al., 2013). The rate of frequency decrease there was 1.05%. The site off Southern California on the other hand, was in a basin that is protected from the propagation of shipping noise by a string of islands between it and the primary shipping routes along the coastline. At this site, low-frequency spectral levels in that same bandwidth were at most around 72 dB re 1  $\mu\text{Pa}^2/\text{Hz}$  on average between 2012-2017 (Wiggins et al., 2017). The rate of decrease here was also lower, at 0.71%. The higher noise levels in the Gulf of Alaska could explain why the rate of decline was higher there when compared to Southern California. However, that assessment, while appealing, is likely an oversimplification. The continental margin off the coast of Southern California is bathymetrically complex,

which results in acoustically heterogeneous environment, with broadly varying noise exposure levels (McDonald et al., 2008). Tag data show that individual blue whales move substantially between different areas while feeding off the coast of Southern California (Mate et al., 1999) so it is likely that these animals are exposed to variable levels of anthropogenic noise within the course of a single feeding season.

Alternatively, the sharper decline in frequency observed in Gulf of Alaska could also be connected to the presence of CWP blue whales in the region. In these data I observed that the fundamental frequency of NEP blue whale calls is slightly lower than that of the CWP animals. This difference could be present because NEP blue whales in the region have decreased their frequency at an accelerated rate in order to get out of the bandwidth of CWP calls. However, my measurements of fundamental frequency were purely exploratory, and any conclusions on this topic would require further investigation.

#### **5.1.1. Limitations**

A number of limitations are generally inherent in passive acoustic studies. The main limit is that passive acoustic data do not provide information which, or how many animals vocalize in a given sampling period. To address this issue, all statistical analyses were conducted on datasets that contained daily-averages of contour structure, to avoid over-representing a single animal.

A challenge with these data was that the recordings were collected opportunistically, which was particularly troublesome for the Central Pacific. Where exactly these animals congregate in the Central Pacific remains unknown. Therefore, instruments deployed near Hawaii and Palmyra Atoll contained only occasional blue whale calls, during the few instances when animals happened to be close enough for the hydrophone to receive those signals, or they were well propagated over potentially long distances. As a result, data from these sites, particularly Palmyra Atoll, often displayed weak signal-to-noise ratios, which made measuring their features challenging. Data from the few days found to contain B calls in Hawaii tended to have complicated spectral characteristics. For one, there were often several calls that overlapped one another, which made extracting accurate contours challenging. Secondly, the best calls available in this dataset were often very high in amplitude, making them much more broadband than calls from the other study sites. The strength of the signal leads me to believe that the overlapping B calls were the result of multiple animals vocalizing at once, close to the hydrophone, as opposed to multi-path arrivals of the signals. Because of the limited sample size from Hawaii data, these complications made it difficult to evaluate whether the substantially higher frequency of calls measured in Hawaii when compared to the Gulf of Alaska is a true indication of the calls produced there, or simply an artifact of the data extraction process. If the broad contour of the call in Hawaii was systematically resulting in the higher maximum frequency along that peak to be extracted, it is possible that extraction of the lower end frequency of that peak would have resulted in calls that were of more similar frequency to those recorded in the Gulf of Alaska.

My goal in this thesis was to quantify one of the call units of stereotypical songs of blue whales so that I could statistically compare its features from different sites across the North Pacific. I extracted eight variables from daily averaged B call contours. Six of those variables were measurements of frequency, collected across the call durations. One variable was a measurement of the slope in the least variable region of B calls across sites, and the final variable was a measurement of the downstep in frequency, which was visually the strongest differing feature between B1 and B2 variants. When tested statistically, these variables were not only sufficient, but highly effective in grouping B call contours by their appropriate site while also showing geographic structure across the two variants. These results support my hypothesis on the existence of unique B call variants within the NEP population, and offer a new approach to studies investigating the previously under-estimated complexities of stereotypical whale songs.

