UNIVERSITY OF CALIFORNIA, SAN DIEGO

Calling Behavior of Blue and Fin Whales off California

A dissertation submitted in partial satisfaction of the

requirements for the degree Doctor of Philosophy

in Oceanography

by

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The text of Chapter 2, in part, has been submitted for publication in Animal Behaviour. I was the primary researcher, and the co-authors listed in this manuscript directed and supervised the research which forms the basis of this chapter. Chapters 3 and 4 are in preparation for submission to Marine Mammal Science and the Journal of Cetacean Research and Management, respectively.

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ABSTRACT OF THE DISSERTATION

Calling Behavior of Blue and Fin Whales off California

by

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Doctor of Philosophy in Oceanography
University of California, San Diego, 2005

John A. Hildebrand and Jay P. Barlow, Co-Chairs

Passive acoustic monitoring is an effective means for evaluating cetacean presence in remote regions and over long time periods and may become an important component of cetacean abundance surveys. To use passive acoustic recordings for abundance estimation, an understanding of the behavioral ecology of cetacean calling is crucial. In this dissertation, I develop a better understanding of how blue (*Balaenoptera musculus*) and fin (*B. physalus*) whales use sound with the goal of evaluating passive acoustic techniques for studying their populations. Both blue and fin whales produce several different call types, though the behavioral and environmental context of these calls have not been widely investigated. To better understand how calling is used by these whales off California I have employed both new technologies and traditional techniques, including acoustic recording tags, continuous long-term autonomous acoustic recordings, and simultaneous shipboard acoustic and visual surveys. The outcome of these investigations has led to several conclusions. The production of blue whale calls varies with sex, behavior, season, location, and time of day. Each blue whale call type has a distinct behavioral context, including a male-only bias in the production of song, a call type thought to function in reproduction, and the production of some calls by both sexes. Long-term acoustic records, when interpreted using all call types, provide a more accurate measure of the local seasonal presence of whales, and how they use the region annually, seasonally and daily. The relative occurrence of different call types may indicate prime foraging habitat and the presence of different segments of the population. The proportion of animals heard calling changes seasonally and geographically relative to the number seen, indicating the calibration of acoustic and visual surveys is complex and requires further study on the motivation behind call production and the behavior of calling whales. These findings will play a role in the future development of acoustic census methods and habitat studies for these species, and will provide baseline information for the determination of anthropogenic impacts on these populations.

CHAPTER 1

Introduction

All species of cetacean (whales, dolphins, and porpoises) found in United States waters are protected by the U.S. government. As part of this protection, the health of each population, including the population size, growth rate, and the impact of anthropogenic and natural threats, must be assessed. Since the 1970s, the primary method of population assessment has been visual line transect surveys. Line transect surveys are conducted from a ship or airplane, enumerating animals or groups and their distances from the trackline (Buckland *et al.* 2001). The number of animals seen in the surveyed area is analyzed statistically to estimate population abundance. While most estimates of abundance derived from visual surveys are robust, some may be biased or otherwise limited. Weather, distance, logistics, or funding may limit the ability to conduct visual surveys in some regions. In regions where visual surveys can be conducted, the behavior of some species may inhibit visual detection. In some cases, alternative means of animal detection are required to adequately assess the status and health of the population. For some species, detecting their sounds is thought to be an effective alternative means of detection.

Passive acoustic monitoring has already proven to be a valuable method for increasing detection and estimating abundance for some species. In some regions of the Antarctic and around Hawaii, visual survey observations of blue (*Balaenoptera musculus*) and fin (*B. physalus*) whales are rare, resulting in abundance estimates with low precision. In contrast, the common occurrence of low frequency calls by blue and fin whales in those regions has allowed for the estimation of minimum abundance (eg. McDonald and Fox 1999, Širović *et al.* 2004). Concurrent use of visual and acoustic surveys has also led to more precise estimates of abundance for sperm (*Physeter macrocephalus*) (Barlow and Taylor 2005) and bowhead (*Balaena mysticetus*) whales (Zeh *et al.* 1988, Clark and Ellison 1989).

Currently, widespread use of passive acoustic monitoring to estimate population size is limited by a lack of information on whale calling behavior. Calling rates are not known for many species. While all whales must breathe and are therefore eventually visible to the careful observer, only whales motivated to call can be heard. Even the reason for calling is a mystery for many species. The accuracy of abundance estimates derived from passive acoustic monitoring alone is limited by the proportion of the population producing calls: this proportion and the behaviors impacting it are unknown for most baleen whales. Understanding the motivation to produce sounds, and the temporal and spatial patterns driving it, are the missing links in using passive acoustic monitoring to estimate whale abundance, monitor their habitat, and protect them from anthropogenic threats. Technological advances have made passive acoustic monitoring possible; however, as Cumming *et al.* (1986) described "… regardless of the technical advances, the use of such tools is severely limited without first knowing the behavioral significance of the animal sound production. In reality, the two are mutually dependant. An analogous situation would be the use of the most refined instrumentation available for listening in on a conversation carried out in a foreign language that is unfamiliar to the observer."

Background

From the mid-1800s to the mid-1900s, most species of baleen whale were subject to intense commercial exploitation, reducing many populations to a small fraction of their original size. By the mid-1900s the North Pacific had surpassed the Antarctic as the primary whaling ground due to intense overexploitation of the Antarctic stocks earlier in the century (Rice 1974). While smaller, coastal species like right (*Eubalaena japonica/glacialis*), humpback (*Megaptera novaeangliae*) and gray whales (*Eschrichtius robustus*) were exploited first, the introduction of factory ships and explosive harpoons in the early 1900s allowed whalers to pursue swifter, larger whales further offshore. Between 1910 and 1965, 9,500 blue whales (*Balaenoptera musculus*) were hunted from the North Pacific (Ohsumi and Wada 1972), with approximately 2,000 animals (Tonnessen and Johnsen 1982) from the eastern North Pacific stock alone. The reduction in blue and humpback whales led the whaling industry to shift their focus to other species such as fin (*B. physalus*) and sei (*B. borealis*) whales. Because of the noticeable population decline, the International Whaling Commission (IWC) banned whaling for blue whales in 1966. From 1947 to 1987, an estimated 46,000 fin whales were taken in the North Pacific (Carretta *et al.* 2004) and an additional 5,000 were taken specifically near the west coast of North America from 1919 to 1956 (Rice 1974, Tonnessen and Johnsen 1982, Clapham *et al.* 1997). Fin whales were afforded protected status by the IWC in 1976. By 1986, the IWC imposed a ban on all commercial whaling.

Today, blue and fin whales, along with humpback, sei, bowhead (*Balaena mysticetus*), and right whales are listed as "endangered" under the U.S. Endangered Species Act (ESA) and as "depleted" under the Marine Mammal Protection Act (MMPA). Among the primary goals of the ESA is to promote the recovery of species to the extent that they can eventually be removed from the list. Regular assessment of population abundance and distribution is mandated under the MMPA and is necessary to monitor trends in abundance which may indicate species recovery or detect declines due to fisheries interaction, ecosystem degradation, or other anthropogenic or natural impact. The status of many blue and fin whale populations worldwide remains unknown; however, the northeast Pacific stock of blue whales and the California/Oregon/Washington stock of fin whales are thought to be increasing (Barlow

1994, 1997) and may represent the best documented recovery since the cessation of whaling. The current population estimate for northeast Pacific blue whales is 2,994 animals (CV=0.14) (Calambokidis and Barlow 2004). The current best estimate for fin whales is 1,635 (CV=0.35) in California/Oregon/Washington waters (Barlow 2003).

