Title

Blue whale acoustic behavior off southern California

Author

Lewis, Leah Allison

Publication Date

2017

UNIVERSITY OF CALIFORNIA, SAN DIEGO

Blue whale acoustic behavior off southern California

A thesis submitted in partial satisfaction of the
requirements for the degree
Master of Science

in

Marine Biology

by

Leah Allison Lewis

Committee in charge:

Ana Širović, Chair
John A. Hildebrand
Sarah L. Mesnick

2017

The thesis of Leah Allison Lewis is approved, and it is acceptable in quality and form for publication on microfilm and electronically:

Chair

University of California, San Diego

2017

DEDICATION

To my parents, Cynthia & Everett Lewis ...

For their unwavering love and support throughout the years, whether it be from within the same state or across the country. For passing on their love of running, a sport which has kept me sane during times of stress, and for instilling in me the strength, passion, and imagination needed to follow my heart during such times. But, most importantly, for always reminding me of the meanings of "Hakuna Matata" and "Ohana".

Thank you.

EPIGRAPH

"The wonders of nature are endless...
Sometimes we can recognize ourselves in animals—
that’s what makes them so interesting."

—*Walt Disney*

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ACKNOWLEDGEMENTS

To say that, five years ago, I never would've believed that I'd be here—studying blue whale acoustics and earning my Master's degree from Scripps Institution of Oceanography in San Diego—would be a grand understatement. And, yet, here I am. The paths I've taken to get to this point have been unique, to say the least. (I'm pretty sure that a few may have actually been "the road less traveled"). But they've also been wonderfully challenging and rewarding. Regardless of the route I've taken, I could not have gotten here without the guidance and support of so many inspiring people, all of whom I must thank from the bottom of my heart.

First and foremost, I need to thank my advisor Ana Širović. In addition to providing me with the academic and financial support required to finish this thesis, Ana has provided me with immeasurable quantities of emotional support throughout the past three years. Even after I decided to change my academic path at Scripps, Ana continued to offer me incredible opportunities, both in the form of fieldwork and conference presentations. Our meetings were a weekly source of guidance, not only in terms of research and coding issues but also in regards to more personal problems, like running up Torrey Pines in the La Jolla half marathon. Now, thanks to Ana, my thesis, which too once seemed an insurmountable task, is now something I can look back upon with a remarkable sense of self-growth and achievement.

I must also thank my other committee members, John Hildebrand and Sarah Mesnick. The advice that I've received from John over the past few years has significantly improved the quality of my research, especially in regards to the more technical aspects of this field. I am also extremely grateful to Sarah for her valuable words-of-wisdom over the past six months–both related to research and not; sometimes, hearing just a few encouraging words is all you need to stand up for yourself and feel more confident doing so.

I have also worked with several other influential researchers during the course of my thesis research. Among the most inspiring has been John Calambokidis, who, between his remarkable ability to predict the location of a blue whale's next surfacing and recall details from a tag deployment that occurred years ago, at times had me wondering if he could, in fact, "speak whale".

To all of the students, staff, and faculty, past and present, of the Marine Bioacoustics Lab, Scripps Whale Acoustic Lab, and the Behavioral Acoustic Ecology Lab, I would also like to extend heartfelt thanks. My thesis would not have been possible without the technical, intellectual, and emotional support that every member of these labs has provided. In particular, I would like to thank my office mate, Regina Guazzo, for her constant willingness to chat about research and life in general. Through the bizarre computer noises and creepy crawlies under the couch, through the highs and the lows, Regina has been both an inspiration and an incredible friend. Many other friends have contributed their support and encouragement to my research—I especially would like to thank Leah Varga and Grace Teller for helping me navigate through all of the various aspects of the Master's program at Scripps; Angela Szesciorka for her insight into the tag data; and Ally Rice, for being a trustworthy computer re-starter and person to vent to on all matters of things.

I owe a special thanks to all of the amazing people that I've met through the San Diego running community. Over the past few years, these runners have paced me, pushed me, and motivated me in ways that I never thought possible. From the long-runs and core-exercises to the (very) late-night shenanigans, this group of people has become more than just a bunch of random running buddies— they are my extended running family. My thesis, and quality of life, has improved thanks to the fuel they've provided in the form of inside jokes, endorphins, and post-run beverages.

All of the paths that I've taken to get here would have been inaccessible if not for the love and support of my family. Most importantly, I need to thank my parents for nourishing my imaginative side and encouraging me to always follow my heart. Despite the long-distance, my Mom has become more of a best friend to me over the past few years, and I owe my love of writing, as well as my ability to travel on a budget, to her. My Dad has always been there to cheer me on, or cheer me up, and I can only hope that I still have his strength and determination fifty years from now. I'd also like to thank the furry members of my family, both near and far. The personalities and antics of Monty and Lola have both entertained and frustrated me over the past year. Across the country, Lilo and Stitch have been my play- and cuddle-mates for over thirteen years, and pictures of them always serve as the perfect distraction or pick-me-up. Last but certainly not least, a huge thank you goes out to my boyfriend, Scott Omahen. Since I've met him, however, Scott has actually been much more than that—he's been my best friend, my supporter through the good times and the bad, my personal chef during late-nights and late-mornings, as well as my running/travel/dance/brewery partner. I truly can't wait to see what paths we take together next.

The research presented in this thesis was possible due to funding provided by the Office of Naval Research, the Chief of Naval Operation-N45, the U.S. Navy's Living Marine Resources Program and the US Navy Pacific Fleet, thanks to Michael Weise, Frank Stone, Ernie Young and Bob Gisiner, among others. The tagging research presented in Chapter 3 was conducted under National Marine Fisheries Service marine mammal research permits 14346 and 19116 (B. Southall, principal investigator) and 540-1502-00, 540-1811, and 16111 (J. Calambokidis, principal investigator). I would especially like to thank the National Science Foundation Graduate Research Fellowship Program for supporting me throughout my time at Scripps, in addition to the SIO Graduate Office for funding my travel to several conferences over the past few years.

Chapter 2 has been submitted for publication to Marine Mammal Science and

Chapter 3 is in preparation for submission. I was the primary researcher and author for both chapters. The research presented in Chapter 2 was directed and supervised by Ana Širović. The research in Chapter 3 is presented with acknowledgements to the support provided by my co-authors: John Calambokidis, Alison Stimpert, James Fahlbusch, Ari Friedlaender, John Hildebrand, Megan McKenna, Sarah Mesnick, Erin Oleson, Brandon Southall, Angela Szesciorka, and Ana Širović.

VITA

2010–2012	Undergraduate Research Assistant University of Rhode Island, Graduate School of Oceanography Geo-biology Laboratory, Narragansett, Rhode Island
2012	B.S., Summa Cum Laude, Marine Biology University of Rhode Island
2012–2014	Marine Biological Technician *Integrated Statistics*, NOAA/NEFSC, Oceanography Branch Narragansett, Rhode Island
2017	M.S., Marine Biology Scripps Institution of Oceanography, University of California, San Diego

PUBLICATIONS

Journal Articles

1. Lewis, L.A., & Širović, A. *Submitted*. Variability in blue whale acoustic behavior off Southern California. Marine Mammal Science.
2. Sauvage, J., Lewis, L., Graham, D., Spivack, A.J., & D'Hondt, S.D. (2017) Data report: quantification of potential drilling contamination using perflurocarbon tracer at IODP Expedition 329 sites. *In* D'Hondt, S., Inagaki, F., Alvarez Zarikian, C.A., & the Expedition 329 Scientists, Proceedings of the Integrated Ocean Drilling Program, 329: Tokyo (Integrated Ocean Drilling Program Management International, Inc.).
3. Lewis, L.A., Richardson, D.E., Zakharov, E.V., & Hanner, R. (2016). Integrating DNA barcoding of fish eggs into ichthyoplankton monitoring programs. Fishery Bulletin, 114(2), 153–166.

Conference Presentations

1. Lewis, L.A., Calambokidis, J., Hildebrand, J.A., & Širović, A. (2016). Blue whale song sequencing off Southern California. Joint Meeting of the Acoustical Society of America and the Acoustical Society of Japan. Honolulu, HI. Invited Speaker: Oral Presentation.
2. Lewis, L.A., & Širović, A. (2015) Differences in blue whale calling behavior at inshore and offshore sites in Southern California. Society of Marine Mammalogy Biennial Conference. San Francisco, CA. Poster Presentation.
3. Lewis, L.A., & Richardson, D.E. (2014) Integrating DNA barcoding of fish eggs into ichthyoplankton monitoring programs. Southern New England Chapter of the American Fisheries Society Winter Meeting. Hadley, MA. Oral Presentation.

ABSTRACT OF THE THESIS

Blue whale acoustic behavior off southern California

by

Leah Allison Lewis

Master of Science in Marine Biology

University of California, San Diego, 2017

Ana Širović, Chair

The acoustic repertoire of the Northeast Pacific population of blue whales (*Balaenoptera musculus*) consists of three different sounds: A, B, and D calls. The pulsed A and tonal B calls can be produced singularly or in phrases or songs, while downswept D calls are only produced as singular calls. Although these sounds have been well described, the behavioral context of sound production is poorly understood. To investigate spatial and temporal variability in blue whale call and song usage off southern California, passive acoustic data collected from four High-Frequency Acoustic Recording Packages (HARPs) were analyzed. The acoustic and dive profile data collected through tags deployed on blue whales were also analyzed to describe the behavioral context of sound production. Singular call and phrase production rates were calculated to assess variability in sound type abundances on different spatial, temporal and behavioral scales. Distinct differences in song type preference were apparent, with offshore sites featuring songs comprised of multiple sequential B units following a single A, while inshore, A and B units alternated. Most blue whale sounds were produced during the summer and fall. The majority of all sounds produced by tagged blue whales occurred during non-lunging dives at shallow depths (less than 30 m). Song production was associated with shallow, non-lunging dives, while singular calls often occurred during lunging dives or bouts of surface behavior. The observed differences in blue whale acoustic behavior off southern California will aid in the development of context specific rates for future models of density estimation.

Chapter 1

Introduction

1.1 Background

From the mid-1800s through the mid-1900s, the populations of many baleen whale species suffered monumental losses due to intense commercial exploitation. Blue whales (*Balaenoptera musculus*) in particular, as the largest cetacean species, endured tremendous population declines due to industrial whaling during the twentieth century. Due to overexploitation of the Antarctic blue whale stocks, the North Pacific surpassed the Antarctic and became the primary whaling ground by the mid-1900s (Rice, 1974). In a span of just fifty-five years, between 1910 and 1965, 9,500 blue whales were hunted in the North Pacific (Ohsumi and Wada, 1972; Monnahan *et al.*, 2014), and approximately 3,000 of these animals were taken from the eastern North Pacific stock alone (Rice, 1974; Tønnessen and Johnsen, 1982; Monnahan *et al.*, 2014). Because of this appreciable population decline, whaling for blue whales was banned by the International Whaling Commission (IWC) in 1966. Today, blue whales are listed as "depleted" under the Marine Mammal Protection Act (MMPA) and as "endangered" under the U.S. Endangered Species Act (ESA) (Reilly *et al.*, 2008). Despite their protected status, other present day threats to this species still exist, including ship strikes (Carretta *et al.*, 2013; Redfern *et al.*, 2013; Irvine *et al.*, 2014; Carretta *et al.*, 2015a; Monnahan *et al.*, 2015), disturbance from ships and other anthropogenic sources (Reeves *et al.*, 1998; Andrew *et al.*, 2002; Melcon *et al.*, 2012), and possible entanglement or by-catch (Irvine *et al.*, 2014; Pace III *et al.*, 2014).

The effective management of blue whales in the Northeast Pacific, as well as in other stocks worldwide, relies upon our ability to efficiently and accurately estimate the number of individuals within the population. Although the Northeast Pacific stock of blue whales was thought to be increasing (Barlow, 1994, 1997), the true status of blue whales in this region remains unknown, with the current best estimate of abundance for the Northeast Pacific stock modeled at 1,647 (CV=0.07) blue whales (Calambokidis and Barlow, 2013; Carretta *et al.*, 2015b). Historically, these estimates have been made based on data collected through visual line transect surveys. However, data collected through methods such as these are generally limited by favorable weather and good sightings conditions, such as during the summer and fall months in the Southern California Bight (SCB) (Barlow, 1995; Barlow and Forney, 2007). Furthermore, because sampling and modeling techniques can vary (Hammond, 1986), calculated density estimates may be difficult to compare between studies or even years. Therefore, a more efficient method for the estimation of population densities should be developed.

Sound detection has proven to be an effective alternative means of detecting marine mammal presence since many species regularly produce a variety of sounds. The loud, low-frequency sounds produced by baleen whales in particular (Clark, 1990) make passive acoustic monitoring a useful method for monitoring populations (Mellinger *et al.*, 2007). The common occurrence of blue and fin (*B. physalus*) whale calls in the Antarctic and around Hawaii has allowed for estimates of minimum abundance to be calculated in these regions (McDonald and Fox, 1999; Širović *et al.*, 2004). However, the widespread use of passive acoustic monitoring as a tool to estimate population size is currently limited by a lack of information on whale calling behavior.

In order to estimate whale abundance from passive acoustic data, meaningful call production rates must first be established. Although whale call production rates should be consistent across different monitoring efforts as they are animal dependent, call rates likely vary with region, season, sex, and behavioral state of the animal (Clark, 1990; Oleson *et al.*, 2007a,b; Parks *et al.*, 2011; Stimpert *et al.*, 2015). Thus it is crucial to gain a better understanding of the behavioral context of sound production, and of the other factors influencing call rates, before any set of passive acoustic data can be used to effectively estimate the population abundance of whales in a given region.

The acoustic repertoire of blue whales worldwide is diverse (McDonald *et al.*, 2006), but the Northeast Pacific population of blue whales produces three main sound types: A, B, and D calls (Figure 1.1). The pulsed A and tonal B calls, each approximately 15-20 s in duration, can be produced at irregular intervals as singular calls or together in regular sequences as phrases or song (Oleson *et al.*, 2007a). Bouts of song have only been recorded by males, and these call types are thus thought to have a reproductive function (McDonald *et al.*, 2001; Oleson *et al.*, 2007a). Blue whale type D calls, on the other hand, are shorter (<5 s), frequency modulated, variable signals that are produced by both males and females at irregular intervals (Thode *et al.*, 2000; McDonald *et al.*, 2001) with a possible social function (Oleson *et al.*, 2007a). While there have been several recent advancements in the understanding of blue whale calling behavior off southern California (Calambokidis *et al.*, 2007; Oleson *et al.*, 2007a; McDonald *et al.*, 2001), the attribution of sounds to a specific function has only been minimally accomplished, with the best descriptions of behavioral context being either reproductive or social, and knowledge of finer-scale variation in blue whale call production rates remains lacking.

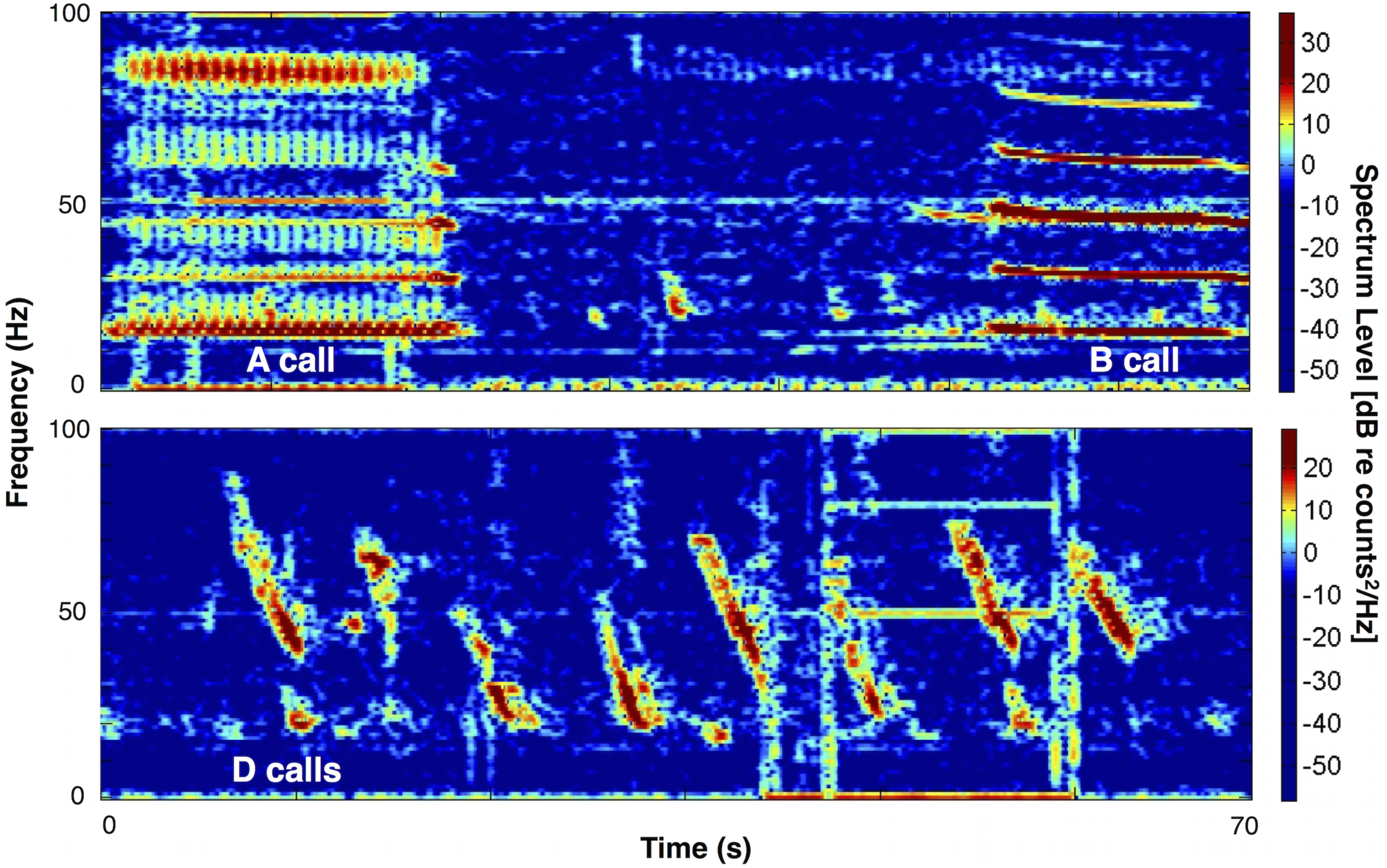

Figure 1.1: Spectrograms of Northeast Pacific blue whale A (*top left*), **B** (*top right*)**, and D calls** (*bottom*) recorded at the northern offshore HARP site (see Chapter 1) in September 2009 (A and B calls) and January 2010 (D calls). (NFFT=2,000, 90% overlap, Hanning window).