Moving forward, this study should be expanded to include more years of data, as well as other sites in the North Pacific. Sites of particular interest would be presumed breeding grounds such as the Gulf of California and the Costa Rica Dome. Investigating these sites for the presence of B1 and B2 variants could provide further information on the geographic separation of the two call types. Also important is the fact I explored variations in B call structure alone, which is only one aspect of NEP blue whale song. Song phrasing in blue whales can also be highly variable within populations (Jolliffe et al., 2019). Further studies should therefore include not only investigations of variations

in A call structure, but also explorations into AB calling patterns, to see if song phrasing is different between songs produced with the B1 variant and songs produced with the B2 variant.

## 6. CONCLUSIONS

Through this study I have discovered the existence of at least two distinct variants of the stereotypical NEP blue whale B call. The two variants, B1 and B2, appear to be at least partially geographically separated and, per my hypothesis, the strongest separation occurs between B calls in the Gulf of Alaska and those in Southern California. While visual comparisons originally indicated a possible third, intermediate variant that was measured from Washington data, statistical analyses consistently grouped these contours with the B1 variant, and I can therefore only propose the existence of two variants. The B1 variant occurs further south, off the coasts of Washington and Southern California, and the B2 variant is found further north in the Gulf of Alaska. As predicted, both of these variants were also observed in the Central Pacific, and a similar north-south separation was observed. While data from these sites were a bit more inconclusive, the B1 variant was observed at Palmyra Atoll, the more southern of the Central Pacific sites, whereas the B2 variant was observed in Hawaii, further north in comparison. These distinct variants may indicate separate populations, or groups that have begun to diverge, which could have important management consequences for this endangered species.

Also, in accordance with my hypothesis, I observed a significant decline in tonal frequency of NEP blue whale calls in these data, and found that the rate of decrease was different at each site. The most rapid rate of decline occurred in the Gulf of Alaska, and the slowest decline occurred off Washington, and Southern California displayed an intermediate rate of decline. While this frequency shift has been observed across all blue

whale populations, we still do not know why they are engaged in this behavior. Different rates of frequency decline, in a species where individuals generally appear to be very well tuned to the “correct” annual frequency, indicates, however, that this decline is likely biologically important and locally driven.

The communicative behavior of many species of large cetaceans is still an underexplored topic. The results of this study provide a foundation for future studies on the topic of fine-scale variations in stereotypical reproductive calls and demonstrate that the vocal repertoire of the Northeast Pacific population is more complex and variable than previously understood.

## REFERENCES

- Abrahms, B., Hazen, E.L., Aikens, E.O., Savoca, M.S., Goldbogen, J.A., Bograd, S.J., Jacox, M.G., Irvine, L.M., Palacios, D.M., Mate, B.R., 2019. Memory and resource tracking drive blue whale migrations. *Proc Natl Acad Sci U S A* 116, 5582-5587.
- Bailey, H., Mate, B.R., Palacios, D.M., Irvine, L., Bograd, S.J., Costa, D.P., 2009. Behavioural estimation of blue whale movements in the Northeast Pacific from state-space model analysis of satellite tracks. *Endangered Species Research* 10, 93-106.
- Ballentine, B., 2004. Vocal performance influences female response to male bird song: an experimental test. *Behavioral Ecology* 15, 163-168.
- Barlow, D.R., Torres, L.G., Hodge, K.B., Steel, D., Baker, C.S., Chandler, T.E., Bott, N., Constantine, R., Double, M.C., Gill, P., Glasgow, D., Hamner, R.M., Lilley, C., Ogle, M., Olson, P.A., Peters, C., Stockin, K.A., Tessaglia-Hymes, C.T., Klinck, H., 2018. Documentation of a New Zealand blue whale population based on multiple lines of evidence. *Endangered Species Research* 36, 27-40.
- Calambokidis, J., Barlow, J., 2004. Abundance of Blue and Humpback Whales in the Eastern North Pacific Estimated by Capture-Recapture and Line-Transect Methods. *Marine Mammal Science* 20, 63-85.
- Calambokidis, J., Barlow, J., Ford, J.K.B., Chandler, T.E., Douglas, A.B., 2009. Insights into the population structure of blue whales in the Eastern North Pacific from recent sightings and photographic identification. *Marine Mammal Science* 25, 816-832.
- Calambokidis, J., Steiger, G.H., Curtice, C., Harrison, J., Ferguson, M.C., Becker, E., DeAngelis, M., Van Parijs, S.M., 2015. 4. Biologically Important Areas for Selected Cetaceans Within U.S. Waters – West Coast Region. *Aquatic Mammals* 41, 39-53.
- Calinski, T., Harabasz, J., 1974. A dendrite method for cluster analysis *Commun. Stat* 3, 1-27.
- Campbell, G.S., Thomas, L., Whitaker, K., Douglas, A.B., Calambokidis, J., Hildebrand, J.A., 2015. Inter-annual and seasonal trends in cetacean distribution, density and abundance off southern California. *Deep Sea Research Part II: Topical Studies in Oceanography* 112, 143-157.