Much of what is currently known about baleen whale biology comes from whaling records. With the cessation of whaling, assessment of whale stocks is now possible only by conducting at-sea surveys of whale distribution and abundance. Cetacean abundance estimates are now typically derived from shipboard or aerial line-transect visual surveys. While the statistical analysis of visual surveys is well developed (Buckland *et al.* 2001) and most estimates are robust to slight variations in population distribution, biases are known to occur when a species shows a strong tendency for specific oceanographic domains or changes its distribution seasonally (Forney 1995, 2000, Ferguson and Barlow 2001, Ferguson *et al.* in review). In addition, adequate visual sampling of some species and regions has not been possible.

Acoustic monitoring for baleen whales has recently shown promise in identifying population ranges, migratory patterns, and trends in relative abundance. When the U.S. military made the acoustic data from the Sound Surveillance System (SOSUS) arrays available to whale researchers, further information on the seasonality and geographic distribution of blue and fin whales was made available in the North Pacific (Moore *et al.* 1998, Stafford *et al.* 1998, Watkins *et al.* 2000, Stafford *et al.* 2001, Burtenshaw *et al.* 2004). Blue and fin whales have also been widely detected by acoustic instruments designed for seismology and physical oceanography (Northrop *et al.* 1970, Riedesel *et al.* 1982, Jacobsen *et al.* 1987, McDonald *et al.* 1995, Andrew *et al.* 2002). The success in detecting and monitoring populations using acoustic sensors has led to an interest in developing methods to estimate abundance using acoustic arrays both during shipboard surveys and from autonomous recorders.

Using Sound to Study Blue and Fin Whales

Sound travels well in the ocean making the production of calls a primary means of communicating, navigating, and foraging for many marine species. Where light and chemical cues are often quickly attenuated in turbid water, sound can travel long distances, providing an effective means of communication among, and detection of, cetaceans. Most balaenopteriid whales are known to produce intense, low-frequency sounds (Edds-Walton 1997). The sounds produced by baleen whales are thought to function primarily for communication, and perhaps more specifically to establish territories, attract mates, or locate conspecifics.

The low-frequency, repetitive calls of blue and fin whales were among the first cetacean sounds to be recognized and widely studied. The first recordings of an unknown 20 Hz source, later identified as a fin whale, were made near Bermuda in 1951 (reveiwed by Schevill *et al.* 1964). Oceanic ambient noise had been studied prior to that time and the sudden presence of the 20 Hz signals led some to speculate that the noise source was artificial. In hindsight it has become clear that scientists only began using sound recording equipment sensitive to such low frequencies in the early 1950s. Prior to their attribution to fin whales, the "20-cycle pulses" in the North Atlantic were studied by a number of researchers, determining that the source was in fact oceanic, seasonally variable, mobile, and the cyclic occurrence of the pulses may correspond to the sounding and surfacing of a whale (Patterson and Hamilton 1964). The eventual assignment of the "20-cycle pulses" to fin whales did not come about overnight. Many hypotheses were tested and most discounted, some for the very reason that the species was nowhere in sight when these sounds were recorded. This complication of assigning call types to species remains a challenge today.

While researchers on the east coast of the U.S. were struggling to identify the source of the "20-cycle pulse", Navy researchers in the Pacific had their own "biologicals" to identify. The first studies of blue and fin whale calls in the North Pacific were in response to the Navy's detection of "20Hz longs" and "20Hz shorts" (Thompson 1965) on SOSUS arrays in the 1950s (Nishimura and Conlon 1994). It was the eventual identification of blue whale calls off Chile which led to the conclusion that the "20Hz longs" detected near San Clemente Island in the Southern California Bight must be produced by blue whales (Cummings and Thompson 1971).

Since the initial detection of blue and fin whale calls in the North Pacific and North Atlantic, underwater bio-acoustic technology has seen marked improvements. Developing technology has allowed for increasingly higher resolution, greater sensitivity systems, capable of longer duration and higher frequency recordings. These systems have resulted in the description of seasonal presence (Thompson and Friedl 1982, Burtenshaw *et al.* 2004, Clark and Clapham 2004, Mellinger *et al.* 2004, Nieukirk *et al.* 2004, Sirovic *et al.* 2004) population range (Stafford *et al.* 2001, Stafford 2003), population identity (Stafford *et al.* 1999, Hatch and Clark 2004, McDonald *et al.* in press) and, in some cases, estimates of abundance when coupled with established visual methods (Zeh *et al.* 1988, Clark and Ellison 2000, Barlow and Taylor 2005) for a variety of baleen whale species and sperm whales. However, the use of acoustics for estimating abundance and habitat use is still limited by a lack of understanding of the behavioral ecology of calling for most species.

The missing element in using passive acoustics to estimate cetacean abundance has been a lack of understanding of call rates; how these rates depend on the environment and behavior, and how they relate to visual encounter rates. Describing the variability in vocalization rates requires an understanding of the behavioral ecology of call production. The first theories regarding the use of sound by mysticetes suggested that the patterned sounds were used for echolocation. In the early 1960s, before the sounds of most mysticetes were described, Patterson and Hamilton (1964) suggested that the "20Hz pulses" recorded on their hydrophone arrays corresponded to a whale echolocating off large ocean features, such as continental shelves and seamounts. Since that time, other uses of sound have been suggested, including a role in indicating breeding condition for the attraction of mates (Evans 1967) and communication with conspecifics over great distances (Payne and Webb 1971). Suggestion of a sex-bias (Watkins *et al.* 1987, McDonald *et al.* 2001, Croll *et al.* 2002) in the production of calls by blue and fin whales would indicate that calls are used primarily in a reproductive context, similar to humpback whales (Darling 1983). Attribution of sounds to a specific function has rarely been accomplished, with the best descriptions of context being either reproductive, or social. The complex songs of humpback whales are widely thought to be for reproduction; however, their specific function, either for mate attraction, mate stimulation, male-male competition, or territory defense has not been resolved. Social sounds produced by right whales show a correlation between the complexity of the call and the complexity of the social context, with simple, predictable sounds used for long-distance communication, and highly variable sounds associated with surface active groups (Clark 1983). While there have been several recent advancements in the understanding of baleen whale calling, the purpose and function of specific blue and fin whale calls remains largely unknown.

Variation in vocalization rates may also occur seasonally, spatially, and daily. Results of acoustic monitoring will be biased by these factors, requiring a thorough understanding of their variability. In addition, the relationship between the detection of animals visually and acoustically must be understood before abundance estimation methods using only acoustics may be developed.

Dissertation Outline

This dissertation research aims to evaluate the use of passive acoustic recordings, from long-term or ship-based surveys, to estimate blue and fin whale abundance off southern California. The results of three studies of the variability in calling are presented, including the identification of behavioral and environmental correlates of call production, the analysis of calling patterns on several temporal and spatial scales, and the effectiveness of acoustic surveys in detecting animals relative to traditional visual methods. These results are presented in chapters 2 through 4. Each chapter is intended to stand alone as a publishable unit, and the reader may encounter some redundancy in the introduction and methods for each chapter.

A long-term study of blue whale calling behavior based on focal animal follows using sonobuoys, acoustic recording tags, biopsy sampling, photo-identification, and visual tracking is described in Chapter 2: "The behavioral context of northeast Pacific blue whale calls: insights from acoustic recording tags and tissue sampling." Blue whale calling is divided into three categories and the non-acoustic behavior of each type of calling is described and the sex-biases in calling are identified. The results of this chapter aid in the interpretation of later chapters by identifying and summarizing some basic patterns of behavior associated with the production of each call type. This chapter has been submitted to the journal Animal Behaviour and is presented as part of this dissertation with acknowledgment to the co-authors in the study.