1.2 Thesis Outline

The research contained within this thesis aims to evaluate variability in blue whale acoustic behavior off southern California. The results from two studies are presented in Chapters 2 and 3, which include the analysis of spatial and temporal patterns in blue whale sound production, and the description of non-acoustic behaviors associated with sound production in blue whales. Each of these chapters is intended to stand alone as a publishable unit.

An analysis of spatial and temporal variability in blue whale sound production is presented in Chapter 2: "Variability in blue whale acoustic behavior off southern California." Blue whale sounds were detected in twelve months of passive acoustic recordings collected from two inshore and two offshore sites between September 2009 and August 2010. Acoustic behavior is separated into three main sound-type categories at each site: singular A and B calls, songs consisting of A and B phrase units, and D calls. The acoustic behavior of blue whales is compared between the inshore and offshore sites, and seasonal and daily patterns in singular call and song type occurrence are investigated. The results of this study reflect the importance of understanding the ecological and environmental context of sound production when interpreting long-term acoustic recordings. This chapter has been submitted, in full, to the journal Marine Mammal Science and is presented as part of this thesis with acknowledgement to the co-authors of the study.

A description of non-acoustic behaviors associated with sound production in blue whales is presented in Chapter 3: "Behavioral context of sound production in tagged blue whales off southern California." The acoustic and dive profile data collected from animal-borne biologging tags deployed on blue whales from 2002 through 2016 are analyzed to determine the behavioral context of sound production. The production of singular A and B calls, D calls, and phrases are investigated, and behavioral state is classified into one of five categories based on dive profile analyses. Variability in blue whale sound production is evaluated on different temporal (seasonal and daily) and spatial scales, as well as in regards to behavioral state. The results of this chapter describe patterns of behavior associated with the production of each sound type, which will aid in future models of blue whale sound production. This chapter is in preparation for submission and is presented as part of this thesis with acknowledgement to the co-authors in the study.

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Chapter 2

Variability in blue whale acoustic behavior off southern California

by Leah A. Lewis & Ana Širović

Abstract

To evaluate the acoustic behavior of blue whales (*Balaenoptera musculus*) located inshore and offshore of southern California, singular A and B calls, D calls, and AB phrases were analyzed from twelve months of passive acoustic data collected at four locations within the Southern California Bight. The relative proportions of singular calls and phrases were used to evaluate spatial and temporal patterns in sound and song type usage, and singular call and phrase production rates were calculated to investigate spatial and temporal variability in call abundance. Blue whale sounds were recorded from spring through early winter, with the majority of all detections occurring between September and December. The proportions and production rates of singular calls and phrases varied between the inshore and offshore sites. In addition, the percentage of A units within repetitive song phrases was greater inshore than offshore, resulting from a higher proportion of AB song type inshore, in which A and B phrase units were alternating. The ABB song type, in which a single A unit was followed by multiple B units, was more common offshore. The observed differences in calling and singing behaviors may identify distinct and variable acoustic behavioral settings for blue whales

off southern California.

2.1 Introduction

Passive acoustic monitoring is an efficient method for the study of marine mammal populations, since many species regularly produce a variety of vocalizations (Mellinger *et al.*, 2007; Marques *et al.*, 2009). The high-intensity, low-frequency sounds produced by baleen whales (Clark, 1990) make passive acoustic monitoring a suitable tool for monitoring distributions of individuals over a large area. In comparison to the complex sounds and elaborate songs produced by more social species of baleen whales, such as those recorded from humpbacks (Payne and McVay, 1971; Winn and Winn, 1978; Cerchio *et al.*, 2001; Darling and Bérubé, 2001), blue whale calls (Thompson *et al.*, 1996; Thode *et al.*, 2000; Mellinger and Clark, 2003; Rankin *et al.*, 2005; Stafford, 2003) and songs (McDonald *et al.*, 2006; Oleson *et al.*, 2007b; McDonald *et al.*, 2009) are relatively simple in structure and composition. However, blue whale acoustic repertoire worldwide is diverse (McDonald *et al.*, 2006) and further complicated by behavioral (McDonald *et al.*, 2001; Oleson *et al.*, 2007b), temporal (Wiggins *et al.*, 2005; Oleson *et al.*, 2007c), seasonal (Watkins *et al.*, 2000; Stafford *et al.*, 2001; Burtenshaw *et al.*, 2004; Širović *et al.*, 2004, 2015), and spatial (Stafford *et al.*, 2001; Širović *et al.*, 2015) variability in sound production. Even though the Northeast Pacific population of blue whales is one of the most extensively studied populations of blue whales worldwide, our understanding of their ecology and acoustic behavior remains lacking.

In the eastern North Pacific Ocean, the acoustic repertoire of blue whales consists of three well-documented call types: A, B, and D calls (Thompson *et al.*, 1996; Clark and Fristrup, 1997; Rivers, 1997; Stafford *et al.*, 1999; Thode *et al.*, 2000; Stafford *et al.*, 2001; Stafford, 2003). The A call consists of up to 20 s long series of low-frequency pulses, while the B call is a slightly frequency modulated tonal that lasts approximately 15-20 s. These pulsed A and tonal B calls can be produced together (McDonald *et al.*, 2001, 2006) or individually at irregular intervals as singular calls (Oleson *et al.*, 2007b). When blue whale type A and B calls co-occur, they are typically produced at very regular intervals, each call becoming a unit in a phrase. The phrases, consisting only of A and B units, may be repeated at regular intervals over extended time periods, ranging from minutes to several hours, thus forming a song (McDonald *et al.*, 2006; Oleson *et al.*, 2007b). Songs have only been recorded from males and are thus likely to have a reproductive function (McDonald *et al.*, 2001; Oleson *et al.*, 2007b). Blue whale type D calls are shorter (<5 s), frequency modulated, variable signals that are produced by both males and females at irregular intervals (Thode *et al.*, 2000; McDonald *et al.*, 2001), with a possible social function during feeding (Oleson *et al.*, 2007b). While the A and B calls are specific to the blue whale population found in the eastern North Pacific (Stafford *et al.*, 1998, 1999; Stafford, 2003; McDonald *et al.*, 2006), D calls appear to be commonly produced by different blue whale populations (Mellinger and Clark, 2003; Rankin *et al.*, 2005).

The Southern California Bight (SCB) is a highly productive upwelling ecosystem that lies within the migration route of the eastern North Pacific stock of blue whales (Mate *et al.*, 1999; Calambokidis *et al.*, 2015). Blue whales are observed during visual surveys in the SCB from spring through early winter, often engaged in foraging (Calambokidis *et al.*, 2003; Campbell *et al.*, 2015; Lomac-MacNair and Smultea, 2016). This timing matches the presence of blue whale sounds in passive acoustic recordings from the SCB: D calls are typically recorded from April through November, with a peak in August, while A and B call types appear in recordings in June and continue through January, peaking in September and October (Oleson *et al.*, 2007c). This temporal variation in the occurrence of different blue whale sound types indicates that blue whales may exhibit strong seasonality in their behavior off southern California (Burtenshaw *et al.*, 2004; Wiggins *et al.*, 2005; Oleson *et al.*, 2007c).

In addition to this seasonal variation in sound-type occurrence, sound production likely varies with time-of-day, behavioral state of the animal, and group size (Clark, 1990; Oleson *et al.*, 2007b,c; Parks *et al.*, 2011). In blue whales, diel patterns in singing behavior may be negatively correlated with foraging behavior (Stafford *et al.*, 2005; Wiggins *et al.*, 2005), and these authors hypothesized that, during times of optimum prey density, blue whales may expend more energy towards feeding as opposed to singing, making the two behavioral states mutually exclusive. In some cases, singing appears to occur in areas with low concentration of zooplankton (Širović and Hildebrand, 2011), providing further support for that hypothesis. On the other hand, the occurrence of D calls appears to increase while foraging, with D call production occurring during shallow dives that are within a series of deeper, lunge-feeding dives (McDonald *et al.*, 2001; Oleson *et al.*, 2007b). Blue whale acoustic behavior may vary not only with prey availability and behavioral state, but also group size. D calls are often used as counter-calls between multiple whales and are frequently heard from individuals within groups (Oleson *et al.*, 2007b). Furthermore, Oleson *et al.* (2007b) found that singular A and/or B callers always occurred within pairs or groups, while singing blue whales generally were not paired with other whales while singing.

An additional question is whether geographic setting also results in different calling behavior. Lomac-MacNair and Smultea (2016) observed that behavioral state, group type and group size of blue whales off southern California varies with distance from shore. These findings, coupled with other behavioral trends such as increased singing observed from solitary males traveling offshore (Oleson *et al.*, 2007b) suggest that there may be some spatial variability in blue whale acoustic behavior within the SCB.

To evaluate the calling and singing behavior of inshore and offshore animals off southern California, we analyzed blue whale sounds from twelve months of passive acoustic data collected simultaneously at four locations within the SCB. In this paper, we examine how blue whale acoustic behavior varies with distance to shore, as well as temporally, in this region.

2.2 Methods

2.2.1 Passive acoustic data collection

From September 2009 through August 2010, four autonomous High-frequency Acoustic Recording Packages (HARPs) were deployed within the SCB, two inshore and two offshore of the southern Channel Islands (Table 2.1). The HARPs were bottom-mounted with a hydrophone suspended 10 m above the bottom recording continuously at 200 kHz sample rate (Wiggins and Hildebrand, 2007). Prior to analysis, data were down-sampled by a factor of 100 creating an effective bandwidth from 10 to 1,000 Hz.

After decimation, data were processed into long-term spectral averages (LTSAs) with 5 s temporal and 1 Hz frequency resolution, as well as saved in waveform audio format. Blue whale sound types were detected automatically (B call) or marked manually (A and D call) from a subsample of these data.

2.2.2 Passive acoustic data analysis

To evaluate patterns in blue whale acoustic behavior at all four sites, continuous acoustic data were subsampled. Occurrence of all blue whale A, B, and D call types within a three-hour time window on ten randomly selected days of each month with recording effort was logged. Only one three-hour time window was analyzed on any selected day. The start-time of these logging windows was randomly selected for each day to provide broad coverage across the 24 h within a given month. The same days and corresponding three-hour time windows were used each month, across all four sites. The random spacing of analysis windows throughout each month allowed us to assume independence between sampling periods. However, call and phrase detections occurring within any given three-hour window could be from one whale or multiple whales; therefore, no assumption was made regarding independence of data within a day. If data were unavailable for a particular site or time, calls were logged either from the same three-hour period during an adjacent day, or that day was skipped.

Due to their pulsed or highly variable nature, A and D call types were not well suited for automatic detection. Therefore, all A and D calls were manually logged during each three-hour window through visual and aural inspection of the LTSA and wav files in Triton, a MATLAB-based (www.mathworks.com) software package (Wiggins and Hildebrand, 2007). The occurrence of A calls was logged based on the presence of the 90 Hz component of these sounds (Thompson *et al.*, 1996; Stafford *et al.*, 1998; McDonald *et al.*, 2001), while D calls were identified as down-sweeps varying in frequency in bandwidth between 100 and 20 Hz with duration of at least 1 s (Thompson *et al.*, 1996; McDonald *et al.*, 2001; Oleson *et al.*, 2007b). One hour of acoustic data was reviewed at a time using the LTSA. The presence of A and D sounds was verified using a 60 s spectrogram window, calculated with 2,000-point NFFT, 90% overlap, and Hanning window, and the start and end times of each call were logged.

Table 2.1: HARP deployment data: latitude, longitude, and bottom depth at each deployment site, as well as deployment periods when data were available at the site for this study; and total number of hours during which there was detection effort.

	Site	**Latitude (N)**	**Longitude (W)**	**Bottom depth (m)**	**Deployment period**	**Total detection effort (h)**
Offshore	North (Offshore-N)	33°30.89’	119°14.84’	910	1 Sep – 16 Sep 2009 25 Sep – 17 Nov 2009 5 Dec – 25 Jan 2010 30 Jan – 25 Mar 2010 10 Apr – 24 Jun 2010 22 Jul – 30 Aug 2010	194.1
	South (Offshore-S)	32°22.20’	118°33.80’	1,290	1 Sep – 15 Sep 2009 26 Sep – 19 Nov 2009 6 Dec – 26 Jan 2010 31 Jan – 26 Mar 2010 11 Apr – 16 May 2010 30 May – 18 Jul 2010 23 Jul – 30 Aug 2010	230.9
Inshore	North (Inshore-N)	33°49.21’	118°37.75’	670	24 Sep – 17 Nov 2009 4 Dec 2009 – 25 Jan 2010 29 Jan – 25 Mar 2010 9 Apr – 21 Jul 2010	234.8
	South (Inshore-S)	32°54.00’	117°22.71’	480	24 Sep – 15 Nov 2009 4 Dec 2009 – 12 Jan 2010 31 Jan – 8 Feb 2010 11 Apr – 7 May 2010	123.8

Blue whale B call types were automatically detected using spectrogram correlation (Mellinger and Clark, 2000; Širović, 2016), which cross-correlated a kernel representation of the sound with a spectrogram of the recording, and the start times for each detection were saved. To ensure high precision and recall values of the automatic detector, new threshold values and kernels were developed seasonally at each site (Širović *et al.*, 2015). For this study, kernels were developed for the months of June and October 2009 and June 2010 to account for the variation in B call frequency content between the start (June) and peak (October) of the blue whale calling season of each year (Širović, 2016). To develop these kernels, high-quality B calls, separated by 24 h or more, were manually identified within the data from each month, and the peak frequency of the third harmonic (in Hertz) was measured at five time points within each call (0, 1.5, 3, 4.5, and 10 s). Kernel values were then calculated based on the average of these measurements. The average kernel values measured from B calls detected from data recorded in June 2009 (47.8, 47.0, 46.2, 45.8, and 44.9 Hz) were applied to recordings from September 2009. The kernel developed for October 2009 (47.6, 46.8, 46.1, 45.3, and 44.9 Hz) was applied to recordings from October 2009 through March 2010, while the kernel calculated for June 2010 (47.9, 47.0, 46.1, 45.6, and 45.0 Hz) was applied to recordings from April through August 2010. The threshold value for the detector was chosen based on the precision to recall ratio closest to 1, based on comparison to ground truth data from June and October (Širović, 2016). For months during which blue whale sounds are not commonly detected in recordings off southern California (February through May), all automatic detections were manually checked and false detections were eliminated from subsequent analyses.

Low-frequency noise, whether due to anthropogenic activity or other sources, at times masked blue whale sounds within the LTSA; therefore, such events were also logged during all analyzed time periods. The periods of these low-frequency noise events were excluded from each three-hour detection window and this difference in effort was accounted for through the normalization of the total numbers of detections by the duration of on-effort analysis.

2.2.3 Acoustic behavior and song analysis

For this analysis, blue whale signals were classified as singular calls or song phrases. To determine whether any individual A or B sound was produced as a singular call or as a unit within a song phrase, all A and B detections were sorted based on recorded start time. Inter-call intervals, measured as the time from the start of one call to the start of the next, were calculated for all A and B sounds detected within each three-hour window. Intermittent blue whale A and B detections that were not produced in a pattern with regular inter-call intervals were classified as singular calls rather than phrase units (Oleson *et al.*, 2007c). Individual phrases of A-B units that were neither preceded nor followed by another phrase within 2 min were classified as single phrases. Repeated A-B phrases that occurred in sequence were classified as song. All D call detections were simply classified as singular D calls.

2.2.4 Analysis of spatial and temporal patterns in acoustic behavior

To evaluate similarity in blue whale acoustic behavior at the four sites, percent sound types, defined as singular A, B, and D calls, single phrases, and repetitive phrases, were determined across the sample period. To investigate phrase composition, we calculated the ratio of B units to A units within both single and repetitive phrases at all four sites. By comparing percentages and ratios instead of absolute numbers, we were able to evaluate proportional changes in acoustic behavior, without confounding it with changes in the number of animals producing calls.

To investigate temporal variability in the occurrence of different sound types, singular A, B, and D call rates (as number of calls/hour) were calculated for each three-hour detection window based on singular call counts and time on-effort. Single and repetitive phrase production rates (as number of single or repetitive phrases per hour, respectively) were also calculated for each daily three-hour window. Diel patterns in call and phrase production rates were analyzed by sorting detection windows into four time-of-day periods: dawn, day, dusk, and night. We used the definitions of these periods as described by Wiggins *et al.* (2005), based on times of nautical twilight, sunrise and sunset. Daily values for nautical twilight, sunrise, and sunset were obtained from the

U.S. Naval Observatory's Astronomical Application Department (Anonymous, 2001) for 2009-10 at an approximate center point of the four sites (33°20'N, 118°19'W). If the timing of a detection window crossed between two time-of-day periods, that window was categorized based on the majority of hours spent in a particular period.

As times without blue whale sound detections were common, the call and phrase production rate data were not normally distributed and therefore non-parametric statistical tests were needed to quantify the influence of location, month, and time-of-day on A, B, and D singular call rates, as well as phrase production rates. We developed general additive mixed models (GAMM) using the 'mgcv' package (Wood, 2006, 2011) in R (Version 3.4.1). Because the call and phrase production rate data were overdispersed, we used a logarithmic link function with a quasi-Poisson error distribution within the GAMM. Two of the variables tested–location (grouped into either inshore or offshore sites) and time-of-day period–were defined as random factors, while month was treated as a circular variable and fit with a cyclic cubic regression spline. Post-hoc Dunn's Kruskal-Wallis multiple comparison tests were conducted using package 'FSA' (Ogle, 2012) on random factors that were statistically significant descriptors of A, B, or D call rates or phrase production rates. All analyses were performed in the R Studio (Version 1.0.153) statistical software platform (R Core Team, 2015).

We also analyzed spatial and temporal patterns in blue whale songs. Intervals between A-B and B-B units, measured from the start of one unit to the start of a subsequent unit within a phrase, were calculated. Inter-phase intervals, measured from the start of the final B unit of one phrase to the start of the leading A of the next, were also calculated. Each individual phrase within a song bout was classified into one of two phrase types. If a song phrase consisted of an A unit followed by a single B unit, we classified it as an AB-type phrase. When a single A unit was followed by two or more B units, it was termed ABB-type phrase. In song bouts containing multiple ABB-type phrases, the number of B units within these phrases varied considerably without a consistent pattern. Therefore, all phrases containing two or more B units were classified as ABB-type regardless of the actual number of B units present. Overall percent song type for each site was calculated based on the number of detected phrases of each type relative to total number of phrases. Monthly song type percentages were also reported for each site. The dominant song type for each site was defined based on the phrase type (AB- or ABB-) that comprised more than half of the total number of phrases detected. Only song bouts longer than 5 min were included in this song analysis.