Clapham, P.J., Baker, C.S., 2018. Modern Whaling in: Kovacs, B.W.J.G.M.T.K. (Ed.), Encyclopedia of Marine Mammals, Academic Press, New York, pp. 1070-1074.

Cooke, J.G., 2018. *Balaenoptera musculus*. The IUCN Red List of Threatened Species 2018: e.T2477A50226195.

Craig, A., Gabriele, C., Herman, L., Pack, A., 2003. Migratory Timing of Humpback Whales (*Megaptera novaeangliae*) in the Central North Pacific Varies with Age, Sex and Reproductive Status. Behaviour 140, 981-1001.

Debich, A.J., Baumann-Pickering, S., Širović, A., Hildebrand, J.A., Buccowich, J.S., Gottlieb, R.S., Jackson, A.N., Johnson, S.C., Roche, L., Trickey, J.S., Thayre, B., Wakefield, L., Wiggins, S.M., 2013. Passive Acoustic Monitoring for Marine Mammals in the Gulf of Alaska Temporary Maritime Activities Area 2012-2013, MPL Technical Memorandum, Scripps Institute of Oceanography, University of California San Diego.

Dingle, H., Drake, A., 2007. What Is Migration? BioScience 57.

Dugard, P., Todman, J., Staines, H., 2010. Approaching multivariate analysis. A practical introduction. Second Edition. Routledge, New York.

Gavrilov, A.N., McCauley, R.D., Gedamke, J., 2012. Steady inter and intra-annual decrease in the vocalization frequency of Antarctic blue whales. J Acoust Soc Am 131, 4476-4480.

Gavrilov, A.N., McCauley, R.D., Salgado-Kent, C., Tripovich, J., Burton, C., 2011. Vocal characteristics of pygmy blue whales and their change over time. J Acoust Soc Am 130, 3651-3660.

Goldbogen, J.A., Calambokidis, J., Oleson, E., Potvin, J., Pyenson, N.D., Schorr, G., Shadwick, R.E., 2011. Mechanics, hydrodynamics and energetics of blue whale lunge feeding- efficiency dependence on krill density. Journal of Experimental Biology, 214(1), 131–146.

Irvine, L.M., Mate, B.R., Winsor, M.H., Palacios, D.M., Bograd, S.J., Costa, D.P., Bailey, H., 2014. Spatial and temporal occurrence of blue whales off the U.S. West Coast, with implications for management. PLoS One 9, e102959.

Jolliffe, C.D., McCauley, R.D., Gavrilov, A.N., Jenner, K.C.S., Jenner, M.M., Duncan, A.J., 2019. Song variation of the South Eastern Indian Ocean pygmy blue whale population in the Perth Canyon, Western Australia. *PLoS One* 14, e0208619.