Long-term acoustic recordings of blue and fin whales collected at five sites around Cortez and Tanner Banks are described in Chapter 3: "Temporal and spatial pattern in blue and fin whale call occurrence in the Southern California Bight." Annual, seasonal, and daily patterns of call occurrence are investigated for all three blue whale call types identified in Chapter 2 and for fin whale calling. Small scale spatial patterns of calling based on recordings from separate sites at the Banks are identified. The results of this study reflect the importance of understanding the behavioral, environmental, and social context of calling when interpreting long-term acoustic recordings. In addition, the chapter highlights the small scale variability in calling which must be accounted for when interpreting this type of record for estimating abundance, distribution, and describing habitat.

Four years of simultaneous visual and acoustic surveys for blue whales in the Bight are described in Chapter 4: "Blue whale visual and acoustic encounter rates from shipboard surveys in the Southern California Bight." Using Generalized Additive Models, the spatial and temporal variability in visual and acoustic detection are evaluated and compared. The goal of this study is to assess the effectiveness of acoustic surveys for blue whales and identify relationships between visual and acoustic detection patterns for use in interpreting autonomous acoustic surveys.

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CHAPTER 2

The Behavioral Context of Northeast Pacific Blue Whale Calls: Insights from Acoustic Recording Tags and Tissue Sampling

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Abstract

We assessed the behavioral context of acoustic calls produced by Northeast Pacific blue whales (*Balaenoptera musculus*) using visual and acoustic observations along the California coast. We deployed acoustic recording tags and employed photo-ID, tissue sampling, and acoustic monitoring with sonobuoys to evaluate the relationship between blue whale call occurrence and behavior. Only a small proportion of monitored blue whales produced calls, and these fell into four categories: 1) repeated low-frequency pulsed A and tonal B calls, or song, 2) irregularly patterned A and B calls, or singular calls, 3) downswept D calls and 4) highly variable amplitude or frequency modulated calls, or non-stereotyped calls. A and B calls were heard only from male blue whales, and D calls were heard from both sexes. Song calls were produced by lone, traveling blue whales; D calls were heard during foraging, commonly within groups of animals. Singular A and B calls had lower source levels than song A and B calls, and D calls. Specific behaviors could not be associated with singular A and B calls. Although the precise function of each call type remains ill-defined, information on the sex bias in call

production, the non-acoustic behaviors associated with each call type, and the source level of calling help us to understand the context of call production and advances the development of acoustic detection to assess population size, trends in abundance, and habitat associations.

Introduction

Passive acoustic monitoring of baleen whale calls is a powerful tool for studying their presence and movements (Thompson and Friedl 1982, Watkins *et al.* 2000, Stafford *et al.* 2001, Burtenshaw *et al.* 2004). Blue whales, in particular, produce low-frequency and high-intensity calls allowing a single acoustic recording instrument to monitor calling blue whales over a large region. Northeast Pacific blue whales (*Balaenoptera musculus*) maintain a seasonal annual migration, primarily feeding in the waters off California in summer and fall (Croll *et al.* 1998, Calambokidis and Barlow 2004), before migrating to waters off Mexico and near the Costa Rica Dome in the winter and spring (Calambokidis *et al.* 1990, Mate *et al.* 1999). Blue whale calls can be heard along their entire migration route and at all times of year (Stafford *et al.* 1999, 2001, Burtenshaw *et al.* 2004). Although calling varies in rate and intensity along the migration route and in feeding areas, we do not yet understand what drives this variability, nor do we understand the ecological role of calling for blue whales. By studying the behavioral context of blue whale calling, we may be able to use acoustic measurements to better understand habitat preferences, social structure and mating system, behavioral ecology, the effects of anthropogenic sound, and the distribution and abundance of populations.

Four blue whale call types have been identified from the northeastern Pacific (Thompson 1965, McDonald *et al.* 1995, Thompson *et al.* 1996, Stafford *et al.* 1999). The best described vocalizations consist of a combination of two low frequency long duration calls: pulsed A calls and tonal B calls. Repeated A and B blue whale call sequences have been classified as song (McDonald *et al.* in press). It has been suggested that song is produced only by males (McDonald *et al.* 2001), similar to song production in humpback (Tyack 1981, Darling 1983) and fin whales (Croll *et al.* 2002). Blue whales also produce downswept calls, known as D calls (Thompson *et al.* 1996, McDonald *et al.* 2001). A fourth class of highly variable frequency modulated (FM) calls has also been reported (Thode *et al.* 2000), with frequencies generally lower than 60Hz. Behavioral observations do not exist for D and non-stereotyped FM calls, though it has been suggested that D calls may occur in call-counter-call sequences between individuals (McDonald *et al.* 2001).

Few behavioral observations have been reported in association with blue whale call production. We have been studying blue whales along the California coast with the goal of understanding how call type production varies with sex and behavior of individual whales. We have made measurements of blue whale acoustic and diving behavior using acoustic recording tags, and have evaluated the associated sex and behavioral relationships using biopsy, photo-identification, surface behavioral observations, and real-time acoustic monitoring with sonobuoys. Our evaluation of blue whale calling includes the rate and intensity of calling in relation to dive depth, feeding or traveling behavior, sex, and the association with other whales. Our observations provide behavioral context for call types that have been widely heard and documented, yet not understood in terms of their biological and ecological context.

Methods

Locating and Sampling Calling Blue Whales

Ship-based observations for blue whales were conducted in the summer and fall of 2000 through 2003 aboard the 38 m R/V *Robert Gordon Sproul* in the waters of the Southern California Bight. We periodically deployed DIFAR (direction-finding) sonobuoys to acoustically monitor for vocally active blue whales. Acoustic signals were monitored as scrolling spectrograms using the software *Ishmael* (Mellinger 2002) (FFT length 1.5 s, 50% overlap, Hanning window). When calls were detected visually in the spectrographic display, the bearing to the sound source was estimated. When bearing estimates could be calculated from more than one sonobuoy position, a track of the vocalizing whale was generated and used to help visually locate the calling whale. The sonobuoy recording and direction-finding system are described in detail elsewhere (McDonald *et al.* 2001, Swartz *et al.* 2003, McDonald 2004). When a calling whale was located, the ship was directed to its position. Visual observers aboard the *Sproul* searched for the calling blue whale using 7x50 power binoculars and naked eye. A 5.3 m Rigid-Hulled Inflatable Boat (RHIB), deployed from the *Sproul,* was used to approach the calling whale to obtain a skin biopsy and photographs for individual identification (photo-ID). Skin samples from calling whales were obtained in three locations (Figure 2.1). Photo-ID and biopsy procedures are described in more detail elsewhere (McDonald *et al.* 2001, Calambokidis and Barlow 2004). In addition, a sonobuoy was usually deployed by the RHIB at the location of a whale surfacing to verify the identification as the calling whale. Sex was determined from genetic analysis of skin samples through simultaneous amplification of the ZFX/ZFY and SRY genes (Fain and LeMay 1995). When ample genetic material was recovered from the biopsy, the sample was split, making half of the sample available for a pregnancy test based on hormone levels in the blubber (Mansour *et al.* 2002, Kellar and Dizon 2003).

Application of Acoustic Recording Tags

We deployed three types of acoustic recording tags on blue whales. We focus here on the results of deployments during which blue whale vocalizations were detected. These records provided detailed information on the vocal behavior of individual whales. Tagging of blue whales using our RHIB was conducted during surveys with the *Sproul* as well as during several additional periods without ship support. These additional operations were conducted in the Santa Barbara Channel (2002, 2004), in Monterey Bay (2002-04), and near Point Reyes (2004). All of our tag deployments on blue whales are summarized in Table 2.1, with the position of calling whales shown in Figure 2.1.