2.3 Results

A combined total of 18,263 blue whale signals were detected over 780 analyzed hours across the four sites, including 5,060 A, 11,489 B, and 1,714 D sounds. A total of 87% of all detections occurred from September through December 2009. From month to month, different acoustic behaviors dominated at different sites (Figure 2.1). Overall, singular B calls and repetitive AB-phrases were the dominant signals recorded during summer and fall while singular D calls dominated detections in the spring. Singular B calls comprised the majority of detections at the offshore sites between September and December 2009, and peaked in December at both inshore sites. Repetitive AB-phrases comprised nearly 60% of all detections in September 2009 at the northern inshore site, as well as in October and November 2009 at the southern inshore site. The percentages of AB-phrases were also higher in December 2009 at the inshore sites than the offshore sites (Figure 2.1). Singular A calls dominated total monthly detections only in July 2010 and comprised about half of all detections in December 2009 at the northern offshore site. At other locations, singular A calls peaked in either September or October 2009 (Figure 2.1). The proportions of singular A and B call detections also increased between June and August 2010 at the two offshore sites (Figure 2.1), which were the only two sites with data available during that time (Table 2.1). Single AB phrases were not very common at any of the sites, but they occurred in the same months as repetitive AB-phrases. Both repetitive and single AB-phrases were also detected in August 2010 at the offshore sites (Figure 2.1), though no data were available for the inshore sites during that month. D calls, which dominated during spring and early summer, were detected as early as April 2010 at the southern inshore site, and comprised the majority of all detections from May through June at the northern offshore site, or through July at the southern offshore and northern inshore sites (Figure 2.1).

There was significant spatial variability in call and phrase production rates,

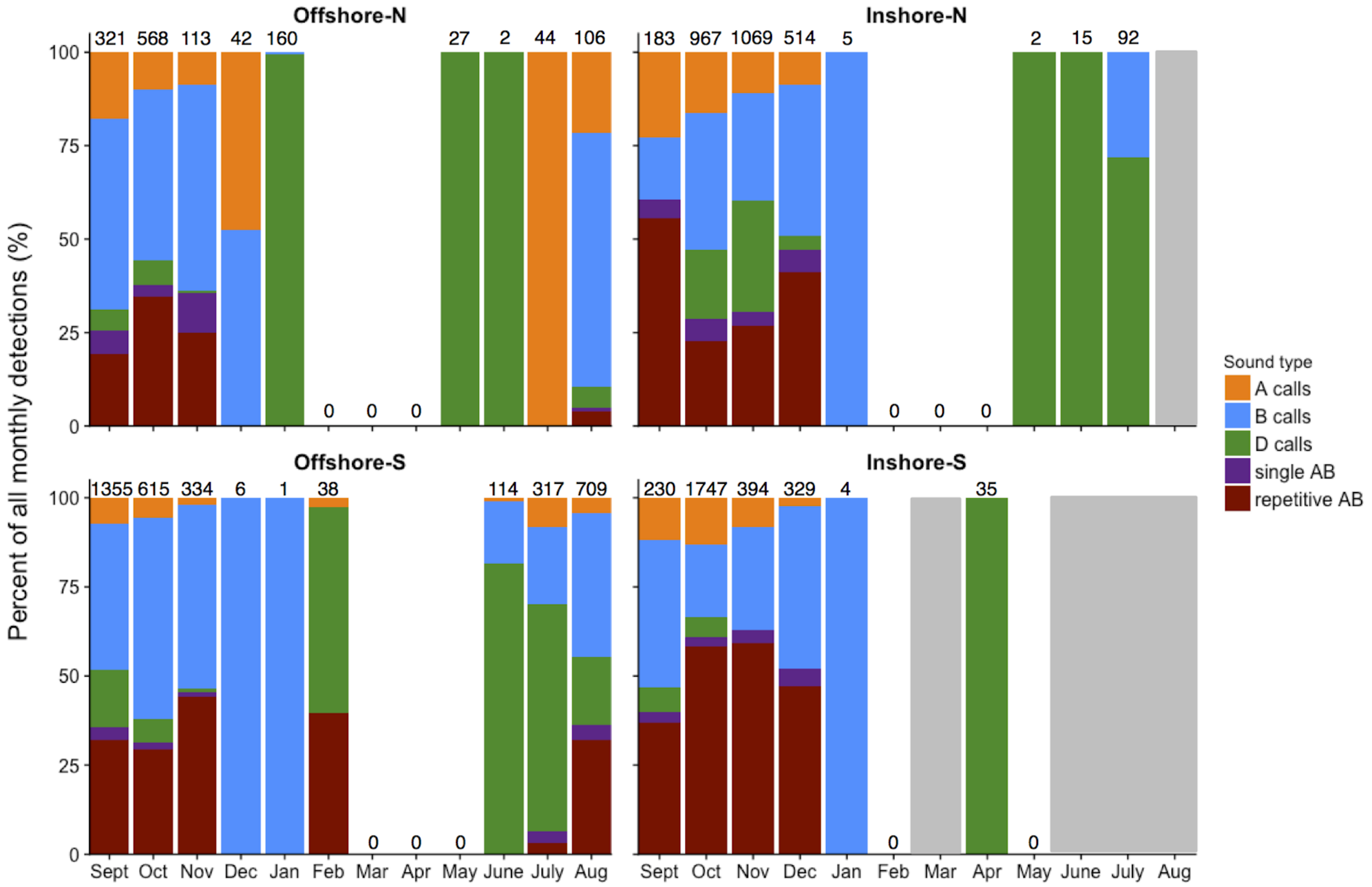

Figure 2.1: Monthly proportions of blue whale sound types. The percent of singular A (orange), singular B (blue) and D (green) call detections, and single (purple) and repetitive (maroon) AB-phrase detections that occurred out of the total number of monthly detections at each of the four sites. Monthly detection totals are listed at the top of each bar. Periods shaded in gray indicate times when there was no data at that site.

particularly between the southern inshore site and the other three sites (Table 2.2). Singular A call rates were slightly higher at the southern inshore site than at the northern offshore site (Dunn's test – Z = -2.12; *P*=0.034). Singular B and D call rates, on the other hand, showed no significant difference between the inshore and offshore sites (Table 2.2). Phrase production rates also differed significantly between the inshore and offshore sites (Table 2.2). Single AB phrase production rates were significantly higher at the southern inshore site than any other site [Offshore-N vs. Inshore-S: (Dunn's test – Z = 3.14, *P*= 0.002), Offshore-S vs. Inshore-S: (Dunn's test – Z = 2.25, *P* =0.024), Inshore-S vs. Inshore-N: (Dunn's test – Z = 2.18; *P* = 0.029)]. Similarly, repetitive AB phrase production rates were also higher at the southern inshore site than any other site [Offshore-N vs. Inshore-S: (Dunn's test – Z = 4.78, *P* <0.001), Offshore-S vs. Inshore-S: (Dunn's test – Z = 3.48, *P* <0.001), Inshore-S vs. Inshore-N: (Dunn's test – Z = 3.60; *P* <0.001)].

There was also a significant level of monthly variability in signal production rates, which could indicate an increase in calling by an individual animal or an increase in number of animals (Figure 2.2). Singular A and B call rates peaked between September and November. Single and repetitive AB-phrase production rates also peaked during these months. Phrase production rates were lower in the late spring and early summer leading up to this peak (between May and July) and were more variable in August than singular call rates. D call rates were generally less variable throughout the year and increased earlier than other sound types (May and June), peaked during the summer, and began decreasing in November. The production rates for all sound types decreased in December and were low between February and May (Figure 2.2). Time-of-day was generally not a significant variable in explaining signal production rates, except repetitive AB phrases (Table 2.2) in which case the differences between diel periods were not significant in post-hoc multiple comparison tests.

Repetitive phrase production rates, indicative of occurrence of song, were greatest on average at the southern inshore site (11.0±16.1 phrases/h). Repetitive phrase production rates at the northern inshore site (3.3±7.2 phrases/h) were similar to those recorded at the southern offshore site (3.6±8.2 phrases/h) and also greater than the northern offshore site (1.2±3.5 phrases/h). Interestingly, the ratio of B units to A units

Table 2.2: Results of the general additive mixed model (GAMM) of daily and monthly variation in singular call and phrase production rates. For each sound type, F-ratios (*F*) and p-values (*P*) for each of the 3 variables (Location, Month and Time-of-day, TOD) are presented; as well as percent deviance explained by the model and generalized cross-validation (GCV) score. Location was classified as inshore or offshore, and sample size was *n*=351 for each sound type. Variables with significant p-values are marked with an asterisk and italicized.

Sound type	**Variable**	***F*-ratio**	***P*-value**	**% deviance explained**	**GCV**
Singular A	*Location*	8.327	0.004*	53.6	2.10
	Month	5.742	0.016*		
	TOD	0.412	0.560		
Singular B	Location	1.233	0.189	64.4	3.90
	Month	13.91	< 2.00e-16*		
	TOD	1.267	0.142		
D calls	Location	0.003	0.587	16.7	7.76
	Month	1.721	0.004*		
	TOD	0.453	0.525		
single AB phrases	*Location*	5.212	0.021*	50.8	0.802
	Month	5.185	0.002*		
	TOD	0.883	0.318		
repetitive AB phrases	*Location*	30.16	1.07e-07*	62.7	5.01
	Month	11.45	0.011*		
	TOD	1.985	0.047*		

within these repetitive phrases was 1.7±0.0 at the inshore sites and 2.7±0.5 at the offshore sites, indicating a production of a larger fraction of B units. Across all hours of song analyzed, ABB-type phrases comprised a higher proportion (64% and 55%) of all identified song at the offshore sites (northern and southern sites, respectively), whereas about 60% of song analyzed at the inshore sites was AB-type (Table 2.3, Figure 2.3).

Although there was some monthly variability in dominant song type observed at three of the four sites, deviations occurred during only one month per site, either September or October (Table 2.3, Figure 2.4). Repetitive AB phrases identifiable as song were detected only at the inshore sites in December (Table 2.3). Blue whale song was also identified in August 2010 at the two offshore sites (Table 2.3), which were the only two sites with data available for analysis during that time (Table 2.1). Overall, during all detection windows, song was detected during more hours inshore (90.2 h) than offshore

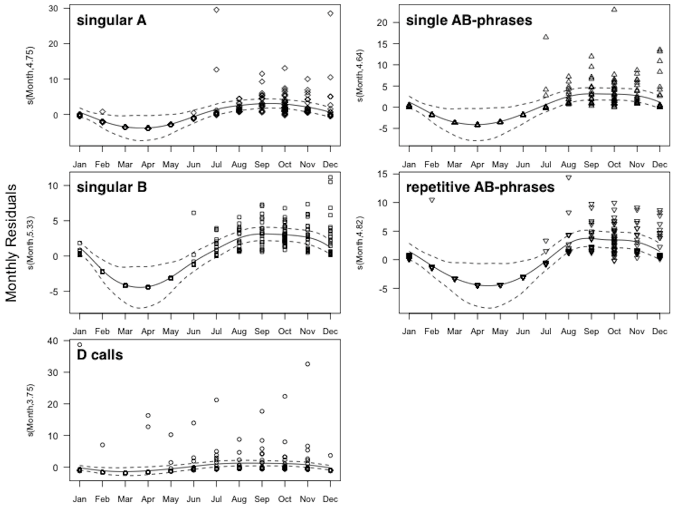

Figure 2.2: Residual plots of monthly variability for all blue whale sound types: singular A (diamonds), singular B (squares), and D (circles) call detections (left panels), and single (upright triangles) and repetitive (downward triangles) AB-phrase detections (right panels).

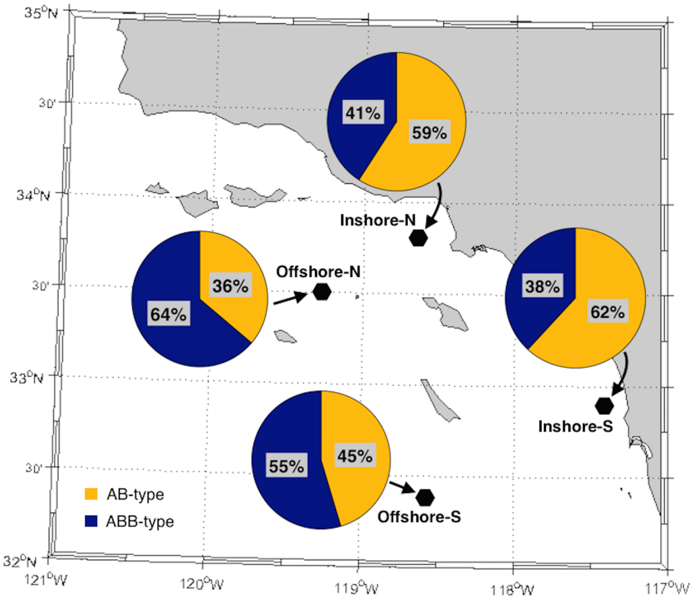

Figure 2.3: Percent of all song bouts recorded at the inshore and offshore sites comprised of the two blue whale phrase types between September 2009 – August 2010.

Table 2.3: Monthly and overall occurrence of song-types for each of the four HARP sites, including: total detection effort each month; total duration of song detected; total number of phrases contained within identified song bouts; as well as percent phrase type and dominating song type. The dominating song type for each site was defined based on whichever phrase type (AB- or ABB-) comprised more than fifty percent of the total number of phrases detected. The greatest monthly durations and the dominating song type for each site are highlighted in gray. Months when the dominating song type differed from the overall dominating song-type observed at a particular site are marked with an asterisk. Only months that contained identifiable song are included for each site. Data were not available for the inshore sites during the beginning of September 2009 or August 2010. (Table 2.1).

	Site	**Month**	**Detection effort (h)**	**Total duration of song detected (h)**	**Total num. of phrases**	**%AB-type phrases**	**%ABB-type phrases**	**Dominating song type**
Offshore	North (Offshore-N)	Sept 2009	15.9	3.4	51	47.1	52. 9	ABB-type
		Oct 2009	24.8	10.3	149	38.3	61.7	ABB-type
		Nov 2009	15.5	2.1	27	11.1	88.9	ABB-type
		Aug 2010	18.7	0.5	5	0	100	ABB-type
		Overall	74.9	16.3	232	36.2	63.8	ABB-type
	South (Offshore-S)	Sept 2009	20.6	19.8	347	44.4	55.6	ABB-type
		Oct 2009	26.0	7.9	145	69.7	30.3	AB-type*
		Nov 2009	17.2	9.3	126	24.6	75.4	ABB-type
		Aug 2010	24.6	9.7	155	41.3	58.7	ABB-type
		Overall	88.4	46.7	773	45.3	54.7	ABB-type
Inshore	North (Inshore-N)	Sept 2009	5.3	3.9	82	74.4	25.6	AB-type
		Oct 2009	28.3	10.7	170	45.9	54.1	ABB-type*
		Nov 2009	17.5	11.9	223	61.0	39.0	AB-type
		Dec 2009	24.2	8.1	138	63.8	36.2	AB-type
		Overall	75.3	34.6	613	59.2	40.8	AB-type
	South (Inshore-S)	Sept 2009	5.7	3.2	59	35.6	64.4	ABB-type*
		Oct 2009	29.2	38.2	775	62.5	37.6	AB-type
		Nov 2009	16.7	8.6	179	61.5	38.6	AB-type
		Dec 2009	26.1	5.6	112	72.3	27.7	AB-type
		Overall	77.7	55.6	1125	61.9	38.1	AB-type

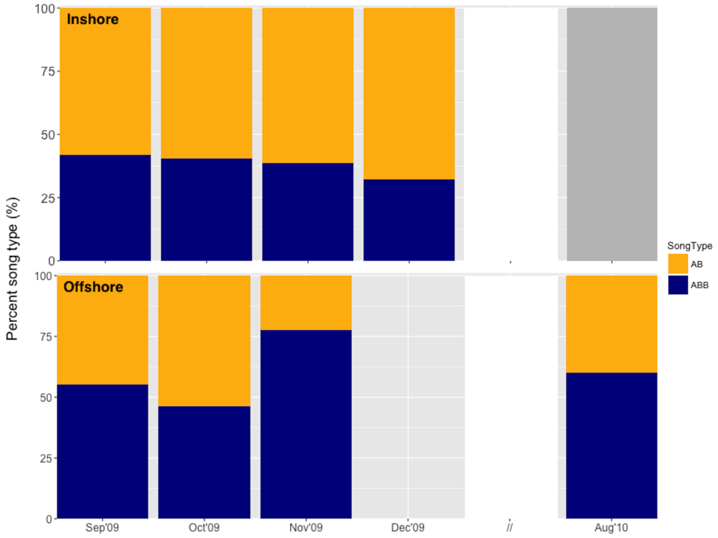

Figure 2.4: Proportion of song consisting of each type per month at the inshore and offshore sites. Only months that contained identifiable song are included. No song was identified at the offshore sites in December 2009. Months when no data were available are marked in dark grey (Table 2.1).

(63 h) (Table 2.3), even though the total detection effort inshore (357 h) was less than offshore (424 h) (Table 2.1).

Average inter-unit intervals contained within singular phrases were 49±7 s between A-B units and 52±6 s between B-B units across all sites. The inter-unit intervals within repetitive song phrases were similar but slightly more variable, at 49±10 s between A-B units and 51±14 s between B-B units. The average inter-phase interval, or interval between ending B unit and leading A unit of repetitive phrases, was 70±29 s.

2.4 Discussion

This is the first detailed investigation of inshore versus offshore differences in calling and singing behavior of blue whales in the SCB. In general, singular calls were detected more frequently at the offshore sites while inshore detections were dominated by single and repetitive phrases. We found that a majority of all identifiable blue whale song phrases offshore were of ABB-type, but inshore they were AB-type. Overall, the temporal and, most notably, spatial differences observed in calling and singing may identify distinct behavioral states for blue whales over this area.

Our results show that blue whales produce sounds that are associated with both foraging and reproduction off southern California, as shown previously in this region (Oleson *et al.*, 2007b). However, the distribution of detected sound types varied considerably between inshore and offshore recording locations. On one hand, we observed increased production of single and repetitive AB phrases inshore compared to offshore. In addition, the total duration of identifiable song bouts was greater inshore. Conversely, detections of singular A and B calls, as well as D calls, were greater offshore. Increased sound detection in our recordings across sites may signify an increase in number of animals in the area, greater sound production rates by individual animals, increase in propagation range, or a combination of these factors. Based on estimates of detection ranges of blue whale B calls at each of the sites (Širović *et al.*, 2015), the offshore sites covered an area approximately five times larger than the inshore sites. This large difference in detection area may account for higher singular B, and possibly singular A call detections offshore. Given that D calls have a lower source level (Thode *et al.*, 2000), their detection range should be greatly reduced compared to A and B calls, and therefore may be more comparable across sites.

The production of singular calls, especially D calls, is thought to correspond with foraging (Oleson *et al.*, 2007b,c), so the higher singular call densities detected offshore may be associated with increased foraging activity. Both 2009 and 2010 were considered transitional years between La Niña and El Niño states in this region and a trend in increased zooplankton biomass was observed offshore (Bjorkstedt *et al.*, 2010). Behaviors exhibited by blue whales producing singular A and/or B calls have also been shown to differ from those associated with singing males, with the former engaging in feeding, milling, resting, and traveling, all while maintaining close association with at least one other individual (Oleson *et al.*, 2007b). Oleson *et al.* (2007b) further hypothesized that the infrequent production of A and/or B calls may be used by males to maintain pair bonds during feeding. Therefore, singular A and/or B calls may serve a different ecological function than A-B units within phrases.