Leroy, E.C., Royer, J.-Y., Bonnel, J., Samaran, F., 2018. Long-Term and Seasonal Changes of Large Whale Call Frequency in the Southern Indian Ocean. *Journal of Geophysical Research: Oceans* 123, 8568-8580.

Lewis, L.A., Širović, A., 2018. Variability in blue whale acoustic behavior off southern California. *Marine Mammal Science* 34, 311-329.

Malige, F., Patris, J., Buchan, S.J., Stafford, K.M., Shabangu, F., Findlay, K., Huckle-Gaete, R., Neira, S., Clark, C.W., Glotin, H., 2020. Inter-annual decrease in pulse rate and peak frequency of Southeast Pacific blue whale song types. *Sci Rep* 10, 8121.

Mate, B.R., Lagerquist, B.A., Calambokidis, J., 1999. Movements of North Pacific Blue Whales During the Feeding Season off Southern California and Their Southern Fall Migration. *Marine Mammal Science* 15, 1246-1257.

McDonald, M.A., Calambokidis, J., Teranishi, A.M., Hildebrand, J.A., 2001. The acoustic calls of blue whales off California with gender data. *J Acoust Soc Am* 109, 1728-1735.

McDonald, M.A., Hildebrand, J.A., Mesnick, S., 2009. Worldwide decline in tonal frequencies of blue whale songs. *Endangered Species Research* 9, 13-21.

McDonald, M.A., Hildebrand, J.A., Mesnick, S.L., 2006. Biogeographic characterisation of blue whale song worldwide- using song to identify populations *Journal of Cetacean Research and Management*, 8(1), 55-65.

McDonald, M.A., Hildebrand, J.A., Wiggins, S.M., Ross, D., 2008. A 50 year comparison of ambient ocean noise near San Clemente Island: a bathymetrically complex coastal region off Southern California. *J Acoust Soc Am* 124, 1985-1992.

Miller, B.S., Leaper, R., Calderan, S., Gedamke, J., 2014. Red shift, blue shift: investigating Doppler shifts, blubber thickness, and migration as explanations of seasonal variation in the tonality of Antarctic blue whale song. *PLoS One* 9, e107740.

Monnahan, C.C., Branch, T.A., 2015. Sensitivity analyses for the eastern North Pacific blue whale assessment, Scientific Committee of the International Whaling Commission.

Monnahan, C.C., Branch, T.A., Punt, A.E., 2015. Do ship strikes threaten the recovery of endangered eastern North Pacific blue whales? *Marine Mammal Science* 31, 279-297.

Monnahan, C.C., Branch, T.A., Stafford, K.M., Ivashchenko, Y.V., Oleson, E.M., 2014. Estimating historical eastern North Pacific blue whale catches using spatial calling patterns. *PLoS One* 9, e98974.

NOAA, 2019. BLUE WHALE (*Balaenoptera musculus musculus*): Eastern North Pacific Stock Assessment Report.

Oleson, E., M., Calambokidis, J., Burgess, W., C., McDonald, M., A., LeDuc, C., A., Hildebrand, J., A., 2007. Behavioral context of call production by eastern North Pacific blue whales. *Marine Ecology Progress Series* 330, 269–284. .

Paniagua-Mendoza, A., Gendron, D., Romero-Vivas, E., Hildebrand, J.A., 2017. Seasonal acoustic behavior of blue whales (*Balaenoptera musculus*) in the Gulf of California, Mexico. *Marine Mammal Science* 33, 206-218.

Pastene, L.A., Acevedo, J., Branch, T.A., 2019. Morphometric analysis of Chilean blue whales and implications for their taxonomy. *Marine Mammal Science* 36, 116-135.

Pham, D.T., Dimov, S.S., Nguyen, C.D., 2004. Selection of k in k-means clustering. *Mechanical Engineering Science*, 103-119.

Quinn, G.P., Keough, M.J., 2002. *Experimental Design and Data Analysis for Biologists*. .