The primary tag deployed and reported on was a commercially available acoustic recording tag, known as the Bioacoustic Probe (BProbe). This tag records pressure, temperature, and sound up to a maximum sample rate of 20 kHz. The 2003 and later version of the BProbe included a 2-axis accelerometer, enabling the monitoring of tilt and roll. Tilt and roll were measured in gravitational units (g) and converted to degrees using the manufacturers specific transfer function. Body position is defined as horizontal at 0^0

tilt and upright at 0^0 roll. All tags were set to an acoustic sample rate of 1024 Hz, with auxiliary channels sampling at 1 Hz.

Whales were approached from behind in the RHIB to a range of ~1-5 m, and a tagger, harnessed to the front of the RHIB, used a 2.6 m metal or 5 m fiberglass pole with a specially designed PVC bracket to hold the tag in place, yet allow it to detach from the pole when it became attached to the whale. The tag was held on the animal with suction cups. Skin was collected from tagged animals, either from the inner surface of the suction cup or tagging apparatus, or by biopsy. When possible, the position of the whale was noted by collecting GPS data from the RHIB at each surfacing while the tag was attached. Tagged whales were selected based on our ability to locate and track them visually and therefore were not necessarily selected to be acoustically active.

Upon tag retrieval, data were downloaded from the tag to a computer for analysis. Acoustic data were initially viewed in spectrogram form (FFT length 1 s, 80% overlap, Hanning window) to determine the presence of calls. When calls were found, the time was noted for comparison to the pressure and accelerometer records, and the call was extracted into a separate sound file for later analysis.

Two additional styles of suction-cup-attached acoustic tags were deployed less often: the National Geographic Crittercam (Marshall 1998) and the Woods Hole Oceanographic Institution dTag (Johnson and Tyack 2003). In addition to video, the Crittercam also records depth and sound, and all data are stored to a Hi8 tape. The dTag was used in June 2002 in the Santa Barbara Channel for two separate deployments. The acoustic data from both tag types were viewed as described above.

Estimating Call Source Level from Tag Records

The BProbe provides calibrated acoustic data from which received levels can be calculated. To estimate source level requires several assumptions. We recorded and, when possible, photographed the position of the tag on the whales. In a few cases we noted a change in position of the tag on the whale following successive dives. Based on the analysis of anatomical measurements of blue whales, sound is thought to be generated at the arytenoids, at the junction of the laryngeal sac and the lungs of the whale, approximately 1 m posterior to the blow hole and 1 m to the interior of the whale (Aroyan *et al*, 2000). Given the arytenoid source location and tag position on the whale's back, the distance over which the sound has traveled between source and receiver can be approximated. The tag was placed approximately 5 m posterior to the blow hole, recording sound at a range of 4 m. Acoustic propagation is complex at distances less than A^2/λ, with A = length of source and λ = wavelength of the signal. Beyond this distance is known as the far-field (Medwin and Clay 1998). A key issue is whether the tag is located in the far-field of the acoustic source within the whale. Using calculated wavelengths ranging from 87.1 m (17.2 Hz) to 90.2 m (16.6 Hz), an estimated distance of 4 m to 5 m between the tag and the source, and assuming a small (<1 m) arytenoid source, the placement of the tag on the whale's back puts it within the far-field (4 m >> 0.01 m), and therefore spherical spreading transmission loss can be assumed. This transmission loss can then be added to the calibrated received level to determine source level. We have not adjusted calling levels for potential changes in acoustic propagation through whale tissues.

Estimation of call source levels included calculating received levels and then correcting these levels for potential surface interference. Power spectral density (PSD) estimates were obtained over the duration of the call in 1 Hz bins from the calibrated acoustic data (Hanning window of length equal to the sample rate and no overlap). The PSD estimates for each 1 Hz bin were summed from 10 Hz to 110 Hz and converted to decibels (dB) referenced to 1 μPa. The received levels, along with the known position of the tag on the back of the whale, were then used to estimate the source level of sounds. Since calls were produced at shallow depths, close to the sea surface (a reflective boundary), the received level may be affected by interfering reflections from the air-sea interface (Urick 1983, Charif *et al.* 2002), known as the Lloyd Mirror Effect. The time averaged source pressure over the duration of the call at 1 m (p_0), including the Lloyd Mirror interference, was calculated given the distance between the source and receiver via direct path (L_1) and reflected path (L_2), the total received pressure (p_R), swell height of 1m (H), grazing angle ($\theta = \tan^{-1} L_1$/source depth), the travel time between source and receiver via the reflected path (τ), and the angular frequency (ω), wave length (λ), and duration (t) characteristics of the signal (derived from Table 2.4) using the following equation:

$$\overline{p_0^2 = p_R^2\left[\frac{1}{L_1}\sin\omega t + \frac{e^{-\frac{2\pi}{\lambda}iH\sin\theta}}{L_2}\sin\omega(t-\tau)\right]^{-2}} .$$

Source level was then estimated as: $SL = 10\log(p_0^2)$ in dB re: μPa-m. Our source level values should be viewed as estimates because of the assumptions stated above and further confounding effects discussed later.

Results

Visual and Acoustic Tracking of Singing Whales

Four singing blue whales were visually and acoustically tracked in the Southern California Bight (Figure 2.1; Table 2.2). Skin samples were collected from two of the four singers, and surface behavioral observations were recorded for all four. The photograph of one calling whale, for which a skin sample was not obtained, was matched to a photo from the Costa Rica Dome which had an accompanying skin sample. All three whales for which skin samples were available were male, and all four tracked whales were traveling at moderate speed and on a predictable course. Acoustic recording tags were not attached to these whales. In all cases, calling whales were visually identified based on their location relative to sonobuoy bearings, the relative amplitude and timing of calls compared to other calling whales, and the coincidence of surfacing and breathing gaps in the song evident from the acoustic records. Concurrent visual and acoustic identification of other calling whales has been obtained previously, though it has proven difficult to get close enough to many calling whales to obtain a photograph, skin sample, or detailed surface behavioral observations. The position and monitoring time for each of the whales discussed here, in addition to the whale reported in McDonald *et al.* (2001), are shown in Table 2.2, along with behavior, average swimming speed and direction of travel. Table 2.4 summarizes the call characteristics of each tracked whale.

A and B Calls Occurring Intermittently

Three (June 23 and 30, and September 21, 2002) of 27 deployments of acoustic recording tags recorded A and B calls, though no calls occurred in song sequences, indicating that blue whales do not always produce A and/or B calls in regular temporal patterns (Table 2.3). These intermittent calls will be referred to as single A and/or B calls. The characteristics of the calls are similar to A and B song calls, except for the irregular timing between calls or call pairs (Table 2.4). A variety of surface and diving behaviors were observed in association with these recordings, including feeding, milling, and traveling. All recordings of single A and/or B calls occurred in the Southern California Bight.

The occurrence of single A and/or B calls shared several features among the three deployments. All calls occurred at shallow (< 25m) depth (Table 2.3), and only a single call or A-B call pair occurred per dive. On all three tag deployments the tagged whale was in close association (ie. paired or grouped) with at least one additional blue whale, and when paired (two occasions) was with a female whale, with other blue whales within 1 km. Additionally, while the identity of the whale producing the calls is unknown for two of the three deployments, all three whales carrying tags when single A and/or B calls were heard were male. In both cases where the tagged animal was paired, the tagged whale was male and the other whale was female.

The detailed dive profile for the tagged whale near La Jolla, CA on June 30, 2002 is shown in Figure 2.2, with time and depth of calling and surface behavioral observations annotated. This animal was feeding during the day, evidenced by the lunging profile. While the record shows most calls occurring at night, acoustic monitoring of this animal with sonobuoys prior to tag attachment indicate that it may have been calling during the day as well. All calls in the tag record had lower source levels than those previously reported for type A and B calls (Figure 2.3; Table 2.4). In addition, surface observations indicate the other animal in the pair, a pregnant female, commonly surfaced 2-3 min before the tagged male. Some of the calls were produced during periods when the tagged male was underwater and the paired female was surfacing, confirming the tagged whale produced the calls, not the leading female.