In another major finding, we observed that A units were produced less frequently than B units within repetitive AB-phrases at the two offshore sites, corresponding to a higher proportion of ABB-type song offshore. As relatively long, low frequency tonal sounds, blue whale B sounds are capable of propagating across extremely long distances underwater (Stafford *et al.*, 1998; McDonald *et al.*, 2001; Širović *et al.*, 2015; Balcazar *et al.*, 2017). Increased production of B units within the ABB-type song offshore, where there are fewer physical obstacles to propagation, could enable phrases to be broadcast across greater distances and potentially increase the chances of a male's song being heard. Indeed, propagation estimates calculated by Širović *et al.* (2015) show that the detection areas for blue whale calls at each of the two offshore sites are greater than at either of the inshore sites. Thus, there may be more benefit to producing repetitive B units in regions where they are likely to travel further. Since solitary whales are more commonly observed offshore than groups or adult pairs (Lomac-MacNair and Smultea, 2016), communication over longer ranges could be more important. This preferential production of B units, as well as singular B calls, could be advantageous to blue whales seeking mates in this area.

Contrary to the high singular call densities recorded offshore, we recorded heightened AB phrase and overall song production, as well as an extended singing season, at the inshore sites. The rate at which phrases are produced depends in part upon the composition of phrase units. Since AB-type phrases contain only a single B unit, while ABB-type phrases contain multiple B units, the number of AB-type phrases that can be produced within any individual song bout is greater than the number of ABB-type phrases. The dominating AB-type song inshore coupled with the greater duration of song bouts identified at the inshore sites may explain the increased phrase production rates observed inshore compared to offshore. However, the abundance of phrases compared to singular calls detected at the inshore sites between September and December when the opposite trend was observed offshore suggests that there may be a more complicated explanation for the differences in sound type usage between sites. The behaviors associated with song production in blue whales are consistent; when singing, males are solitary and traveling, not feeding (Oleson *et al.*, 2007b). The exclusivity of feeding and singing behaviors in blue whales has been hypothesized previously (Wiggins *et al.*, 2005; Oleson *et al.*, 2007b,c), so the differences that we observed in singular call and phrase production rates between the inshore and offshore sites may indicate spatial separation between behavioral states.

Overall, some of the spatial trends that we observed in blue whale acoustic behavior off southern California may be due to prey distribution (Fiedler *et al.*, 1998; Bjorkstedt *et al.*, 2010), preferential use of habitat by blue whales (Irvine *et al.*, 2014; Campbell *et al.*, 2015; Širović *et al.*, 2015), or a combination of these two factors. The variability that we recorded in singular call densities and rates, particularly for D calls, between sites may be due to finer-scale patchiness in euphausiid densities during our study period. Both euphausiid species preferentially preyed upon by blue whales in this region,*Thysanoessa spinifera* and *Euphausia pacifica* (Croll *et al.*, 1998; Fiedler *et al.*, 1998; Croll *et al.*, 2005) are characterized by a patchy distribution (Croll *et al.*, 1998). Unfortunately, we did not have measures of prey during our recording period, but future studies into blue whale acoustic behavior would benefit from concurrent prey measurements. Alternatively, although solitary traveling individuals have been more commonly observed offshore (Lomac-MacNair and Smultea, 2016), the higher phrase and song production rates that persisted late into the fall at the inshore sites may indicate inshore movement of blue whales in the SCB, possibly before proceeding south on their migration (Mate *et al.*, 1999; Calambokidis *et al.*, 2015).

In addition to these spatial patterns, we found significant seasonal variability in blue whale acoustic behavior in the SCB during 2009-2010, largely similar to findings from previous studies (Burtenshaw *et al.*, 2004; Wiggins *et al.*, 2005; Oleson *et al.*, 2007b,c; Širović *et al.*, 2015). The majority of all A, B, and D sound detections, at both inshore and offshore HARPs, occurred from fall through early winter, while very few acoustic detections were made from mid-January through mid-April. This is consistent with blue whale sightings from long-term visual surveys in the SCB, which peak during summer and fall and are nearly absent from winter through spring (Campbell *et al.*, 2015). The occurrence of B sounds in our dataset from June through October was similar to the peak in B production reported by Oleson *et al.* (2007a,b,c) albeit indicating an extended calling season, especially inshore. Peaks in B sound detections at the inshore sites, in October and November, are a bit later than those from studies that included larger areas and more offshore sites (Burtenshaw *et al.*, 2004; Širović *et al.*, 2015). Blue whale D calls appeared as early as April in our dataset. Our data also indicated a marked summer peak in D call recordings, consistent with previous studies (Oleson *et al.*, 2007b,c). However, unlike for singular A and B calls and AB phrases, month was not an important variable for modeling the occurrence of D calls.

Both the inferred summer peak in D calling, as well as the observed fall peak in AB-song production, suggest that blue whales may exhibit a temporal separation between feeding and reproductive behaviors in this region. Although the SCB is primarily considered a seasonal feeding ground, the occurrence of song during nonreproductive seasons has been previously documented in blue whales (Oleson *et al.*, 2007b). Since AB-songs are thought to be associated solely with males and related to breeding, while D calls are considered to be a foraging call produced by both males and females (Oleson *et al.*, 2007b), blue whales in the SCB may arrive and start feeding as early as spring, continuing through summer and early-fall, at which time reproductive behaviors begin to dominate. Overall, the temporal trends observed in blue whale acoustic behavior in the SCB differ minimally from those recorded across the North Pacific Ocean, with the timing of detection peaks at offshore sites occurring just slightly earlier than reported in other studies (Stafford *et al.*, 1998, 1999; Watkins *et al.*, 2000; Stafford *et al.*, 2001; Burtenshaw *et al.*, 2004).

The relationships between acoustic behavior and time-of-day have varied in previous studies in the SCB. Blue whales were found to produce fewer B calls during daytime (Wiggins *et al.*, 2005), but in other work time-of-day was not an important variable to model sound production (Oleson *et al.*, 2007a). Although we found time-of-day to have a slight explanatory significance on repetitive AB phrase production rates, this significance did not appear in post-hoc tests. It is possible these differences across studies arose from different temporal resolutions and variation in sample sizes; the overall importance of time-of-day is likely relatively small thus a larger sample size and finer temporal resolutions may be needed to point towards some diel variability in acoustic behavior.

Recently, passive acoustics have proven to be an efficient means for estimating marine mammal densities (Marques *et al.*, 2009; Küsel *et al.*, 2011; Marques *et al.*, 2011). Sound production rates are a critical part of that method. Before reliable density estimates can be developed, the behavioral contexts of sound production must first be understood.

For example, the temporal variation in the occurrence of blue whale sounds observed in the SCB in this study, as well as in previous studies (Oleson *et al.*, 2007c), already serves as an indication that any sound production models, to be useful to density estimation, will likely need to have a seasonal or monthly component to account for the variability in singular call as well as song production. But unlike singular A and B call rates and AB phrase production rates that varied both spatially and temporally, D call production rates exhibited less spatial variability in the SCB. Therefore, it is possible that D calls, rather than the more commonly studied AB sound types, may be a more robust metric for density estimation using passive acoustics.

It is important to note an inherent bias in any passive acoustic monitoring analysis: absence of animals cannot be assumed simply because calls are absent. Additionally, because our analyses relied solely upon passive acoustic data with no concurrent visual surveys, the absolute number of calling and/or singing blue whales at any time cannot be determined based on our results. Thus, the variability that we observed in blue whale sound production rates at any one site could be due to changes in whale presence, differences in behavioral state (feeding and breeding for D and AB sounds, respectively) resulting in different rates of sound production, or a combination of these factors.

The Northeast Pacific population of blue whales has been widely studied over broad spatial and temporal scales; however, much remains to be learned about smaller-scale variability in their acoustic behavior. While no single year nor site can fully capture this variability, the observed differences in blue whale call and phrase production, as well as occurrence of song, that we found between offshore and inshore sites in the SCB illustrate considerable heterogeneity in acoustic behaviors that should be considered when modeling blue whale sound production.

2.5 Acknowledgements

HARP deployment and recovery, and data processing and analysis were supported by Hannah Bassett, Tim Christianson, Chris Garsha, Ryan Griswold, Brent Hurley, John Hurwitz, Erin O'Neill, and Bruce Thayre. The analysis presented was supported by the Office of Naval Research (ONR) under Award No. N00014-14-1-0414 (Michael Weise).

Data collection was supported by the Chief of Naval Operations CNO-N45 (Frank Stone, Ernie Young, and Bob Gisiner) and the US Navy Pacific Fleet (Chip Johnson). LAL was supported with funding from the National Science Foundation Graduate Research Fellowship Program under Grant No. DGE-1144086.

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Chapter 3

Behavioral context of sound production in tagged blue whales off southern California

by Leah A. Lewis,
John Calambokidis, Alison K. Stimpert, James Fahlbusch,
Ari S. Friedlaender, John A. Hildebrand, Megan F. McKenna,
Sarah Mesnick, Erin M. Oleson, Brandon L. Southall,
Angela R. Szesciorka, & Ana Širović

Abstract

Sound production is an important behavioral strategy for many species, particularly in the marine realm. Northeast Pacific blue whales (*Balaenoptera musculus*) produce three different call types–A, B, and D calls– which can all be produced as singular calls, but A and B calls can also occur in phrases. To evaluate the behaviors associated with singular call and phrase production in blue whales, the acoustic and dive profile data collected from tags deployed on individuals off southern California were analyzed, and variability in call and phrase production rates were assessed using Generalized Estimating Equations. Approximately 22% (27 out of 121) of all analyzed

deployments contained sounds attributed to tagged blue whales. The majority of all calls were produced at shallow depths (less than 30 m). Sound production rates were affected by behavioral state, and spatial as well as temporal patterns in sound production rates were observed. Repetitive phrases indicative of singing were most commonly produced during shallow, non-lunging dives, while the behaviors associated with singular call production were more variable and generally suggestive of foraging. Higher singular call and phrase production rates were recorded during fall deployments, between September and October. Sound production rates also varied with respect to time-of-day: singular call rates were higher during dawn and dusk, while phrase production rates were highest at night. Overall, the differences observed in blue whale acoustic behavior stress the importance of context specific rates in future models of density estimation.

3.1 Introduction

Sound production is an important behavioral strategy for many species. In the marine environment, where sound travels fast and with little attenuation, sound production may play an even more critical role in many life functions than it does in the terrestrial environment. Most marine mammals rely on sound for social and communicative purposes (Tyack and Clark, 2000), or, in toothed whales, for navigation and foraging (Au, 2012). Baleen whales produce a wide variety of sounds (Evans, 1967; Thompson *et al.*, 1979; Edds-Walton, 1997; Clark, 1990); however, the functional significance of the majority of these sounds has yet to be fully understood. Sounds produced by the Northeast Pacific population of blue whales (*Balaenoptera musculus*) in particular have been extensively studied (Thompson *et al.*, 1996; Thode *et al.*, 2000; McDonald *et al.*, 2001; Stafford *et al.*, 2001, 2005; Wiggins *et al.*, 2005; McDonald *et al.*, 2006; Oleson *et al.*, 2007b,c), yet our understanding of finer-scale variability in sound production by individuals within this population, especially across different behavioral states, remains lacking.

Theories on the function of sound production in baleen whales have evolved substantially over the years. Patterson and Hamilton (1964) originally hypothesized that patterned sounds might be used for echo-sensing, but other theories regarding the purpose of such sounds have since been suggested, including mate attraction (Evans, 1967) and long-range communication between conspecifics (Payne and McVay, 1971). Since then, the behavioral context of sound production has been determined for a subset of calls produced by some well-studied baleen whale species, including the humpback whale (*Megaptera novaeangliae*) (Payne and McVay, 1971; Winn and Winn, 1978; D'Vincent *et al.*, 1985; Silber, 1986; Darling and Bérubé, 2001), the southern right whale (*Eubalena australis*) (Clark, 1983), and the North Atlantic right whale (*E. glacialis*) (Parks and Tyack, 2005; Parks *et al.*, 2005, 2011).

The acoustic repertoire of the Northeast Pacific population of blue whales consists of three main sound types: A, B, and D calls (Thompson *et al.*, 1996; Clark and Fristrup, 1997; Rivers, 1997; Stafford *et al.*, 1999; Thode *et al.*, 2000; Stafford *et al.*, 2001; Stafford, 2003). Best-described are the pulsed A and tonal B sound types, each approximately 15-20 s in duration, which can be produced individually at irregular intervals as singular calls (Oleson *et al.*, 2007b) or together at regular intervals as A and B units within phrases that, when repeated, form bouts of song (McDonald *et al.*, 2001, 2006). The A and B sound types have only been recorded from males and are thus considered to have a reproductive function (McDonald *et al.*, 2001; Oleson *et al.*, 2007b). Blue whale D calls are shorter (<5 s), more frequency modulated sounds that have been recorded from both males and females (Thode *et al.*, 2000; McDonald *et al.*, 2001). These variable downswept calls appear to be commonly produced by different blue whale populations (Mellinger and Clark, 2003; Rankin *et al.*, 2005) and are likely used as social calls while foraging (Oleson *et al.*, 2007b).

Passive acoustic monitoring (PAM) is an efficient method for the study of marine mammal populations due to the commonality of sound production amongst many species (Mellinger *et al.*, 2007; Marques *et al.*, 2009). The loud, low frequency sounds produced by blue whales in particular make PAM a suitable tool to study distributions of individuals over a large area. Seasonal patterns in the occurrence of blue whales off Southern California have been observed using PAM (Clark and Fristrup, 1997; Burtenshaw *et al.*, 2004; Wiggins *et al.*, 2005; Oleson *et al.*, 2007a; Širović *et al.*, 2015). In addition, general sound function has been inferred from differential representation of blue whale sound types during different times of the day or year (Wiggins *et al.*, 2005; Oleson *et al.*, 2007c). However, evaluation of the behavioral or social context of sound production is not generally possible through remote PAM methods without visual identification of associated behaviors.

Recent developments in biologging technology have allowed for the collection of finer-scale data associated with sound production in several species of mysticetes, including humpback whales (Stimpert *et al.*, 2007; Parks *et al.*, 2014), North Atlantic right whales (Parks *et al.*, 2011), Antarctic minke whales (Risch *et al.*, 2014), fin whales (Goldbogen *et al.*, 2014; Stimpert *et al.*, 2015), and blue whales (Calambokidis *et al.*, 2007; Oleson *et al.*, 2007b). Miniature multi-sensor tags, which are capable of recording acoustic and dive depth data as well as body orientation, allow for evaluation of the tagged whale's behavior during sound production (Johnson *et al.*, 2009). The detailed behavior of tagged whales producing sounds may also be compared to that of whales not producing sounds while tagged to examine differences in behavior. Sound production rates determined through use of these archival tags can be applied to models to estimate whale distributions and densities (Marques *et al.*, 2009; Küsel *et al.*, 2011; Marques *et al.*, 2011) from long-term acoustic data collected by other PAM systems. However, before reliable models can be developed, the behavioral context(s) of sound production must first be understood.

Previous studies into the behavioral context of sound production in blue whales have been limited either in sample size, with a small number of tag deployments resulting in relatively few hours of collected data (Calambokidis *et al.*, 2007), or in the number of sounds detected, due to natural variation in sound production by any individual tagged whale (Oleson *et al.*, 2007b). Furthermore, because the recording durations of these tags are inherently dictated by memory, battery capacity, and attachment method (Johnson *et al.*, 2009), a limited subset of data has been collected from blue whales at night (Calambokidis *et al.*, 2007; Oleson *et al.*, 2007b), providing us with limited understanding of how blue whale behavior varies between day and night. However, recent tests of alternative attachment methods have resulted in longer deployments and have thus enhanced our ability to obtain behavioral and acoustic data from tagged blue whales for durations ranging from several days to weeks (Szesciorka *et al.*, 2016).

In this study, I evaluated the behavioral context of sound production in blue whales tagged off southern California. My dataset included the acoustic and dive depth data collected from tags deployed on individuals over the course of fourteen years, including data recorded during several long-duration deployments. My analysis provides valuable insight into how blue whale call and phrase production rates vary with respect to behavioral state, location, season and time-of-day in this region.

3.2 Methods

3.2.1 Tag data collection

Available for this analysis are the data collected through tags deployed on blue whales off southern California from 2002 through 2016 (Appendix A). These whales were tagged as part of multiple research efforts, including collaborations between the Cascadia Research Collective (CRC) and Scripps Institution of Oceanography (SIO), and the Southern California Behavioral Response Study (SOCAL-BRS) (Southall *et al.*, 2012). Three types of sound- and movement recording tags were deployed on blue whales during this time: Bioacoustic Probes (Bprobes)(Greeneridge Sciences, Inc.), Acousondes (Greeneridge Sciences, Inc.) and Dtags (Johnson and Tyack, 2003). Bprobes are capable of sampling data at rates up to 20 kHz and are equipped with ancillary sensors for recording temperature, pressure, and, in versions produced after 2003, 2-axis acceleration. Accelerometer data enables for the derivation of instantaneous body orientation of the whale during a dive cycle (Goldbogen *et al.*, 2006). In addition to the auxiliary sensors found in the Bprobe, Acousondes contain an updated 3-axis accelerometer, a compass, and the ability to collect higher frequency acoustic data. The sampling capabilities of Dtags are similar to those of Acousondes, recording depth, accelerometer and acoustic data. The technical specifications of Dtags are described in detail by Johnson and Tyack (2003). The sampling rates for acoustic, auxiliary, and accelerometer data varied with tag type and year (Appendix A). Across all deployments, sampling rates were between 1,024–240,000 Hz, 1–50 Hz, and 1–800 Hz for acoustic, auxiliary, and accelerometer data, respectively (Appendix A).

Tag deployments were conducted during ship-based efforts or shore-based tagging operations off southern California. Blue whales were tagged opportunistically, typically based on the ability to locate and track them visually. When an individual was chosen for tagging, the whale was approached from behind using a rigid-hulled inflatable boat (RHIB) and a tag was attached using a metal or fiberglass pole. For the majority of deployments, the tag was held on the whale with suction cups. However, between 2013 and 2016, a variety of longer-duration tag attachment methods, including darts, were used (Szesciorka *et al.*, 2016).

Upon tag retrieval, digital data were downloaded from the tag to a computer for analysis. Only acoustic and pressure data were used for this study because 3-axis accelerometer data were not available on 44 of the 121 deployments. Only deployments with at least 15 min of high quality data were included in this analysis to avoid biasing the data with a possible response of the whale to the tagging event rather than its true behavior. As part of the SOCAL-BRS, some of the animals included in this analysis were exposed to controlled exposures of simulated Navy sonar or pseudo-random noise (Southall *et al.*, 2012; Goldbogen *et al.*, 2013)(Appendix A); however, in those cases, data from during and up to 3-hr after the exposure were excluded from analysis to eliminate any potential impact of the exposure on the tagged whale's natural behavior.