R Development Core Team, 2018. R: A language and environment for statistical computing R Foundation for Statistical Computing Vienna Austria

Rice, A., Širović, A., Trickey, J.S., Debich, A.J., Gottlieb, R.S., Wiggins, S.M., Hildebrand, J.A., Baumann-Pickering, S., in prep. Marine Mammal distributions in the Gulf of Alaska from long-term passive acoustic monitoring *Marine Biology*

Rice, D.W., Wolman, A.A., 1971. The life history and ecology of the gray whale (*Eschrichtius robustus*). The American Society of Mammalogists.

Rivers, J., 1997. Blue Whale, *Balaenoptera Musculus*, Vocalizations from the Waters off Central California Marine Mammal Science 13(2), 186-195.

Sears, R., Calambokidis, J., 2002. COSEWIC Assessment and Update Status Report on the Blue Whale *Balaenoptera musculus*, Committee on the Status of Endangered Wildlife in Canada., Ottawa, pp. 1-32

Širović, A., 2016. Variability in the performance of the spectrogram correlation detector for North-east Pacific blue whale calls, Bioacoustics, Bled, Slovenia p. 7.

Širović, A., Hildebrand, J.A., Wiggins, S.M., 2007. Blue and fin whale call source levels and propagation range in the Southern Ocean. J Acoust Soc Am 122, 1208-1215.

Širović, A., Hildebrand, J.A., Wiggins, S.M., McDonald, M.A., Moore, S.E., Thiele, D., 2004. Seasonality of blue and fin whale calls and the influence of sea ice in the Western Antarctic Peninsula. Deep Sea Research Part II: Topical Studies in Oceanography 51, 2327-2344.

Širović, A., Oleson, E.M., Favilla, A., Fisher-Pool, P., 2016. Blue whale song variability in the North Pacific Ocean. 7

Širović, A., Rice, A., Chou, E., Hildebrand, J.A., Wiggins, S.M., Roch, M.A., 2015. Seven years of blue and fin whale call abundance in the Southern California Bight. Endangered Species Research 28, 61-76.

Sremba, A.L., Hancock-Hanser, B., Branch, T.A., LeDuc, R.L., Baker, C.S., 2012. Circumpolar diversity and geographic differentiation of mtDNA in the critically endangered Antarctic blue whale (*Balaenoptera musculus intermedia*). PLoS One 7.

Stafford, K.M., 2003. Two Types of Blue Whale Calls Recorded in the Gulf of Alaska Marine Mammal Science 19, 682-693.

Stafford, K.M., Fox, C.G., Clark, D.S., 1998. Long-range acoustic detection and localization of blue whale calls in the northeast Pacific Ocean. *Journal of the Acoustical Society of America* 104.

Stafford, K.M., Nieuwkirk, S.L., Fox, C.G., 1999. An Acoustic Link Between Blue Whales in the Eastern Tropical Pacific and the Northeast Pacific Marine Mammal Science 15, 1258-1262.

Stewart, B.S., 1997. Ontogeny of Differential Migration and Sexual Segregation in Northern Elephant Seals *Journal of Mammalogy* 78, 1101-1116.

Tibshirani, R., Walther, G., Hastie, T., 2000. Estimating the number of clusters in a dataset via the Gap statistic, Stanford.

Torres-Florez, J.P., Hucke-Gaete, R., LeDuc, R., Lang, A., Taylor, B., Pimper, L.E., Bedrinana-Romano, L., Rosenbaum, H.C., Figueroa, C.C., 2014. Blue whale population structure along the eastern South Pacific Ocean: evidence of more than one population. *Mol Ecol* 23, 5998-6010.

Wiggins, S.M., Debich, A.J., Trickey, J.S., Rice, A.C., Thayre, B.J., Baumann-Pickering, S., Širović, A., Hildebrand, J.A., 2017. Summary of Five Years of Ambient and Anthropogenic Sound in the SOCAL Range Complex 2012 - 2017, MPL TM, Scripps Institution of Oceanography, University of California San Diego, La Jolla, California