The two remaining records of A/B calling (June 23 and September 21, 2002) occur in slightly different contexts. It is not possible to attribute the calls to the tagged whale with certainty for either record because of the close association between whales during surfacing, and due to the lack of calibration for the hydrophone in some of the tags (dTag and Crittercam). The dive profile for the whale tagged in the Santa Barbara Channel on June 23, 2002 is shown in Figure 2.4. All calls in this record have similar (uncalibrated) received levels and all occur at a constant, shallow depth (~20 m: Table 2.3). The tag record from September 21, 2002, occurred in a group of three whales. The video track of the Crittercam record shows the tagged whale next to another blue whale during the time that the single A call occurred. The primary difference between these records and that of June 30, 2002 is that deep excursions immediately followed calls, without an intervening surface interval.

D and Non-Stereotyped Calls

Type D calls were observed on three of 27 BProbe attachments on blue whales (September 26 and 28, 2003 and July 28, 2004), all within Monterey Bay. Two of the three attachments were on animals in loosely associated pairs, while the third was on a single whale. Skin samples from the September 26 and 28 tagged and paired animals indicate that both male and female blue whales produce D type calls. Additionally, all three records indicate that D calls are produced by feeding whales (Figure 2.5, 2.6a and 2.7). Calls were only heard during relatively shallow dives (<35 m, Table 2.3), with several calls per dive. There were no significant deviations from 0° tilt (horizontal) or 0° roll (upright) during call production (Table 2.3). The observed D calls are highly variable in both frequency content and sweep rate (Table 2.3), even those produced by a single animal. In all three cases, additional blue whales were within 1 km of the tagged whale, though there did not appear to be any coordinated behavior between the tagged whale and these more distant animals.

During attachments to paired whales, we observed large variability in the signal-to-noise ratio (SNR) of received calls, occasionally due to variation in the received level, such that both whales in the pair may have been calling, and other times due to increases in background noise. Figure 2.6b illustrates one dive in which a D call with high SNR was received on the tag, followed by two much lower amplitude calls, probably produced by the other whale in the pair (Figure 2.6c). Additionally, there were variations in the dive behavior of the tagged whale during call reception. For example, the July 28 record shows calls occurring at the surface and at depths of up to 33 m (Figure 2.7). Estimating source levels for all calls in the record (including Lloyd mirror interference) yields a bimodal distribution, with the calls occurring deep (>10 m) being significantly louder (183.5 +/- 7.7 dB re: μPa-m) than shallow (<4 m) calls (166.4 +/- 7.9 dB: re μPa-m) (Student's T-test, unequal variance: $t_2 = 5.799$, $P \ll 0.001$). This may indicate that calls occurring deep were produced by the tagged whale, while those heard at shallow depth were produced by the other animal in the pair. Alternatively, the other whale in the pair could have produced all calls, with the difference in received level attributed to greater distance between the whales and the reduction of acoustic pressure close to the surface. Surface behavioral observations are not available for the other animal in the pair. Because we cannot be certain which calls were produced by the tagged whale, source levels are not presented for records including paired whales.

The tagged single animal (September 26, Table 2.3) producing D calls also produced several non-stereotyped frequency and amplitude modulated (AM) calls. An example of a sequence of calls is shown in Fig. 8a, illustrating the highly variable nature of both D and FM calls produced. Some of the calls appear to be similar to type B calls because of their frequency content; however, these calls were highly frequency-modulated and significantly shorter in duration than typical B calls. Figures 2.8b and 2.8c also show some of the AM variants heard from this whale. The frequency, duration, and source level characteristics of D calls, and AM and FM variants can be found in Table 2.4.

Discussion

Song and Single AB Calls

The observations of singing blue whales presented here suggest a unique context for the production of A and B calls. Based on four unambiguous samples presented here (three singers, one single AB), and one additional report from McDonald et al (2001), there is mounting evidence that blue whale A and B calls are produced by males only. Given the current sample size, and assuming sexual parity within the population, the probability that males were sampled only by chance is 3.13% (0.5^5). Singing blue whales did not display any sort of coordinated behavior, either acoustically or visually, with the other whales in the area, and the whales were traveling (Table 2.2), similar to the few previous behavioral observations of this call type (Stafford *et al.* 1998, McDonald *et al.* 2001). In addition, these singing whales were not feeding, evidenced by the markedly different surfacing and movement patterns of singing whales and known feeding whales. Singers are often difficult to approach because of the distance covered between surfacings, their speed of travel, and their short surface sequences.

Song has been documented in other baleen whale species as being produced primarily by males, supporting the common conclusion that songs may function in reproduction. The most extensively studied of these species is the humpback whale (*Megaptera novaeangliae*). In contrast to blue whales, humpback whales produce complex songs (Payne and McVay 1971). Singing is heard primarily on low-latitude breeding grounds, with most singers producing the same song (Payne and McVay 1971, Cerchio *et al.* 2001); however, like blue whale song, it has also been heard along migration routes (Norris *et al.* 1999) and on feeding grounds (Clark and Clapham 2004). The precise function of humpback song is still unknown (Payne and McVay 1971, Tyack 1981, Clapham 1996); however, it has been suggested that song may function to mediate interactions between males (Tyack 1981, Darling 1983, Frankel *et al.* 1995) or to advertise species, sex, location, and condition to females (Payne and McVay 1971, Winn and Winn 1978, Tyack 1981). If breeding is confined seasonally, the detection of humpback song along migration routes and on feeding grounds complicates the interpretation of song as a reproductive display only. Clark and Clapham (2004) do, however, point out evidence for out-of-season breeding in humpback whales.

Fin (*B. physalus*) whales also produce songs. Like blue whales, fin whales are pelagic, and therefore it has been suggested that the two species may use song in a similar manner

(Clark and Ellison 2004). Fin whales produce short, low frequency downsweeps in song sequences (Watkins 1981, Thompson *et al.* 1992), and Croll *et al*. (2002) has proposed that these songs are produced only by males to attract females to patchily distributed prey, a notion which is supported by the high intensity of the call and the absence of a specific breeding area for this species. Observations of Watkins *et al.* (1987) indicate that singing fin whales remain stationary over a singing bout, suggesting advertisement of location, similar to the findings of Croll *et al.* (2002). Other studies have observed fin whales traveling while singing (Patterson and Hamilton 1964, McDonald and Fox 1999). The diversity of observed behaviors for singing fin whales indicates the function of their song may be more complicated than for blue whales. Observations indicate that blue whales produce calls while traveling, not during foraging, indicating that they are not attempting to attract mates to a specific location or to food resources. This is supported by the fact that blue whale B calls are diurnally distributed with more calls occurring at night and twilight than during the day (Stafford *et al.* 2005, Wiggins *et al.* 2005), such that they preferentially produce B calls when not foraging on daytime aggregations of prey (Croll *et al.* 1998).

Our observations occurred on feeding grounds rather than winter breeding grounds, so we may not be sampling song meant for reproduction, particularly if the function of song changes seasonally. Whaling records indicate breeding occurs in winter. However, blue whales in the Gulf of St. Lawrence in the North Atlantic, and along the California coast have been observed in male-female pairs during the feeding season (Sears 2002, J. Calambokidis unpublished data). The incidence of pairing increases as the breeding season approaches, with some pairs remaining stable for at least several weeks. This may indicate that mate selection in blue whales in not confined seasonally, and that song produced on feeding grounds, while temporally and spatially apart from known breeding grounds, may still serve a reproductive function.