3.2.2 Acoustic data analysis

I reviewed the acoustic data collected from all Bprobe and Acousonde deployments in spectrogram form in *Triton*, a MATLAB-based (www.mathworks.com) software package (Wiggins and Hildebrand, 2007). I manually detected all blue whale A, B, and D sounds based on visual and aural inspection of the spectrogram (fast Fourier transform [FFT] length equal to the acoustics sampling rate, 90% overlap, Hanning window), and logged the start and end times of each sound. We decimated the acoustic data collected from Dtag deployments to 600 Hz before plotting the spectrogram (FFT length 512, 98% overlap, Hamming window) and manually analyzed waveforms for blue whale sounds, as described in Goldbogen *et al.* (2013) and Stimpert *et al.* (2015).

When studying the behavioral context of sound production, it is important to note whether the tagged animal produced each sound recorded on the tag or not. To attribute sound production to the tagged whale, as opposed to other nearby animals, I used a combination of high root-mean-square received levels (RMS-RL) and signal-to-noise ratios (SNR). I calculated the RMS-RL and SNR for each detected sound according to the following processes. For Bprobes and Acousondes, I applied an infinite impulse response (IIR) bandpass filter to the data based on the call type (A, B, or D) to correspond to the band of peak frequency for each call. The three frequency bands defined for the filter were 100-70 Hz for A calls, 55-38 Hz for B calls and 100-25 Hz for D calls. I calculated RMS-RLs over the full duration of each sound using a 90% energy criterion, where the duration of each analysis window contained 90% of the energy of the sound. I measured noise levels in 500 ms intervals during the 10 s prior to each call, and subtracted the lowest of these noise level measurements from the RMS-RL of the call to determine SNR. I used relative values for all Acousonde and Bprobe calculations, without application of any corrections for system sensitivity. We decimated audio clips containing sounds detected in the Dtag data to a sample rate of 6,000 Hz in this case and applied a low-pass filter (6th- order Butterworth filter at 100 Hz) before level measurement. We automatically extracted noise levels within the Dtag data from 2 s before each sound for a duration of 1 s, and reported RMS-RLs, which we also calculated using a 90% energy criterion, as the maximum RMS level observed in any 200 ms window during the duration of the signal. We used a sensitivity value of 172 $\mathrm{re}:1\mathrm{V}\mu\mathrm{Pa}$ (for Dtags version 2) and 178 $\mathrm{re}:1\mathrm{V}\mu\mathrm{Pa}$ (for Dtags version 3) in all cases to convert the calculations to absolute values. Furthermore, our analysis did not compensate for the built-in high pass filters in Dtag hardware. Our calculated values should be considered relative and only comparable to each other, within a given tag deployment. We performed all calculations in MATLAB (www.mathworks.com).

I calculated the mean and standard deviations of RMS-RLs and SNRs for each call type and deployment. If the RMS-RL or SNR of an individual call was less than the mean minus one standard deviation calculated for that deployment, I did not assign the call to the tagged whale. For deployments that contained only one or two calls of one call type, I used the mean and standard deviation RMS-RL and SNR calculated for all deployments of the same tag. For the purposes of this study, I was interested only in identifying relatively strong sounds and attributing these to the tagged whale.

To determine whether any individual A or B sound was produced as a singular call or as a unit within a phrase, I sorted all A and B detections based on recorded start time. I calculated inter-call intervals, measured as the time from the start of one call to the start of the next, for all A and B sounds. I classified all intermittent blue whale A and B detections that were not produced in a pattern with regular inter-call intervals as singular calls rather than phrase units (Oleson *et al.*, 2007c). I defined phrases as sequences of A and B calls where the start of one units was followed by another within 49±10 s for A-B units and within 51±14 s for B-B units (Chapter 2). I defined repetitive phrases as sequences of AB phrases where the interval between the ending B unit of one phrase and the leading A unit of the next was 70±29 s (Chapter 2). I grouped all single AB phrases, or those that were neither preceded nor followed by another phrase, and repetitive phrases together into the same category as phrases. Similarly, I grouped all phrases together regardless of phrase composition (i.e. the ratio of A to B units within any given phrase did not constitute different categories). I classified all D call detections as singular D calls.

3.2.3 Pressure data analysis and behavioral classification

I used pressure (*i.e.* depth) data as a proxy for the behavioral state of the tagged blue whale throughout the duration of each deployment. The pressure data collected from each deployment was loaded into Acq*Knowledge* software (Version 3.9.1, Biopac Systems, Inc.) and individual dives were identified based on changes in the pressure data over time. For each dive recorded, I selected the following dive characteristics using the program's manual selection tools: dive start time (in local time); dive duration; maximum dive depth; time spent at bottom of dive (defined as the time between the whale's descent from and ascent to the surface); and number of vertical lunges present within the dive. If strong singular A, singular B, D calls, or phrases attributed to the tagged blue whale (Section 3.2.2) were detected within a dive, I recorded the number and type of sounds present. I determined the depth of production for each sound based on pressure data and sound start-time. Many of the Bprobe and Acousonde deployments exhibited systematic offsets in surface depths. To correct for this, I calculated the average surface depth for each deployment and applied this correction factor to all sound production depths. I excluded all dives during which a playback experiment occurred or the tag fell off (*i.e.* the final dive of each deployment) from all analyses.

I then used a combination of the maximum dive depth and number of vertical lunges recorded within a dive to broadly classify each dive into one of four behavioral states: shallow non-lunging, shallow lunging, deep non-lunging, and deep lunging. I classified all dives without vertical lunges that did not exceed 50 m depth as shallow, non-lunging dives. Dives that exceeded 50 m depth without vertical lunges were classified as deep, non-lunging dives. I classified all dives that did not exceed 50 m depth but contained vertical lunges as shallow lunging dives, and all dives that contained vertical lunges at a depth exceeding 50 m as deep lunging dives. For these categories, I use lunging and non-lunging as shorthand to describe the presence or absence of vertical lunges only; no other changes in the tagged whale's orientation were recorded. In several of the longer-term tag deployments, I observed the tagged blue whale spending increased time near the surface, without any identifiable diving behavior. I classified this behavior, which ranged in duration from minutes to hours, into a separate behavioral category as surface behavior.

3.2.4 Sound production rate and behavior analysis

To statistically evaluate the influence of behavioral state, location, season, and time-of-day on sound production rates, I modeled the production of singular A, singular B, D calls, and AB phrases using Generalized Estimating Equations (GEEs) (Hardin and Hilbe, 2012). I used this approach because GEEs allow for estimates of population average parameters from correlated or clustered data by appropriate inflation of the estimated standard errors (Hardin and Hilbe, 2012). Thus I was able to account for differences between individual tagged whales as well as correlation over time within an individual deployment.

To statistically test which variables (location, season, time-of-day, and behavioral state) were associated with sound production, I binned the data from each deployment into 12-min intervals (time selected based on average dive duration) over which I recorded each of these variables, as well as the number of singular A, singular B, D calls, and phrases. I classified deployments into one of four groups based upon the location (latitude and longitude) of initial tagging event: inshore-south (south of 33°N, In-S), inshore-central (between 33°and 34°N, In-C), inshore-north (north of 34°N, In-N), and offshore

(offshore of Santa Catalina Island and south of the Channel Islands)(Figure 3.1). I evaluated seasonal trends in call and phrase production rates by classifying data based on month of intial deployment: spring, for deployments occurring between March and May; summer, for deployments occurring from June through August; and fall, for tags deployed between September and November. I analyzed diel patterns in call and phrase production rates similarly by classifying data into four time-of-day periods: dawn, day, dusk, and night. I used the definitions of these periods as described by Wiggins *et al.* (2005), based on times of nautical twilight, sunrise and sunset at the location each tag was deployed. I defined the behavioral state for each bin based on the five dive categories described in Section 3.2.3. If multiple diving behaviors were recorded within a 12-min interval, I classified the behavioral state for that time bin as the behavior in which the majority of time was spent.

I calculated hourly call and phrase production rates based upon the number of sounds of each type detected within each 12-min bin. I used only A, B, and D calls, and phase units attributed to the tagged whale (Section 3.2.2) for the analysis. I used individual whale as the clustering unit for the GEE, along with the standard robust sandwich variance estimate for all reported results (Hardin and Hilbe, 2012). I also used an autoregressive correlation structure to account for temporal correlation between bins within a single deployment. I performed post-hoc sequential Wald tests to determine which factors were statistically significant descriptors of singular A, singular B, or D call rates, or phrase production rates. I performed all analyses using the 'geepack' package (Yan, 2002; Halekoh *et al.*, 2006) in the R Studio (Version 1.0.153) statistical software platform (R Core Team, 2015).

3.3 Results

A total of 874.1 h of acoustic and dive profile data collected from 121 tags deployed on individual blue whales off southern California were analyzed (Appendix A). Of these, 22.3% (27 tags) contained sounds produced by the tagged whale, an additional 12.4% (15 tags) contained sounds not attributed to the tagged whale, and 65.3% (79 tags) contained no blue whale sounds (Figure 3.1, Appendix A). Overall, out of the total of

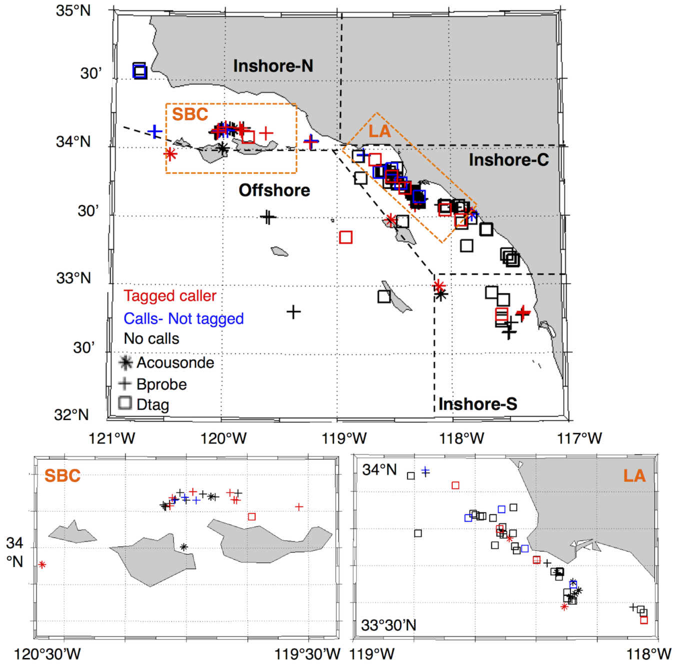

Figure 3.1: Locations of tagging events for all Acousondes (stars), **Bprobes** (crosses)**, and Dtags** (squares) **deployed on blue whales off southern California between 2002 – 2016.** Tags that contained loud, high intensity sounds that were attributed to the tagged whale (see Section 3.2.2) are marked in red, while tags that contained sounds not assigned to the tagged whale are marked in blue. Tags that did not contain any sounds are plotted in black. The four locations used to classify tag deployment groups for statistical analyses are marked in bold, black-hashed lines. Two smaller areas that contained high densities of tag deployments (within the Santa Barbara Channel and off of Los Angeles) are marked in orange and highlighted in the bottom two maps.

4,487 blue whale sounds detected, 70% (3,161) were produced by tagged individuals. The majority of all sounds produced by tagged individuals were phrases (812; comprised of 812 A units and 1,083 B units). Similar numbers of singular B and D calls were produced (447 and 512, respectively), and the fewest number of sounds produced were singular A calls (307). The number of tags deployed, as well as the number of callers, differed from year to year (Figure 3.2). Deployments during 2003 – 2004, 2013 and 2015 contained no tagged callers (Figure 3.2); however, the duration of recordings (34.7 h) collected during these years comprised just 4% of the total combined effort (874.1 h). The maximum number of tagged callers in any year of deployments was 4 (Figure 3.2).

The majority of all blue whale sounds attributed to tagged animals were produced

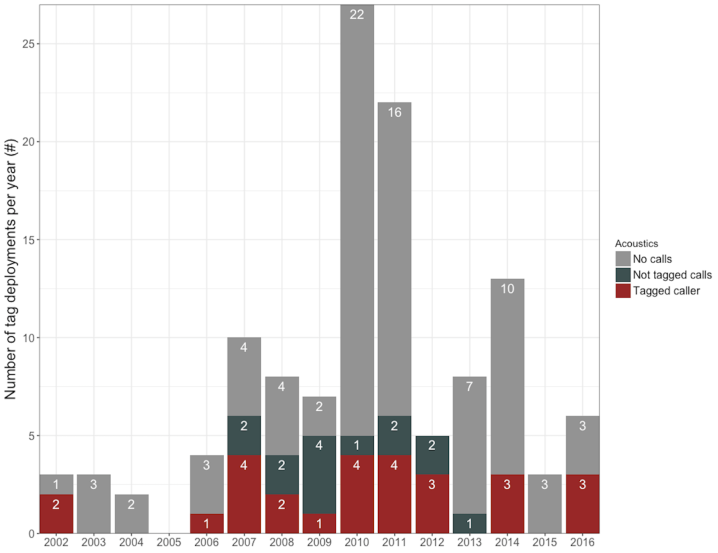

Figure 3.2: The number of tags deployed on blue whales off southern California per year. Tag deployments containing calls that were attributed to the tagged blue whale (as described in Section 3.2.2) are shown in red, while tags that contained calls not assigned to the tagged whale are marked in blue. Tag deployments that did not contain any blue whale sounds are plotted in gray. No tags were deployed on blue whales off southern California in 2005.

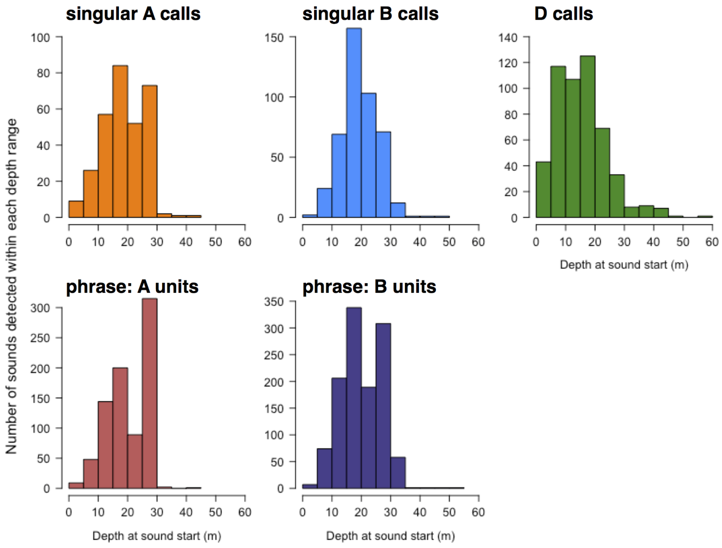

Figure 3.3: Histograms of depth during sound production for all singular A, singular B, D calls, and phrase units attributed to tagged individuals. Depth during each sound was determined based on the recorded start time of each sound. Note different y-axis scales.

within 30 m depth (Figure 3.3). In general, D calls were regularly produced at shallow depths ranging from 5 to 20 m. Singular B calls were most frequently produced between 15 and 20 m. On the other hand, the production depths of B phrase units contained two peaks: one between 15 and 20 m, similar to singular B calls, and another between 25 and 30 m. Both singular A calls and A phrase units also occurred most frequently within these two depth ranges: between 15 and 20 m, and between 25 and 30 m.

Most tag deployments, and the largest number of tagged callers, occurred within the inshore central and inshore north locations (Figure 3.1), particularly off of Los Angeles and within the Santa Barbara Channel. However, the effect of location on call and phrase production rates varied with sound type (Table 3.1). Singular B call rates recorded from blue whales tagged in the inshore central and southern regions were significantly higher than singular B call rates recorded from individuals tagged in the inshore north and offshore regions (Appendix B). D call rates were also higher from blue whales tagged in the inshore central region than in any other region (Appendix B). Singular A call rates, on the other hand, did not differ significantly between individuals tagged in different regions (Appendix B). Location of tag deployment also had an effect on blue whale phrase production rates (Table 3.1); however, differences between regions were not significant in pairwise tests (Appendix B).

Table 3.1: Results of the post-hoc sequential Wald tests run on the Generalized Estimating Equations (GEEs) used to assess spatial, temporal, and behavioral variability in singular call and phrase production rates. For each sound type, degrees of freedom (Df), chi square statistics (X^2) and p-values (P) for each of the four variables (Behavioral state, Location, Season, and Time-of-day, TOD) are presented. Behavioral state, location, season, and TOD were classified based upon the categories described in Section 3.2.3 and Section 3.2.4. Variables with significant p-values are marked with an asterisk and italicized.

Sound type	**Variable**	**Df**	X^2	***P*-value**
Singular A	*Behavior*	*4*	*120.3*	*<2.00e-16**
	Location	3	5.5	0.141
	Season	*1*	*5*	*0.025**
	TOD	3	3.6	0.302
Singular B	*Behavior*	*4*	*35.6*	*3.50e-07**
	Location	*3*	*18.2*	*4.10e-04**
	Season	1	0.9	0.332
	TOD	*3*	*59.2*	*8.70e-13**
D calls	*Behavior*	*4*	*12.4*	*0.015**
	Location	*3*	*126.1*	*<2.00e-16**
	Season	*1*	*6.9*	*0.009**
	TOD	*3*	*59.9*	*6.30e-13**
Phrases	*Behavior*	*4*	*53.364*	*7.15e-11**
	Location	*3*	*7.93*	*0.047**
	Season	1	0.538	0.463
	TOD	*3*	*45.363*	*7.75e-10**

I observed significant variation in call and phrase production rates with respect to the tagged whale's behavioral state (Table 3.1, Appendix B). About 73% of all sounds were produced during shallow, non-lunging dives (Figure 3.4), and another 10% were produced during deep non-lunging dives. The fewest number of sounds were produced during shallow lunging dives (around 1% of all sounds).

Phrase production rates in particular were significantly higher during shallow non-lunging and deep non-lunging dives than during any other dive behavior (Figures 3.4 and 3.5, Appendix B). During the production of A and B units within phrases, dives were

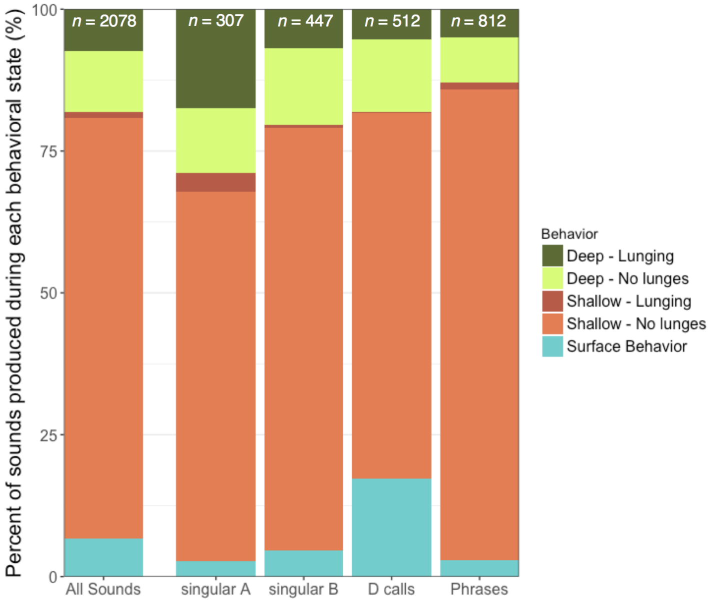

Figure 3.4: The percent of singular A, singular B, and D calls, and phrases that were produced within different behavioral states. Behavioral state was classified based upon the categories described in Section 3.2.3 and the total number of detections for each sound type are listed. Only sounds that were attributed to tagged blue whales are included.

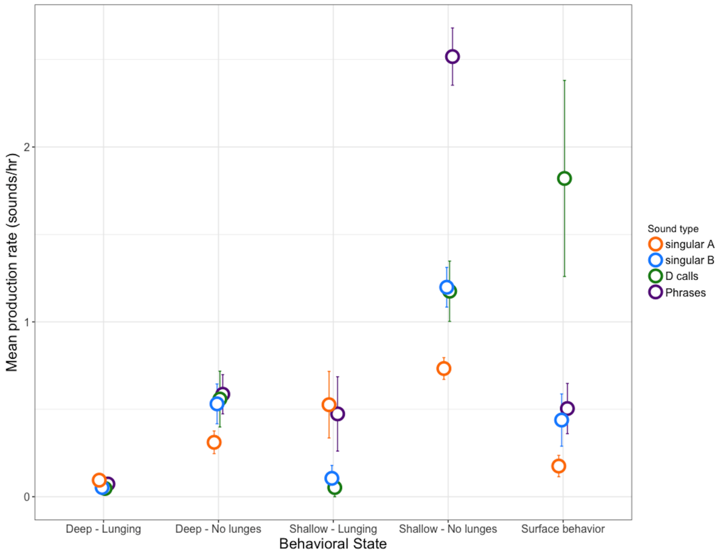

Figure 3.5: Mean hourly production rates of singular A (orange)**, singular B** (blue) **, and D calls** (green)**, and phrases** (purple) **within different behavioral states.** Behavioral state was classified based upon the categories described in Section 3.2.3. Bars represent the standard error of the mean, calculated for each sound type.

consistently shallower (less than 35 m maximum depth) than during the production of singular calls (Figures 3.6 and 3.7). Aside from surface breath intervals, blue whales producing repetitive phrases (*n* = 11 individuals), or singing, often remained at a relatively consistent depth for hours, displaying a similar dive type throughout the duration of the song bout (Figure 3.7). During these bouts, singing individuals also consistently ended each dive with a B unit (Figures 3.6 and 3.7), sometimes producing this final B unit at a shallower depth than other B units, just before surfacing (Figure 3.6). Blue whale behaviors exhibited during the production of single phrases, or those neither preceded nor followed by another phrase, were less consistent (Figures 3.7 and 3.8). In some cases, single phrases were produced towards the end or beginning of deeper dives by an individual that would later begin singing (Figure 3.7), while during other deployments, the tagged blue whale would produce both single phrases and singular calls within a short timeframe (Figure 3.8). Average inter-unit intervals contained within phrases were 47±5 s between A-B units and 49±7 s between B-B units across all deployments. The average inter-phrase interval, or interval between ending B unit and leading A unit of repetitive phrases, was 75±13 s.

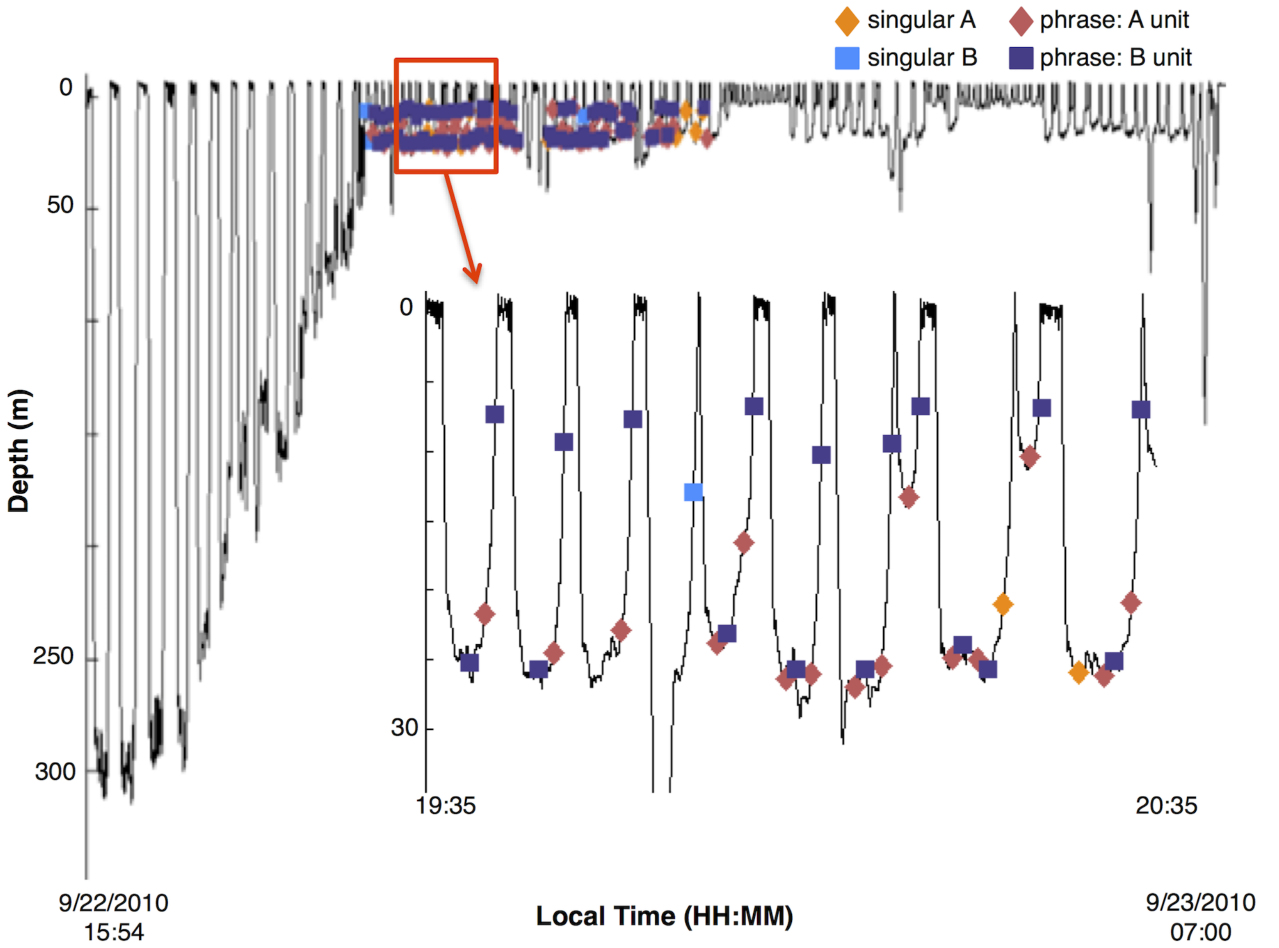

Figure 3.6: Blue whale dive profile recorded from an Acousonde deployed on September 22, 2010, showing singing behavior. One hour of the repetitive phrase, or song, bout is shown in the inset to illustrate the secondary shallower depth of B unit production before surface breath intervals. Only sounds attributed to the tagged individual are included.

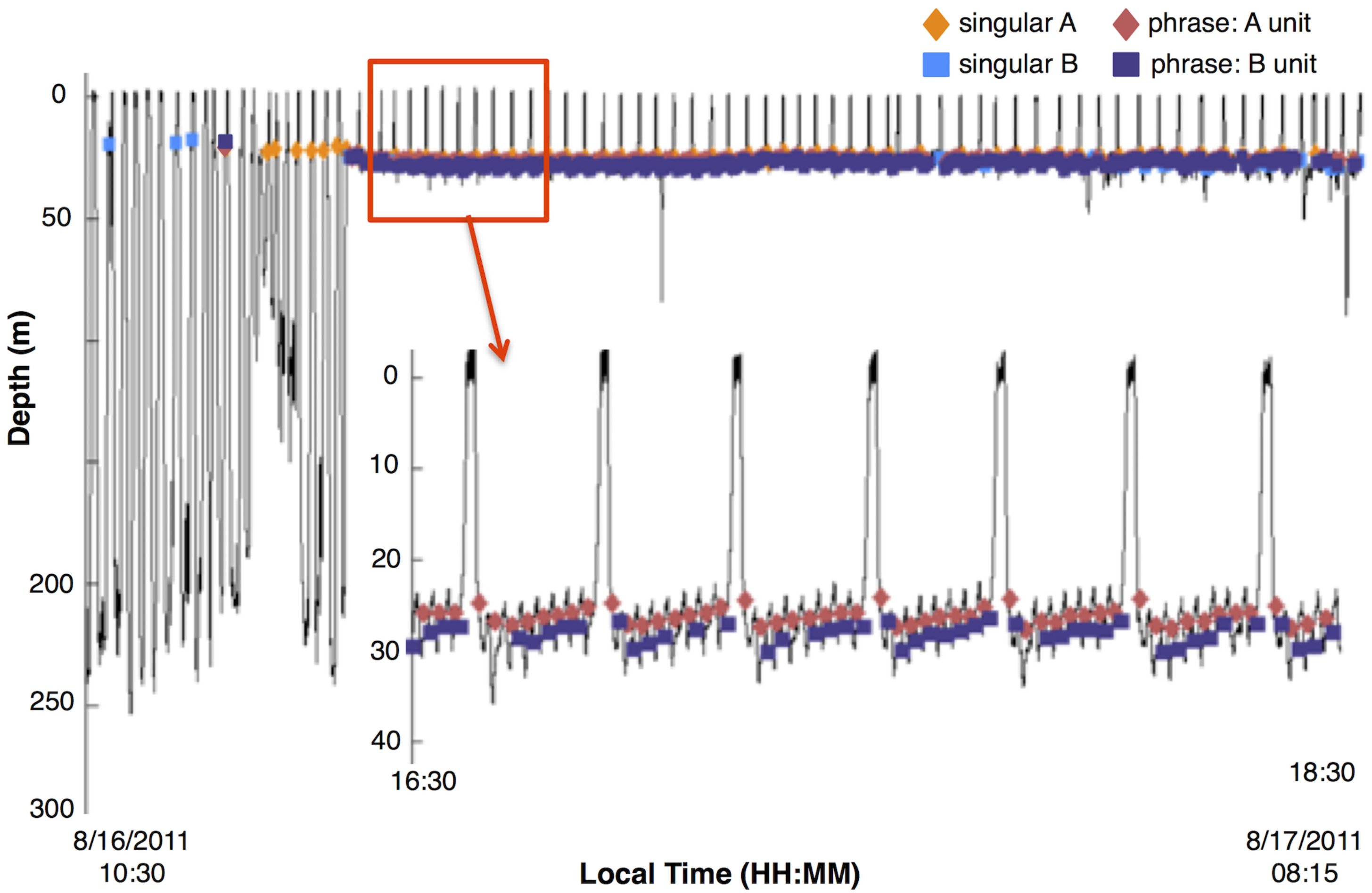

Figure 3.7: Blue whale dive profile recorded from an Acousonde deployed on August 16, 2011, showing extended singing behavior. Two hours of the repetitive phrase, or song, bout are shown in the inset. Only sounds attributed to the tagged individual are included.

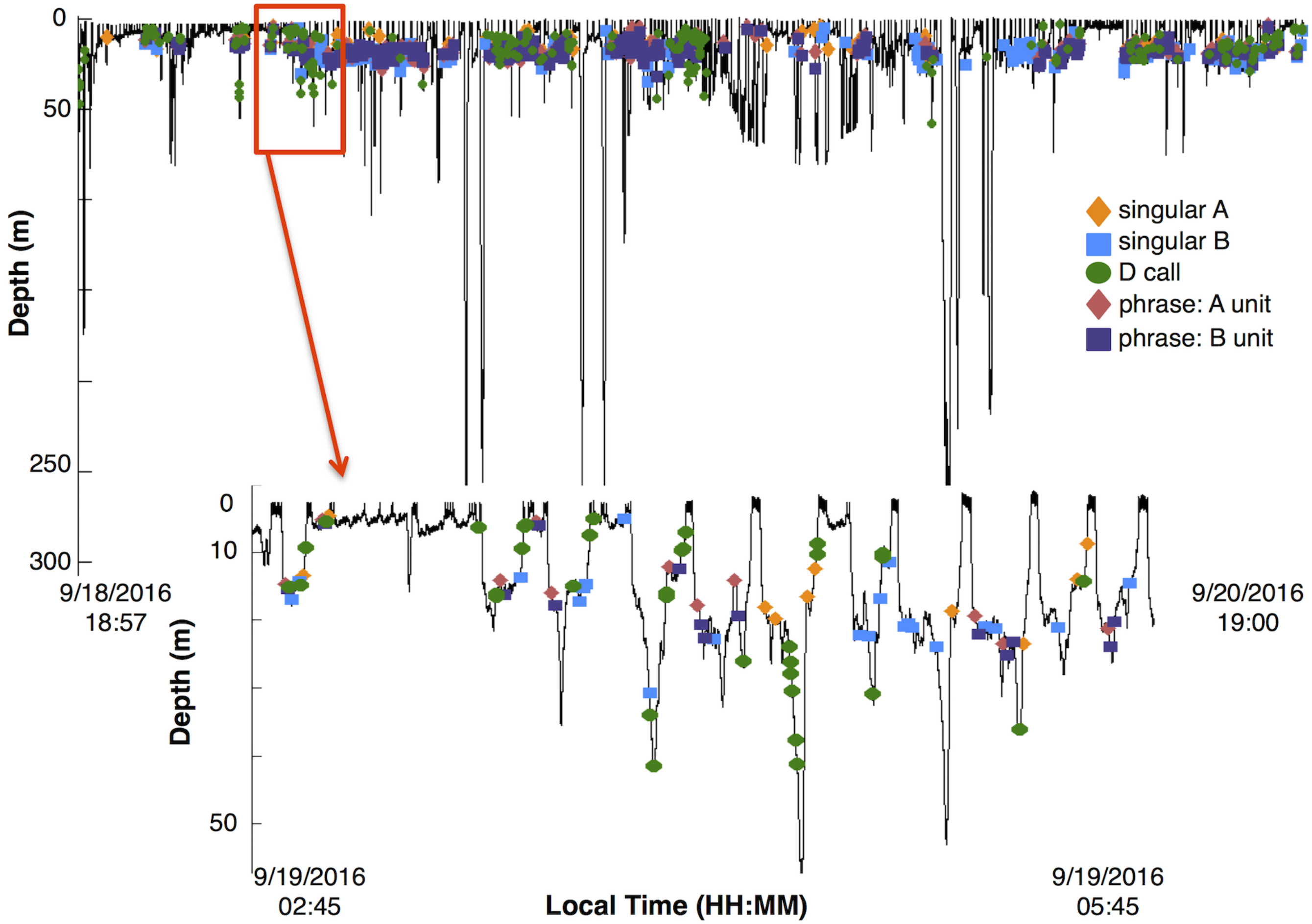

Figure 3.8: Blue whale dive profile recorded from an Acousonde deployed on September 18, 2016, showing variability between the behaviors associated with singular call and phrase production. Only 48 h from the full 5 d deployment are shown and three hours are highlighted in the inset to illustrate behavior during singular call and single phrase production. Only sounds attributed to the tagged individual are included.

During the production of singular A, B, and D calls, blue whale behavior was more variable (Figure 3.4), with dives frequently reaching depths much greater than 35 m, although call production generally still occurred within the upper 30 m (Figures 3.3 and 3.8). Singular A call rates were significantly higher during shallow non-lunging and lunging dives than during surface or deep dives (Figure 3.5, Appendix B) and A calls were also produced in higher numbers during shallow lunging dives than any other sound type (Figure 3.4). Singular B and D call rates were higher during deep non-lunging and shallow non-lunging dives than during either deep or shallow lunging dives (Figure 3.5, Appendix B). D call production rates were also higher during extended bouts surface behavior (Figures 3.4 and 3.5, Appendix B). In comparison, when not producing sounds, blue whales generally spent more time within the deep lunging or deep non-lunging behavioral states than during song production (Figures 3.6, 3.7 and 3.9).

There was also significant temporal variability in call and phrase production rates (Table 3.1). Both singular A and D call rates were higher in blue whales tagged during the fall than during the summer (Appendix B). However, there was no significant difference between the summer and fall in singular B call or phrase production rates (Appendix B). Only one tag was deployed on a blue whale during the spring (March of 2015, Appendix A), so data collected from this deployment could not be included in statistical analyses. Singular A call rates showed no significant difference between diel periods (Appendix B); however, singular B call rates were highest at dawn and lowest during the day (Appendix B). D call rates were lower at dawn than during any other diel period (Appendix B), while phrase production rates were significantly lower during the day, highest at dusk, and similar between night and dawn (Appendix B).