Classifying blue whale song as serving a reproductive purpose does not necessarily limit possible uses for the call type, as reproduction encompasses many behaviors including mate attraction, guarding, and stimulation, as well as territory defense and male-male dominance. To assign the function of song to one particular reproductive context is not yet possible; however, we may be able to eliminate some of the possibilities given the observations presented here. Signals designed for mate attraction in other animals are generally of the lowest possible frequency, have a high repetition rate, long signal duration, and are produced by a single sex when receptive to mating, and in a stationary position (Bradbury and Vehrencamp 1998). Blue whale songs are annually decreasing in call frequency (J. Hildebrand, personal communication) which may be encouraged by sexual selection toward lower frequency signals. While blue whale songs have many of these characteristics (low frequency, high repetition rate, long signal duration, produced by a single sex), they are heard all along the migration route, at all times of year, and the whales are traveling rather than stationary. Mate guarding and male-male aggression do not appear to be plausible functions of song as singing blue whales are commonly observed traveling alone, and uncoordinated with other whales in the region. Territory defense signals are generally designed to transmit over the entire territory, can be localized by listening whales, and have a sufficient duration and repetition rate that species and individual identity can be discerned by possible intruders (Bradbury and Vehrencamp 1998). Dwarf minke (Gedamke *et al.* 2003) and fin whale

(Watkins 1981, Croll *et al.* 2002) songs have been shown to play some role in territory defense, and blue whale songs are loud and localizable; however, there is no evidence that blue whales maintain stationary territories. Unlike fin whale song (Croll *et al.* 2002), blue whale song does not appear to be consistently and most frequently heard in regions of high food concentration. Larger, mobile territories may exist for this species; however, it is unclear how the territory would be defined.

The long duration (~20 s) of the individual blue whale song components, and the repetitive nature of the song along with high source levels (McDonald *et al.* 2001), optimize this call type for communication over long distances (Payne and Webb 1971, Clark and Ellison 2004), a potential benefit to migrating blue whales which are often widely dispersed. It seems likely given these characteristics, and by comparison to humpback, fin, and minke whale songs, that the blue whale song is involved in reproduction. It also has been proposed that a secondary function of song may be for long-range navigation using reflections from distant bathymetric features (Clark and Ellison 2004), as has been suggested for bowhead whale (*Balaena mysticetus*) calls (George *et al.* 1989). Both sexes and all age groups of whales must navigate over large distances, suggesting that song calls are not solely for navigation, because females would be at a disadvantage. In addition, changes in call duration or intercall interval have not been observed, which would be expected if the calls were used for navigation as the whale approached features upon which it was echolocating.

The data show that blue whales do not always produce A and B calls in song sequences, such that calls may occur intermittently. In this mode A calls are not necessarily followed by Bs, nor are there predictable intervals between successive calls.

All three whales observed producing this call type have been engaged in different behaviors; however there is one unifying theme: this call has only been heard from a whale or whales that are part of a pair or group of animals (Tables 2.3 and 2.5). Feeding, milling, and traveling behavior have been observed from blue whales producing single A and B calls making the interpretation of the function of this call type more complex.

The behavioral context for producing single A and B calls appears to be more complex than that associated with singing. Single A and B calls share the frequency and duration characteristics of song A and B calls (Table 2.3), but it is the amplitude and timing of these calls that clearly distinguish them from song. The consistent depth of single A and B call production along with their lower amplitude may be related to their function. All three instances of this call type were heard from a whale in a group, and with other blue whales in the immediate vicinity, such that the low source level (compared to song calls) might suggest that the intended receivers are nearby. The social context further suggests coordination or aggression within the group. On at least four occasions during the record from June 30, 2002, the female in this pair surfaced before the tagged male. The times of these asynchronous surfacings are coincident with the times that some calls were detected on the tag. Her surface position acoustically isolates her from the call, suggesting the call may be intended for another whale as a guarding action. Further, the Crittercam video shows the tagged blue whale next to another blue whale during the production of a single A call, perhaps signaling aggression between the whales. These observations are in marked contrast to the social context of singing. Further, unlike song calls, the hourly occurrence of single calls does not change significantly throughout the day (Chapter 3), suggesting these calls occur independent of feeding behavior and are therefore likely not intended to attract females to or defend prey aggregations.

D and Non-Stereotyped Calls

D calls have a context unique from song type calls. D calls appear to be produced by both sexes. Two tagged whales heard producing D calls were genetically sex-typed: one male and one female. This call type has been heard in association with feeding and from single and loosely associated pairs, suggesting this call may be used to maintain contact with conspecifics. Previous reports of whales producing D calls (Thode *et al.* 2000, McDonald *et al.* 2001) have also shown that this call type is quite variable and is observed from lone blue whales, as well as whales that are part of aggregations. McDonald *et al.* (2001) observed D calls from two or more whales in an alternating pattern, and suggest that these are contact calls. Similar to these observations of D callers from tags, Thode *et al.* (2000) observed multiple calls per dive, with calls produced throughout the dive profile at depths between 15 m and 35 m. Our measurements of tilt and roll also indicate that D calling whales are not deviating significantly from upright and horizontal during call production. As these calls occur in the upper 30 m where light levels are sufficient for visually identifying conspecifics, slight deviations from upright and horizontal seen in these records (Table 2.3) may be indicators of whale movements for visual tracking of the intended receiver of their calls.

The observations presented here and those of Thode *et al.* (2000) and McDonald *et al.* (2001) suggest the function of D calls is likely to be social interaction or contact, rather than reproductive. These calls are made by both sexes on feeding grounds, and often come as sets of call-counter-calls. Social sounds, as described by Edds-Walton (1997), are produced by two or more animals in close proximity whose activity appears to be coordinated. In balaenopteriids, this type of vocalization generally includes frequency sweeps and is repeated (Edds-Walton, 1997). Our observations of whales producing D calls are consistent with both types of sounds (Table 2.5). Similar vocalizations have been recorded from several rorqual species; however, fin whales may provide the best comparison in terms of the behavioral context of this type of call. Fin whales have been observed using their 20 Hz pulse calls while traveling at distances of up to 3 km from each other (McDonald *et al.* 1995), and are believed to be using the call to maintain contact between the individuals in the group.

The presence of non-stereotyped tonal and amplitude-modulated calls indicates that blue whale calling behavior is more complex than has been previously recognized. Thode *et al.* (2000) also notes other "highly modulated" variants occurring with D calls. The occasional association of these non-stereotyped calls with D calls may indicate that their combined function serves a purpose different than that of D calls which occur alone. Greater complexity may be an indicator of aggression (Edds-Walton 1997), as may be the case with the AM and FM combination calls observed on the tags, as other blue whales were present in the area. In contrast, contact vocalizations are produced by only a single whale, physically separated from a conspecific (like the record from July 28, 2004), which result in interaction between the caller and the conspecific (Edds-Walton, 1987). Fin whales have been observed producing 20Hz calls in conjunction with other growl-like calls on feeding grounds in the North Atlantic (Edds 1980, Watkins *et al.* 1987), perhaps analogous to our observations of type D calls in conjunction with non-stereotyped AM and FM calls of blue whales.

Using Calls to Study Blue Whale Populations

Acoustic monitoring is becoming an increasingly important method for delineating species boundaries, migration routes, and relative abundance, and offers promise in aiding in abundance estimation and the prediction of critical habitat (Mellinger and Barlow 2003). However, before acoustic detection can be a robust survey method for blue whales, we must understand the rate of occurrence and the ecological importance of call types so that we can adequately account for changes in acoustic behavior over time and space.