The percent of time spent in each behavioral state varied over the seasons (Figure 3.10). Deep lunging and shallow non-lunging dives comprised the majority of all hours of dive profile data; however, the proportion of time spent within each of these behavioral states differed per month. Specifically, the percent of time spent in deep lunging dives decreased between the summer and fall months, while shallow non-lunging and surface behaviors increased (Figure 3.10). The percent of time spent in deep non-lunging and shallow-lunging dive behaviors was greatest between July and September. With the exception of the single March deployment, tagged blue whales spent

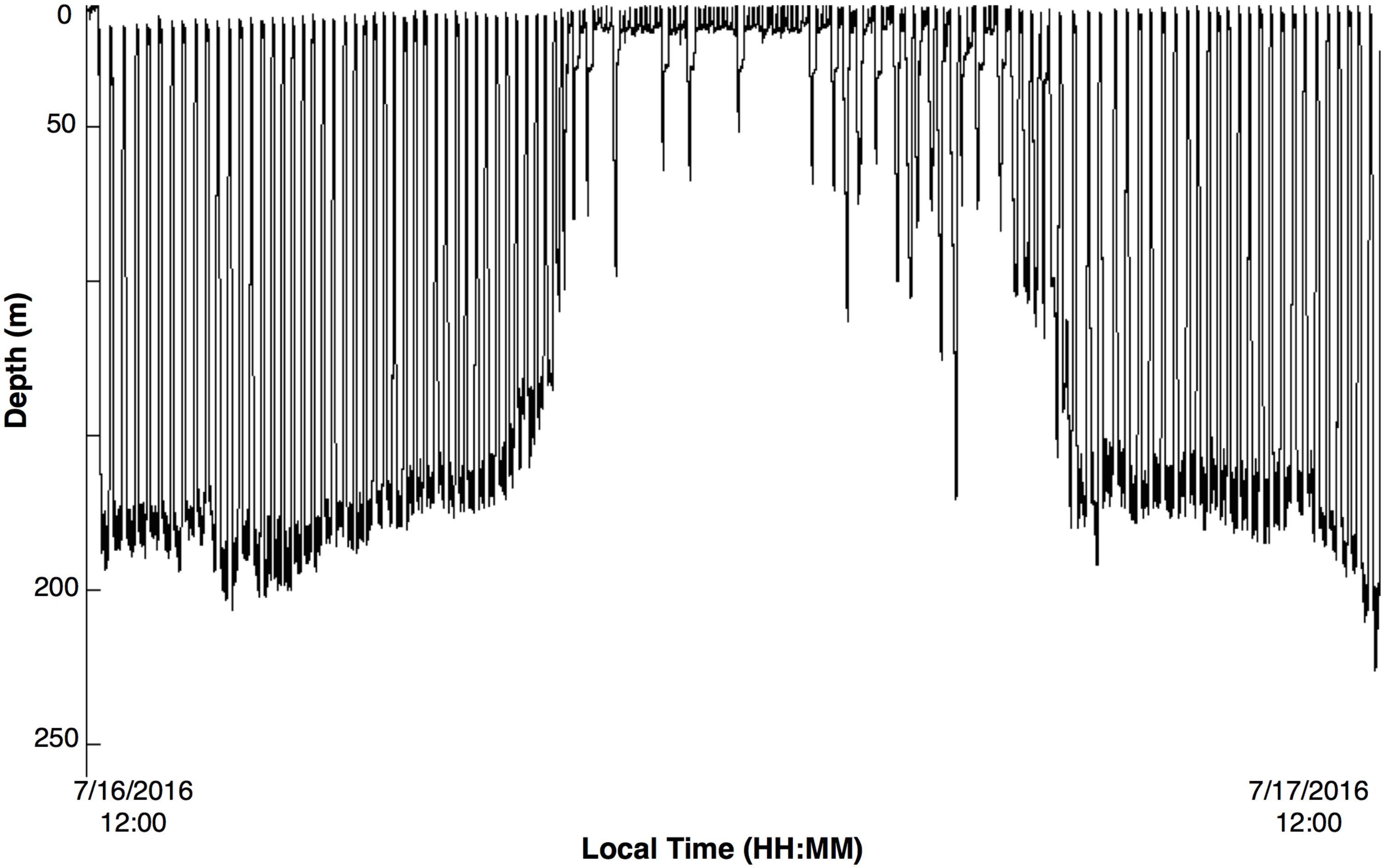

Figure 3.9: Blue whale dive profile recorded from an Acousonde deployed on July 16, 2016, showing the behavior of an individual not producing sounds. Only 24 h from the 4 d deployment are shown. No blue whale sounds were detected during the full duration of the deployment.

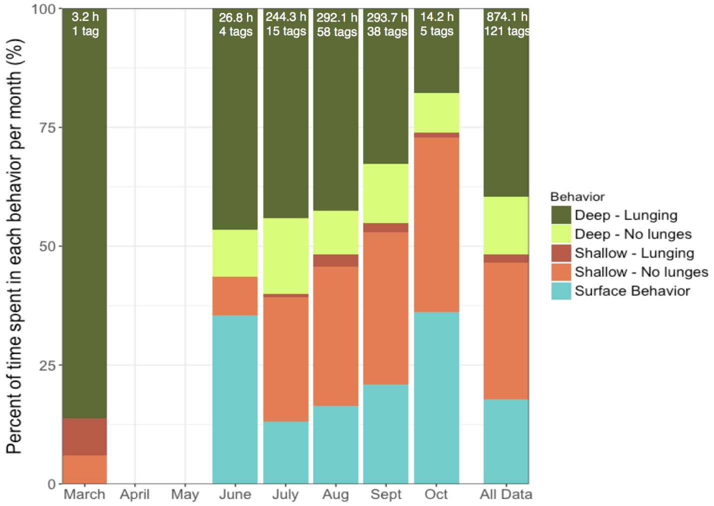

Figure 3.10: The percent of time that tagged blue whales spent in each behavioral state per month. The number of tags deployed and total hours of data collected per month are also listed. No tags were deployed on blue whales off southern California during the months of April or May.

the least amount of time in the shallow lunging dive state each month (Figure 3.10).

3.4 Discussion

My evaluation of data collected from tag deployments indicated that the majority of all sounds produced by blue whales were produced at shallow depths (less than 30 m) during shallow non-lunging dives. However, there were distinct differences between the behaviors associated with the production of singular calls versus phrases. Singular A, B, and D calls were more frequently produced during shallow and deep lunging dives or during bouts of surface behavior than phrases, which were typically produced during shallow non-lunging dives. Overall, the spatial, temporal, and, most notably, behavioral differences observed in blue whale acoustic behavior stress the importance of incorporating context specific sound production rates in future density estimation models.

Blue whales produce most sounds, particularly repetitive phrases, during shallow non-lunging dives. Similar to the observations made by Stimpert *et al.* (2015) on fin whales, tagged blue whales that were producing repetitive phrases, or singing, repeatedly made long, stereotypically "U-shaped dives" to a consistent shallow depth, often for extended periods of time. In general, the behaviors associated with song production in male blue whales have been described as solitary and traveling, not feeding (Oleson *et al.*, 2007b). When foraging, blue whales exhibit lunge feeding behaviors (Croll *et al.*, 1998; Acevedo-Gutiérrez *et al.*, 2002), often exploiting prey patches at depth (Croll *et al.*, 2001; Oleson *et al.*, 2007b). The absence of dives containing vertical lunges during song bouts, coupled with the shallow production depths of repetitive song phrases, supports the hypothesis that feeding and singing behaviors in blue whales may be mutually exclusive states (Wiggins *et al.*, 2005; Oleson *et al.*, 2007b,c).

Contrary to the consistent diving behavior exhibited by singing blue whales, the behaviors that I observed from tagged individuals producing singular calls were much more variable. Compared to the production of other sound types, singular A and B call rates were significantly higher during dive types that most likely correspond to foraging (Croll *et al.*, 1998, 2001; Acevedo-Gutiérrez *et al.*, 2002; Oleson *et al.*, 2007b), indicating that singular A and/or B calls may have a distinct behavioral purpose from A and B sounds produced as units within phrases. Oleson *et al.* (2007b) also observed that blue whales producing singular A and/or B calls exhibited different behaviors than those associated with singing males, with the former more frequently engaging in feeding, milling, resting, and traveling behaviors, and further hypothesized that the infrequent production of A and/or B calls may be used by males to maintain pair bonds during feeding. In contrast to this hypothesis, I recorded singular A and B calls from two female blue whales that were tagged in August of 2008 (Appendix A). However, focal follow data collected during and after each of these deployments indicate that both females were tagged while interacting with another whale as part of a pair (Calambokidis, *unpublished data*). Therefore, it is possible that the recorded sounds were actually produced by the untagged individuals rather than the tagged females. In this case, if the untagged individuals had been males, the presence of singular A and B calls may support the hypothesis proposed by Oleson *et al.* (2007b). Unfortunately, neither additional tag nor sex data were collected during the remainder of these two deployments.

I found production rates of D calls, which are also thought to correspond with foraging (Oleson *et al.*, 2007b,c), to be significantly higher during shallow non-lunging dives and periods of surface behavior than during other dive types. This increase in D calling at shallower depths during non-lunging dives, coupled with the fact that D calls have been recorded from both males and females (Oleson *et al.*, 2007b), suggests that the purpose of D calls may be more socially complex. However, it is important to point out that approximately 71% (364 of 512) of all D calls were produced by a single blue whale tagged in September of 2016 (Figure 3.8). This particular whale spent extended amounts of time at or near the surface (22.9 out of 102.5 h of data collected), so it is possible that the observed differences in D call production rates may be due to differences in this individual's behavior.

Despite differences observed between dive type and behavioral state during the production of singular calls and phrases, tagged blue whales in my dataset produced the majority of sounds at shallow depths, generally within 30 m. This depth range is consistent with the average depths of blue whale calling (20–30 m) that Oleson *et al.* (2007b) reported using a subset of this data, and is also similar to the average depths of fin whale calling (10–15 m) recorded by Stimpert *et al.* (2015) from other tag deployments off southern California. Additionally, my results are consistent with the average depth of B call production proposed in a theoretical model of blue whale sound production by Aroyan *et al.* (2000). Although details regarding the sound production mechanism in blue whales remain largely unknown, Oleson *et al.* (2007b) speculated that signal output may be maximized at these shallow calling depths, and furthermore, that such depths may also be near natural buoyancy for blue whales. The gradual changes in dive depths during the production of repetitive song phrases observed in the data collected from one individual (Figure 3.7), which were not associated with any systematic tag offsets, may illustrate an inadvertent upward drift of the animal while singing and could support this hypothesis. For male blue whales that are seeking mates and thus singing for extended periods of time, the ability to communicate over longer ranges with minimal energy expenditure would be advantageous. The consistent behavior that I recorded from tagged individuals during bouts of song production certainly indicates some predisposition, and possible benefit, in blue whale calling at these particular depths.

Interestingly, there were noticeable differences in production depths between A/B sounds produced as singular calls and A/B sounds produced as units within phrases. The bimodal occurrence of B units within two distinct depth ranges may be due to the production of these sounds during both the bottom portion of dives as well as during dive ascents, since singing blue whales will commonly end dives with a B unit before surfacing to breathe (a clear example of this behavior can be seen in Figure 3.6). Alternatively, it is possible that this individual blue whale may be purposefully producing these ending B units at shallower depths in an attempt to eliminate breaks in their song. Indeed, during this deployment, several of the inter-phrase intervals between the ending phrase unit of one dive and the leading phrase unit of the next were less than 2 min, including surface breaths (Figure 3.6). Similarly, there was a separation between the two most frequent depth ranges of production for A units. Although A units were most frequently produced between 25 and 30 m, they were also commonly produced at shallower depths during dive descents and dive ascents (Figures 3.6 and 3.8), trends which could explain this bimodality.

In addition to the differences observed in acoustic behavior, I found that the proportion of time blue whales spend in different non-acoustic behavioral states also varies temporally off southern California. The amount of time that tagged blue whales spent in deep diving states, specifically deep lunging dives indicative of foraging (Croll *et al.*, 1998, 2001; Acevedo-Gutiérrez *et al.*, 2002; Oleson *et al.*, 2007b), was generally greatest during the summer months, between June and August. The single blue whale tagged in March of 2015 also primarily exhibited deep and shallow lunging dive behaviors. However, shallow non-lunging and surface behaviors, which might be more commonly associated with song production (Oleson *et al.*, 2007b), comprised the majority of all hours of data collected during the fall, between September and October. Southern California is primarily considered to be a seasonal feeding ground for blue whales, and individuals may begin feeding as early as spring, continuing through summer until the fall, at which time reproductive behaviors begin to dominate. Unfortunately, little-to-no data were collected during the spring or late-fall months, so it is difficult to assess whether these behavioral trends continue in adjacent months and seasons.

I also observed temporal variability in sound production rates from tags deployed on blue whales off southern California. Production rates of all sound types were higher during the fall than during the summer, although only differences between singular A and D call rates were significant. The production of sounds by tagged individuals during each month of tag deployments, with the exception of March, is similar to the occurrence of B calls reported by Oleson *et al.* (2007a,b,c). In contrast to the summer peak in D calling recorded in several of these studies (Oleson *et al.*, 2007b,c), D call production rates in my data were greater during the fall. This discrepancy may be because fewer individuals are producing D calls during the summer months. However, approximately 93% (475 out of 512) of all D calls were produced by two separate blue whales tagged in September of 2010 and September of 2016, so the increase in D call production rates during the fall may be biased by the data collected from these two individuals.

The seasonal and diel differences that I observed in blue whale sound production rates may be correlated to temporal changes in behavior. It is possible that blue whales are actually producing more singular calls, especially B and D calls, and phrases during the fall than during the summer months off southern California. However, the data analyzed in this study were collected from opportunistic tagging efforts that occurred primarily between July and September; relatively few deployments occurred during other months. Therefore, it is also possible that the differences between the seasonal patterns that I observed in my dataset and those reported in other studies are due to the lack of data collected during the spring and early summer, as well as during the late fall. Specifically, the fall peak in D call production in my dataset may be due to the paucity of data collected during late-spring and early-summer deployments, which is when D calls have been shown to increase in other studies (Oleson *et al.*, 2007b,c)(Chapter 2). Similarly, the diel trends that I observed may differ from previous reports that were limited in regards to night-time tag data (Calambokidis *et al.*, 2007; Oleson *et al.*, 2007b), since longer duration deployments have mainly occurred during more recent years (Szesciorka *et al.*, 2016). Alternatively, it is possible that differences in results across studies arose from different temporal resolutions and variation in sample sizes (Calambokidis *et al.*, 2007; Oleson *et al.*, 2007b).

The data collected through the use of multi-sensor tags has distinct advantages over other PAM methods, as it allows assessment of the behavioral context of sound production. However, there are several limitations associated with studying blue whale acoustic behavior through tag deployments. Most importantly, the assignment of any recorded sound to the tagged individual rather than a nearby whale is not a straightforward task. Recent studies on fin whales have indicated that caller identity can be confirmed based on detection of sounds within accelerometer data (Goldbogen *et al.*, 2013; Stimpert *et al.*, 2015); however, this method is only applicable to tags capable of recording high-sample rate accelerometer data and, further, has proven less successful for the longer duration sounds produced by blue whales. Due to these issues, I assigned recorded sounds to tagged animals based on calculated relative RMS-RLs and SNRs for all sounds detected. Sounds were assigned to tagged individuals based on high relative values on a deployment-by-deployment basis. Based on these methods, it is possible that some of the sounds that I attributed to tagged individuals may have been produced by another whale swimming very closely nearby and alongside; however, if this was the case, it is likely the adjacent whale was engaging in the same behavior as the tagged individual. In addition, over the years of tag deployments, different efforts were targeting animals in specific behavioral states, or under different environmental and geographic conditions for different studies. Furthermore, the ability to tag blue whales varies with respect to the individual whale's behavioral state: it is much easier to deploy a tag on an animal that is resting or milling than on an animal that is traveling quickly or feeding repeatedly at depth. Therefore, our collection of tag data cannot be considered a truly random sample of the population.

Although the sound types produced by the Northeast Pacific population of blue whales have been well-described (Thompson *et al.*, 1996; Thode *et al.*, 2000; McDonald *et al.*, 2001; Stafford *et al.*, 2001, 2005; Wiggins *et al.*, 2005; McDonald *et al.*, 2006; Oleson *et al.*, 2007b,c), relatively little is known about the behaviors associated with sound production. I recorded significant behavioral differences between calling and singing blue whales, in addition to both spatial and temporal patterns in call and phrase production rates. Such differences stress not only the importance of continued monitoring of blue whale acoustics and behavior, but also the necessity of including the behavioral context of sound production rates in any meaningful models for density estimation.

3.5 Acknowledgements

The research in this chapter is presented with acknowledgements to my co-authors: John Calambokidis, Alison Stimpert, James Fahlbusch, Ari Friedlaender, John Hildebrand, Megan McKenna, Sarah Mesnick, Erin Oleson, Brandon Southall, Angela Szesciorka, and Ana Širović. We would like to thank everyone involved at the CRC and the entire SOCAL BRS team, especially Ann Allen and Jeremy Goldbogen, for their help with data collection, organization, and analysis throughout the course of this project. The research presented was supported by the U.S. Navy's Living Marine Resources Program (SOCAL BRS) and the Office of Naval Research (ONR). LAL was supported with funding from the National Science Foundation Graduate Research Fellowship Program under Grant No. DGE-1144086. Tagging experiments were carried out under NMFS permits 1434 and 19116 (B. Southall, principal investigator) and 540-1502-00, 540-1811, and 16111 (J. Calambokidis, principal investigator).

Appendix A: Blue whale tag deployments, 2002-2016

Table 3.2: Appendix A: Blue whale tag deployments, 2002-2016. Deployment details for all tags deployed on blue whales between 2002-2016 with data used in this study, including: deployment date, tag on time, tag type, latitude, longitude, location, sampling rates for acoustic, auxiliary (pressure) and accelerometer data, number of hours of acoustic and dive profile data collected during each deployment, types of sounds attributed to the tagged individual, and the sex of the tagged individual. Data collected during Dtag deployments that included controlled exposure experiments are marked with either one or two asterisks, depending on whether the exposure consisted of simulated Navy sonar or pseudo-random noise, respectively. In those cases, data from during and up to 3-hr after the exposure were excluded from analysis to eliminate any potential impact of the exposure on the whale's natural behavior, and the number of hours of data listed as been updated to reflect this. Each deployment's location is classified as described in Section 3.2.4: inshore south (In-S), inshore central (In-C), inshore north (In-N), and offshore (Off). Deployments that contained A, B, or D sounds that were assigned to the tagged whale (Section 3.2.2) are shaded in gray, and the types of sounds are indicated. For sex determination, M: male, F: female, na: no skin sample collected or analyzed, and U: sex could not be determined.