When choosing to use acoustic monitoring to estimate relative or absolute abundance, the rate of call production must be considered. Calling rate may be evaluated as the number of calls or the number of calling animals per time period. In the tag deployments on blue whales described here, eight single A-B or D callers were heard over six of 27 deployments (29%), while calls (irrespective of the source) were heard in 17.3 of 57.5 total recording hours (30%). Calling between paired animals would be difficult to detect for D callers because of the large variability in frequency content and sweep rate preventing individual identification of two closely spaced animals. This suggests that call counting would be the preferred method for extrapolating between the number of calls heard and the number of animals present for this call type. In contrast, a single singing blue whale can be heard for several hours, while concurrent visual and acoustic observations of blue whales indicate that relatively few whales sing (Chapter 4), suggesting a different approach may be desirable when using the occurrence of song calls as an index of abundance. Spatial variation in the use of call types by the whales, evaluated in Chapters 3 and 4, would also complicate the use of calls to estimate abundance.

Previous descriptions of blue whale distribution using long-term recordings focused on the detection of song calls. While this is useful for outlining seasonality and distribution of singers, monitoring song calls does not necessarily yield the best estimate of the distribution of the entire population. Our observations of blue whales producing single A and/or B calls suggest that interpretation of long-term records is more complex. While there are no previous reports of blue whales producing song calls in intermittent patterns, this is probably not because the calls were absent. The nature of the call type, with the same frequency and duration as song calls, might prevent the unique identification of these calls, particularly in the presence of singing whales. However, whale producing single calls may constitute a larger percentage of the total number of vocalizing whales than do singers, a distinction important for researchers interested in using the detection of blue whale sounds for abundance estimation. Additionally, monitoring the presence of D and single A and/or B call types may provide a more direct means for delineating whale habitat, as these calls have been heard from feeding whales in known productive areas. The presence of these call types, together with environmental data (eg. Moore *et al.* 2002) may allow for the calculation of predictive habitat models.

Estimating Source Level from Tag Recordings

To calculate source level from a moderate distance (100 m – 1 km) you minimally need only the received level and the distance to the source, assuming spherical spreading and little or no directionality to the source. However, to estimate source level from acoustic data acquired at very close range we need more information including the size, dimensions, and detailed position of the source within the whale. If the sound is originating at the arytenoids, at the junction of the passageway to the lungs and the laryngeal sac, approximately 1 m posterior to the blow hole and 1m to the interior of the whale (Aroyan *et al.* 2000), and the tag is placed 5 m posterior to the blow hole, it is recording sound at a range of 4 m, equivalent to a spherical spreading loss of 12 dB. If this placement is within the far-field, the received level is not complicated by the constructive and destructive interferences of the source from near-field propagation (Medwin and Clay 1998). If the sound is simply spreading spherically from the arytenoids, the mean source level estimates for the single A and B calls would then be 172 dB re: µP-m and 176 dB re: µP-m, respectively (Figure 2.3a), lower than previously reported source levels for the corresponding song call types. Type A calls have been previously measured with average source levels of 178 dB re: µP-m (McDonald *et al.* 2001). Blue whale B calls have been reported with average intensities of 180 dB re: µP-m (Thode *et al.* 2000), 186 dB re: µP-m (McDonald *et al.* 2001), and 188 dB re: µP-m (Cummings and Thompson 1971).

The placement of an acoustic recording tag on the back of a calling whale may not be the best way to estimate the source level of vocalizations, as we do not know the precise location or dimensions of the sound source or the impact of bony and air filled structures. We have assumed the sound source location to be the arytenoids, however the propagation of sound through the whale is likely complex as it encounters and reflects off air spaces (lungs, laryngeal sac) and bones (skull, vertebrae), each influencing the received level with its own acoustic transmission properties. If in fact the source is not at a specific point (the arytenoids), but is dispersed (the entire lung acting as a resonator), then the source dimensions would be large and we would be measuring sound within the near-field. Blue whale vocalizations are thought to be omni-directional, however, (Aroyan *et al.* 2000, Bass and Clark 2003), such that the choice of tag location on the whale should not be affected by the whale's transmission of sound in a particular direction. Without an independent measure of the source level of calls recorded on acoustic tags, the effect of such close placement to the source cannot be known. For this reason, received levels at the tag and the inferred source level have been presented under the assumption of spherical spreading from an arytenoids source, including the removal of 1 dB to 4 dB in additive surface reflection (Lloyd Mirror Effect). The actual source level will likely be between these values.

Review of Call Production Mechanism

A theoretical model of blue whale sound production is presented in Aroyan *et al.* (2000). The model suggests that the frequency, intensity, and duration for B call production require such a large air volume that the whale may be using changes in depth to move the required air volume over the arytenoids. In their example, a whale producing a B call with a fundamental frequency of 17 Hz, 19 sec duration, and an source level of 187 dB re μPa-m, would require a flow volume of 800 L to 1100 L without resonance. They suggest that it is not reasonable for a blue whale to move or store such large quantities of air without the aid of a compression system and a change in pressure to facilitate the production of a continuous tone. According to their model, the maximum volume of air that a blue whale can move during a dive from the surface to lung collapse depth at 90 m is 650 L to 700 L, therefore, resonance must be an additional factor in the production of such a loud, long duration signal. The model presented in Aroyan *et al.* (2000) suggests that singing whales would maintain an undulating dive profile as they move from deep to shallow depth (or vice versa) to move the air required for each B call.

While this model was developed with only the knowledge of blue whale song call characters, data on the dive characteristics during production of single B calls, as well the song call depths presented by Thode *et al.* (2001), suggest the theory of an undulating dive profile may be incorrect. Long duration, low frequency, high intensity B calls, even produced singly, should be subject to the same physical limitations; however, we found no significant changes in depth during call production (less than 1 m upward for A calls, and 1.5 m downward for B calls). The observations of singly produced B calls presented here are several dB less intense (176 dB re μP-m) than the most intense song calls reported in the literature (188 dB re μP-m). They require only half of the total air volume and therefore eliminate the theoretical need to create a pressure differential to aid in the movement of air. An air volume of 380 L (the estimated volume necessary to produce the single B calls observed on June 30, 2002) is potentially moved across the arytenoids at depths of 20 m from air stored in the lungs, without changing depth. It is instructive to note that it is possible for a blue whale to produce this type of long-duration, high-intensity sound while maintaining a nearly constant depth. While it is possible for two separate mechanisms to exist for the production of the song and single B call, this begs the question: Why would blue whales have different mechanism for producing the same call depending on the intensity and behavioral context of the signal? If the signal carries some information of the mechanism of sound production, then two mechanisms may exist to transmit different types of information. The other possibility is that the mechanism is in fact the same for both types of B calls and that mechanism does not involve changes in depth. Additional information on the source level of both forms of B call, as well as detailed dive descriptions for singing whales, will be necessary before we can determine if more than one call production mechanism exists.

Conclusions

Understanding and interpreting blue whale calling requires finding patterns in the occurrence of different call types, with their variable frequency, duration, and amplitude characteristics, as well as their associated non-acoustic behaviors. Acoustic recording tags and genetic sampling, paired with acoustic monitoring with sonobuoys and surface behavioral observations, have provided the opportunity to increase our knowledge of the behavioral patterns exhibited within categories of calling whales. It appears likely that singing and single A and/or B callers are male. These calls, particularly song, may be involved in reproduction, as for singing humpback and fin whales. Both sexes produce the more variable type D calls and this call type appears to be associated with feeding and social interactions. Knowledge of non-acoustic behaviors associated with particular blue whale call types should aid in the interpretation of long-term acoustic data sets. Further studies on the behavior of calling whales in different environmental contexts, in addition to comparisons of the relative seasonality and geographic distribution of these various call types will also help to define how acoustics can be most appropriately applied to monitoring blue whale populations.

Tables and Figures

Table 2.1. Tag deployments on blue whales in 2002-2004. Locations are in degrees and decimal minutes. Regional designations are defined as Southern California (SC) from Point Conception and the United States/ Mexico border, Central California (CC) from Bodega Bay to Point Conception, and Mexico (MX) near Isla San Jose, Mexico. Tag deployments shown in bold italics included calls.