Tagging event information						**Sampling rates (Hz)**			**Data analysis**		
Date	**Time on (PDT)**	**Tag type**	**Lat (N)**	**Long (W)**	**Loc**	**Acoustic**	**Aux**	**Accel**	**Data (h)**	**Sounds**	**Sex**
6/26/02	9:03	Bprobe	34°06.85	120°04.25	In-N	5,461	1	na	2.8	none	U
6/27/2002	10:49	Bprobe	34°06.92	120°03.17	In-N	2,520	1	na	1.3	D's	na
6/30/2002	15:49	Bprobe	32°47.10	117°22.63	In-S	2,520	1	na	15	A's, B's	M
7/24/03	11:17	Bprobe	33°30.25	119°36.72	Off	2,520	1	1	1.5	none	F
7/24/03	15:45	Bprobe	33°29.81	119°35.80	Off	2,048	1	1	0.8	none	na
8/22/03	15:48	Bprobe	32°48.68	119°22.50	Off	2,048	1	1	0.7	none	F

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Tagging event information						Sampling rates (Hz)			Data analysis		
Date	**Time on (PDT)**	**Tag type**	**Lat (N)**	**Long (W)**	**Loc**	**Acoustic**	**Aux**	**Accel**	**Data (h)**	**Sounds**	**Sex**
7/20/04	14:17	Bprobe	34°07.31	120°03.25	In-N	1,024	1	1	0.6	none	na
7/21/04	13:09	Bprobe	34°06.74	120°04.01	In-N	1,024	1	1	0.9	none	U
8/22/06	12:00	Bprobe	32°39.34	117°30.10	In-S	1,024	1	1	6.5	none	F
8/23/06	12:47	Bprobe	32°43.08	117°28.90	In-S	1,024	1	1	1.2	none	F
8/24/2006	15:30	Bprobe	32°48.07	117°22.38	In-S	1,024	1	1	3.9	A’s, B’s	M
8/25/06	12:33	Bprobe	32°38.85	117°30.40	In-S	1,024	1	1	0.6	none	F
9/06/2007	10:01	Bprobe	34°07.88	119°50.50	In-N	2,048	1	1	4.4	A’s, D	na
9/06/2007	10:24	Bprobe	34°07.83	119°50.07	In-N	2,048	1	1	1	A’s, D	na
9/6/07	12:40	Bprobe	34°08.39	119°54.25	In-N	2,048	1	1	0.8	none	na
9/06/2007	16:03	Bprobe	34°09.21	119°58.67	In-N	2,048	1	1	11.5	A’s, B’s	na
9/6/07	16:45	Bprobe	34°07.82	119°58.07	In-N	2,048	1	1	0.6	none	na
9/7/07	9:50	Bprobe	34°09.04	120°01.22	In-N	2,048	1	1	0.9	none	na
9/7/07	18:14	Bprobe	34°07.02	120°04.47	In-N	2,048	1	1	1.7	none	na
9/8/07	9:07	Bprobe	34°08.01	120°02.14	In-N	2,048	1	1	0.8	none	na
9/8/07	9:45	Bprobe	34°07.80	120°02.39	In-N	2,048	1	1	2.4	none	na

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Tagging event information						Sampling rates (Hz)			Data analysis		
Date	**Time on (PDT)**	**Tag type**	**Lat (N)**	**Long (W)**	**Loc**	**Acoustic**	**Aux**	**Accel**	**Data (h)**	**Sounds**	**Sex**
9/08/2007	10:02	Bprobe	34°08.24	120°02.68	In-N	2,048	1	1	5.9	A	na
6/14/08	10:17	Bprobe	32°46.30	117°23.21	In-S	2,048	1	1	7.7	none	F
8/14/2008	14:32	Bprobe	34°09.05	119°51.38	In-N	2,048	1	1	1.6	A	F
8/16/2008	10:44	Bprobe	34°06.70	119°37.8	In-N	2,048	1	1	10.6	A’s, B’s	F
9/9/08	13:38	Bprobe	33°57.54	118°45.81	In-C	2,048	1	1	1.8	none	F
9/9/08	14:05	Bprobe	33°57.02	118°45.78	In-C	2,048	1	1	0.4	none	F
9/10/08	14:37	Bprobe	34°08.82	119°56.69	In-N	2,048	1	1	0.5	none	F
9/12/08	14:17	Bprobe	34°07.84	120°00.01	In-N	2,048	1	1	0.3	none	M
9/12/08	14:30	Bprobe	34°08.28	120°00.27	In-N	2,048	1	1	1.3	none	F
8/3/09	14:00	Bprobe	34°09.00	119°49.74	In-N	2,048	1	1	4.2	none	M
8/04/2009	14:03	Bprobe	34°03.07	119°14.18	In-N	2,048	1	1	2.9	A’s, B’s	M
8/4/09	17:25	Bprobe	34°02.89	119°13.88	In-N	2,048	1	1	0.6	none	F
8/5/09	10:45	Bprobe	34°03.56	119°13.66	In-N	2,048	1	1	4.5	none	F
9/16/09	16:43	Bprobe	34°03.22	119°13.39	In-N	2,048	1	1	7	none	F
9/21/09	16:10	Bprobe	34°07.14	120°37.11	In-N	2,048	1	1	0.8	none	F

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Tagging event information						Sampling rates (Hz)			Data analysis		
Date	**Time on (PDT)**	**Tag type**	**Lat (N)**	**Long (W)**	**Loc**	**Acoustic**	**Aux**	**Accel**	**Data (h)**	**Sounds**	**Sex**
9/21/09	16:30	Bprobe	34°06.99	120°36.67	In-N	2,048	1	1	1	none	na
8/17/10	8:44	Dtag-v2	33°11.87	117°29.52	In-C	64,000	50	50	8.8	none	U
8/17/10	8:48	Dtag-v2	33°13.37	117°30.46	In-C	64,000	50	50	6.3	none	F
8/18/10	7:50	Dtag-v2	33°11.93	117°28.96	In-C	64,000	50	50	6.7	none	F
8/23/10	9:14	Dtag-v2*	33°33.86	117°54.18	In-C	96,000	50	50	2.5	none	na
8/23/10	9:20	Dtag-v2*	33°33.54	117°53.16	In-C	64,000	50	50	2.9	none	F
8/23/10	14:10	Bprobe	33°35.22	118°04.84	In-C	8,192	1	1	1.2	none	F
8/23/10	15:44	Bprobe	33°35.22	118°04.84	In-C	8,192	1	1	1.5	none	F
8/26/10	9:25	Bprobe	33°34.18	117°57.80	In-C	8,192	1	1	5.1	none	na
8/27/10	10:25	Dtag-v2*	33°34.31	118°02.83	In-C	96,000	50	50	4.3	none	F
8/28/10	8:15	Dtag-v2*	33°41.09	118°19.33	In-C	96,000	50	50	30.9	none	F
8/28/10	8:21	Dtag-v2*	33°40.90	118°19.14	In-C	96,000	50	50	1.4	none	F
8/29/10	9:27	Bprobe	33°42.40	118°21.77	In-C	8,192	1	1	1.5	none	F
8/29/2010	10:22	Bprobe	33°42.82	118°23.69	In-C	8,192	1	1	2.4	A's, B's	na
8/31/10	9:28	Bprobe	33°47.16	118°30.47	In-C	8,192	1	1	10.6	none	F

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Tagging event information						Sampling rates (Hz)			Data analysis		
Date	**Time on (PDT)**	**Tag type**	**Lat (N)**	**Long (W)**	**Loc**	**Acoustic**	**Aux**	**Accel**	**Data (h)**	**Sounds**	**Sex**
8/31/10	10:37	Dtag-v2**	33°47.20	118°47.20	In-C	96,000	50	50	5	none	F
9/1/10	14:30	Dtag-v2	33°49.99	118°34.92	In-C	96,000	50	50	0.7	none	F
9/1/10	15:59	Dtag-v2**	33°49.76	118°37.33	In-C	96,000	50	50	1.4	none	M
9/1/10	16:13	Dtag-v2**	33°49.75	118°32.43	In-C	96,000	50	50	1.2	none	F
9/2/10	12:38	Dtag-v2**	33°50.02	118°34.54	In-C	96,000	50	50	2.1	none	F
9/3/10	12:49	Dtag-v2*	33°50.46	118°36.36	In-C	96,000	50	50	1.4	none	M
9/3/10	12:53	Dtag-v2*	33°50.21	118°35.90	In-C	96,000	50	50	1.3	none	na
9/4/10	13:03	Dtag-v2**	33°45.16	118°28.15	In-C	96,000	50	50	0.7	none	F
9/08/2010	13:20	Dtag-v2**	34°05.12	119°47.06	In-N	96,000	50	50	1	A’s, B’s	U
9/22/2010	10:47	Dtag-v2*	33°47.96	118°31.09	In-C	96,000	50	50	2.6	D’s	M
9/22/10	11:15	Dtag-v2	33°47.31	118°31.05	In-C	96,000	50	50	1	none	F
9/22/2010	15:54	Acousonde	33°46.44	118°29.23	In-C	25,811	10	10	14.9	A’s, B’s	U
9/23/10	14:56	Dtag-v2**	33°42.94	118°23.82	In-C	96,000	50	50	1.6	none	F
7/29/11	11:17	Dtag-v2*	34°32.40	120°44.61	In-N	96,000	50	50	4.1	none	F
7/29/11	12:29	Dtag-v2*	34°33.22	120°45.42	In-N	192,000	50	50	2.9	none	M

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Tagging event information						Sampling rates (Hz)			Data analysis		
Date	**Time on (PDT)**	**Tag type**	**Lat (N)**	**Long (W)**	**Loc**	**Acoustic**	**Aux**	**Accel**	**Data (h)**	**Sounds**	**Sex**
7/30/11	9:09	Dtag-v2**	34°34.36	120°45.29	In-N	192,000	50	50	2	none	F
8/1/11	9:54	Dtag-v2*	33°48.29	118°30.58	In-C	192,000	50	50	2.9	none	na
8/2/11	8:32	Dtag-v2	33°51.48	118°28.42	In-C	96,000	50	50	1.1	none	F
8/2/11	9:02	Dtag-v2**	33°51.16	118°30.74	In-C	96,000	50	50	2.3	none	U
8/3/11	11:19	Dtag-v2	33°34.93	117°55.96	In-C	96,000	50	50	1.2	none	F
8/03/2011	12:39	Dtag-v3	33°34.89	117°56.58	In-C	96,000	50	50	1.4	A	na
8/6/11	16:24	Dtag-v2**	33°10.77	117°27.11	In-C	96,000	50	50	1.3	none	F
8/6/11	16:44	Dtag-v2**	33°10.46	117°27.43	In-C	96,000	50	50	1.7	none	F
8/7/11	14:00	Dtag-v2	32°44.12	117°33.58	In-S	96,000	50	50	0.8	none	F
8/7/11	14:56	Dtag-v2*	32°45.18	117°33.85	In-S	192,000	50	50	3	none	F
8/08/2011	10:59	Dtag-v2*	32°47.01	117°33.71	In-S	96,000	50	50	4.8	B’s	M
8/8/11	14:38	Dtag-v2*	32°53.32	117°32.69	In-S	192,000	50	50	1.2	none	F
8/9/11	11:50	Dtag-v2**	33°27.12	117°54.29	In-C	96,000	50	50	3.1	none	F
8/09/2011	13:46	Dtag-v2**	33°28.52	117°54.69	In-C	96,000	50	50	1.2	A’s	na
8/16/2011	10:30	Acousonde	33°35.34	118°18.46	In-C	116,151	20	20	21.8	A’s, B’s	na

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Tagging event information						Sampling rates (Hz)			Data analysis		
Date	**Time on (PDT)**	**Tag type**	**Lat (N)**	**Long (W)**	**Loc**	**Acoustic**	**Aux**	**Accel**	**Data (h)**	**Sounds**	**Sex**
8/17/11	8:25	Bprobe	33°36.58	118°16.96	In-C	2,048	1	1	3.9	none	na
8/19/11	9:59	Acousonde	33°36.97	118°17.18	In-C	2,003	20	20	2.3	none	na
10/3/11	9:43	Acousonde	33°39.35	118°16.72	In-C	10,100	10	10	1.7	none	F
10/4/11	13:41	Acousonde	33°37.96	118°15.65	In-C	10,100	10	10	1.6	none	F
10/4/11	15:01	Acousonde	33°37.42	118°16.33	In-C	10,100	10	10	0.6	none	F
8/04/2012	12:50	Dtag-v2**	33°42.85	118°23.87	In-C	64,000	50	50	16.1	D’s	na
8/4/12	17:03	Dtag-v3	33°44.76	118°26.14	In-C	64,000	50	50	2.2	none	na
8/27/2012	13:35	Acousonde	33°32.45	117°50.83	In-C	4,005	20	20	8.7	A’s, B’s	na
8/28/12	13:12	Acousonde	33°30.92	117°48.79	In-C	4,005	20	20	4	none	na
10/18/2012	10:00	Dtag-v2**	33°21.27	118°55.14	Off	96,000	50	50	3.6	A’s, B’s	na
7/10/13	11:56	Dtag-v3*	33°24.05	117°41.12	In-C	240,000	20	200	1.4	none	na
7/12/13	7:33	Dtag-v3*	33°24.44	117°41.47	In-C	240,000	25	250	2.1	none	na
7/26/13	15:47	Dtag-v3	33°38.92	118°16.64	In-C	240,000	50	500	3.4	none	na
8/2/13	10:15	Dtag-v3	33°36.27	118°16.63	In-C	240,000	50	500	4.1	none	na
8/2/13	10:26	Dtag-v2	33°36.25	118°16.94	In-C	64,000	50	50	0.9	none	na

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Table3.2 – continued from previous page

Tagging event information						Sampling rates (Hz)			Data analysis		
Date	Time on (PDT)	Tag type	Lat (N)	Long (W)	Loc	Acoustic	Aux	Accel	Data (h)	Sounds	Sex
8/2/13	14:53	Dtag-v3	33°36.68	118°17.83	In-C	240,000	50	500	2.1	none	na
8/5/13	8:30	Dtag-v3*	33°34.80	118°03.39	In-C	240,000	50	500	2.6	none	na
9/16/13	10:15	Dtag-v3*	33°47.27	118°28.46	In-C	240,000	50	500	1.9	none	na
7/30/14	11:39	Dtag-v3*	33°45.33	118°32.03	In-C	240,000	25	250	1.8	none	na
7/30/14	14:29	Dtag-v3*	33°46.98	118°30.39	In-C	240,000	25	250	1.4	none	na
7/31/2014	11:31	Dtag-v3	33°55.03	118°39.89	In-C	240,000	25	250	26.4	A’s, B’s	na
8/1/14	13:39	Dtag-v3	33°56.53	118°48.63	In-C	240,000	25	250	4	none	na
8/5/14	10:52	Dtag-v3	33°27.95	118°25.25	In-C	240,000	25	250	5.5	none	na
8/6/14	8:34	Dtag-v3*	33°37.64	118°17.87	In-C	240,000	25	250	3.4	none	na
8/6/14	10:22	Dtag-v3	33°40.98	118°20.38	In-C	240,000	25	250	1.4	none	na
8/26/14	13:25	Acousonde	33°40.87	118°19.88	In-C	25,811	40	800	3.1	none	na
9/8/14	8:58	Dtag-v3	33°44.45	118°27.72	In-C	240,000	25	250	8.5	none	na
9/13/14	8:46	Dtag-v3*	33°40.17	118°19.42	In-C	240,000	25	250	2	none	na
9/18/14	8:50	Dtag-v3	33°29.34	117°49.43	In-C	240,000	25	250	4.9	none	na
9/19/2014	8:49	Dtag-v3*	33°33.05	118°02.74	In-C	240,000	25	250	2.2	A	na

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Table3.2 – continued from previous page

Tagging event information						Sampling rates (Hz)			Data analysis		
Date	**Time on (PDT)**	**Tag type**	**Lat (N)**	**Long (W)**	**Loc**	**Acoustic**	**Aux**	**Accel**	**Data (h)**	**Sounds**	**Sex**
9/19/2014	8:52	Dtag-v3*	33°33.10	118°02.73	In-C	240,000	25	250	2.2	A’s, B’s	na
3/17/15	12:10	Dtag-v3	33°17.33	117°51.58	In-C	240,000	25	250	3.2	none	na
8/20/15	13:35	Dtag-v3	32°56.42	117°38.74	In-S	240,000	25	250	2	none	na
10/6/15	9:33	Dtag-v3	32°54.99	118°35.32	Off	240,000	25	250	6.8	none	na
7/16/16	12:12	Acousonde	34°00.17	120°00.51	In-N	1,814	10	100	92.5	none	na
7/17/16	9:28	Acousonde	34°08.42	119°55.15	In-N	1,814	10	100	102.5	none	na
8/15/16	11:15	Acousonde	32°56.02	118°05.56	In-S	12,226	10	100	3.9	none	na
8/17/2016	13:28	Acousonde	32°59.59	118°06.70	In-S	12,226	10	100	45.8	D	na
9/18/2016	13:15	Acousonde	33°57.24	120°28.32	Off	12,226	10	100	96.8	A’s, B’s	na
9/18/2016	18:57	Acousonde	33°28.85	118°31.43	In-C	12,226	10	100	102.6	A’s, B’s, D’s	na
	Total hours of data:								874.1		

Appendix B: Blue whale tag data GEE results

Table 3.3: Appendix B: Results from the Generalized Estimating Equations (GEEs) used to assess behavioral, spatial, and temporal variability in singular call and phrase production rates. For each sound type, coefficient parameter estimates (Cp.est), robust standard errors (std. err.), and p-values (*P*) for each of the levels within the four factor variables (Behavioral state, Location, Season, and Time-of-day, TOD) are presented. The levels within each factor were classified based upon the categories described in Section 3.2.3 and Section 3.2.4. Variables and associated levels with significant p-values are marked with an asterisk and italicized.

Sound type	**Factor**	**Level**	**Cp. est**	**Std. err**	***P*-value**
Singular A	*Behavior*	Dp-no lunges	0.280	0.313	0.371
		Sh-lunging	1.088	0.336	0.001*
		Sh-no lunges	0.453	0.225	0.044*
		Surface	-0.324	0.208	0.118
	Location	In-N	0.068	0.688	0.921
		In-S	-1.687	4.325	0.696
		Off	-0.978	0.624	0.117
	Season	*Summer*	-1.623	0.815	0.046*
	TOD	Day	0.222	0.325	0.495
		Dusk	0.904	0.522	0.083
		Night	0.464	0.284	0.102
Singular B	*Behavior*	*Dp-no lunges*	1.563	0.324	1.40e-06*
		Sh-lunging	0.131	0.519	0.801
		Sh-no lunges	2.028	0.216	<2.00e-16*
		Surface	0.974	0.249	9.30e-05*
	Location	*In-N*	-3.775	1.091	0.001*
		In-S	-1.798	1.142	0.115
		Off	-1.193	0.392	0.002*
	Season	Summer	-0.568	0.912	0.534
	TOD	*Day*	-1.163	0.423	0.006*

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Table3.3 – continued from previous page

Sound type	**Factor**	**Level**	**C.p.est**	**Std.err**	***P*-value**
		Dusk	-0.088	0.585	0.880
		Night	-0.436	0.167	0.009*
D calls	*Behavior*	*Dp-no lunges*	1.075	0.399	0.007*
		Sh-lunging	-0.444	0.307	0.148
		Sh-no lunges	1.251	0.382	0.001*
		Surface	1.541	0.480	0.001*
	Location	*In-N*	-1.730	0.720	0.016*
		In-S	-2.321	1.064	0.029*
		Off	-4.792	0.223	<2.00e-16*
	Season	*Summer*	-2.527	1.020	0.013*
	TOD	*Day*	0.510	0.256	0.046*
		Dusk	1.614	0.215	6.60e-14*
		Night	0.836	0.289	0.004*
Phrases	*Behavior*	*Dp-no lunges*	1.578	0.442	3.59e-04*
		Sh-lunging	1.111	0.865	0.199
		Sh-no lunges	2.569	0.476	6.59e-08*
		Surface	0.809	0.430	0.060
	Location	In-N	-2.178	1.136	0.055
		In-S	-1.496	1.276	0.241
		Off	-1.596	0.857	0.063
	Season	Summer	-0.579	0.848	0.495
	TOD	*Day*	-0.551	0.202	0.006*
		Dusk	0.779	0.168	3.69e-06*
		Night	-0.037	0.155	0.813

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