Date	Start Time (PDT)	Tag Type	Latitude (N)	Longitude (W)	Region	Attach duration (hrs)
6/23/02	***11:19***	***dTag***	***34 08.01***	***119 53.21***	***SC***	***1.16***
6/24/02	12:34	dTag	34 08.34	119 56.11	SC	7.28
6/26/02	9:03	Bprobe	34 06.85	120 04.25	SC	2.85
6/27/02	7:27	Bprobe	34 06.64	120 05.53	SC	0.20
6/27/02	*10:49*	*Bprobe*	*34 06.92*	*120 03.17*	*SC*	*1.48*
6/30/02	***15:49***	***Bprobe***	***32 47.10***	***117 22.63***	***SC***	***17.50***
9/16/02	12:14	Crittercam	36 46.59	121 57.02	CC	1.10
9/21/02	***11:00***	***Crittercam***	***34 08.27***	***119 51.50***	***SC***	***0.25***
9/24/02	12:01	Crittercam	34 07.81	119 46.37	SC	0.28
7/24/03	15:45	Bprobe	33 29.81	119 35.80	SC	0.88
8/22/03	12:59	Bprobe	32 48.86	119 22.53	SC	0.38
8/22/03	15:48	Bprobe	32 48.68	119 22.50	SC	0.78
9/24/03	9:55	Bprobe	36 43.65	121 59.10	CC	1.20
9/26/03	11:06	Bprobe	36 46.59	121 57.00	CC	0.23
9/26/03	***11:35***	***Bprobe***	***36 46.80***	***121 58.10***	***CC***	***3.35***
9/26/03	15:14	Bprobe	36 41.52	122 01.69	CC	1.52
9/28/03	***13:43***	***Bprobe***	***36 44.52***	***121 58.70***	***CC***	***3.62***
9/30/03	15:45	Bprobe	36 33.54	121 58.65	CC	0.77
3/4/04	9:57	Bprobe	25 08.43	118 41.37	MX	1.47
3/4/04	4:09	Bprobe	25 07.89	118 41.94	MX	1.18
3/5/04	10:11	Bprobe	25 08.51	118 41.46	MX	0.85
7/20/04	14:17	Bprobe	34 07.31	120 03.25	SC	0.70
7/21/04	13:09	Bprobe	34 06.74	120 04.01	SC	0.90
7/26/04	12:46	Bprobe	36 43.23	121 59.18	CC	0.30
7/26/04	16:54	Bprobe	36 51.52	122 09.23	CC	2.80
7/28/04	***9:45***	***Bprobe***	***36 49.10***	***121 58.5***	***CC***	***3.30***
9/28/04	18:27	Bprobe	38 04.41	123 21.54	CC	1.12

Table 2.2. Tracking information for singing blue whales described in this study. Behavior was determined through the evaluation of surface behavior. Group size is defined as the number of whales acting in a coordinated fashion, such that they are directly associated. All singing whales were tracked within the Southern California Bight between Point Conception and the U.S./ Mexico border.

Date	Latitude (N)	Longitude (W)	Start Time (PST)	Monitoring Time (hrs)	Sex	Group Size	Behavior	Speed (km/h)	Direction
10/15/97	33 07.2'	119 54.0'	16:52	4.2	M	1	Traveling	5	W
10/18/00*	32 01.2'	119 41.4'	11:12	8.0	M	1	Traveling	7.4	N
8/24/01	33 26.4'	119 24.0'	12:50	2.0	M	1	Traveling	3.7	N
8/28/01[‡]	32 37.8'	119 08.5'	13:05	0.8	-	1	Traveling	9.3	NW
11/3/02	32 39.6'	119 10.2'	13:35	3.0	M	1	Traveling	7.5	SW

[†] From McDonald *et al* (2001).

* Photo of tracked whale matched to a whale photographed in the Costa Rica Dome, with coincident sloughed skin sample used for the identification of sex as described in Gendron and Mesnick (2001).

[‡] A skin sample was not obtained from this animal. It is included here for comparison of behavior with other singing whales.

Table 2.3. Tagged single A and/or B calling and D calling whales described in this study. Region “SCB” is Southern California Bight; “MB” is Monterey Bay. Group size equals the number of whales acting in a coordinated fashion, such that they are directly associated. Behavior includes surface behaviors and feeding was only ascribed when vertical lunges were evident in the dive profile. Calling depth, tilt and roll angles represent mean values (presented with one standard deviation) among calls measured from the BProbe auxiliary sensors. Body position is defined by tilt (0^0 = horizontal) and roll (0^0 = upright).

Type of Calling	Date	Region	Sex	Group Size	Behavior	Call Depth (m)	Tilt (deg)	Roll (deg)
Single AB[†]	6/23/02	SCB	M	2	Traveling	20.4 (2.0)	-	-
Single AB	6/30/02	SCB	M	2	Feeding, milling	18.3 (3.3)	-	-
Single A[†]	9/21/02	SCB	M	3	Milling	NA	-	-
D AM/FM variants	9/26/03	MB	M	1	Feeding	20.9 (5.0)	1.5 (5.9)	0.9 (2.2)
D	9/28/03	MB	F	2	Feeding	12.2 (3.8)	-1.3 (12.6)	-3.6 (10.3)
D[*]	7/28/04	MB	-	2	Feeding, milling	7.8 (8.7)	2.0 (8.3)	-1.9 (3.9)

[†] DTag and Crittercam deployments preventing identification of the calling whale due to lack of hydrophone calibration.

[*] A skin sample was not obtained from this animal.

Table 2.4. Call characteristics of blue whales tracked in this study, presented as mean with one standard deviation in parentheses. Call frequencies were measured from spectrogram displays (1 s FFT, 80% overlap, Hanning window) and inter-call interval is measured from the onset of one call to the onset of the next. D and highly variable call intervals were measured between successive calls, with no regard to their assignment as D or variable. Received levels (RL) were measured from calibrated BProbe recordings between 10 Hz and 110 Hz, and source level (SL) estimated assuming spherical spreading from the arytenoids to the hydrophone position, including the correction for the additive water surface reflection as described in the text. See discussion on estimating source levels from tags for cautionary points in interpreting these values. We do not present received or source levels for song calls because of the large variation in received level between sonobuoys. Source level was not estimated for the whales tagged on 9/28/03 and 7/28/04 because it is likely both whales in the pair were calling, therefore making the distinction between the tagged whale's calls and that of its pair difficult.

* A-B call intervals could not be accurately measured because of the presence of A calls of similar amplitude from other whales, preventing identification of A calls from the focal animal.

Type	Date	Call	N	Frequency Start (Hz)	Frequency End (Hz)	Call Duration (s)	Intercall Interval (s) A-B	Intercall Interval (s) B-A	Pulses (A)/ Harmonics (B/D)	RL (dB)	SL (dB re: uPa-m)
Song*	8/24/01	B	16	52.8 (0.9)	46.8 (0.8)	17.7 (1.5)		[B-B] 45.1 (6.3)	3-6		
Song	8/28/01	A	9	89.5 (3.9)	86.0 (3.1)	14.2 (S3.1)	48.5 (3.9)	112.4 (46.3)	16-21		
		B	14	52.7 (0.9)	45.3 (0.4)	16.0 (0.5)			4		
Song	11/3/02	A	15	90.9 (1.5)	86.5 (1.2)	16.3 (1.4)	49.1 (4.7)	111.5 (48.1)	19-23		
		B	16	52.8 (0.5)	47.2 (0.6)	16.4 (0.4)			5-11		
Singular AB	6/23/02	A	1	89.5	85.3	15.1	45.7	[B-B] 1294.8 (911)			
		B	3	50.8 (0.3)	45.2 (0.1)	15.9 (0.9)			3		
Singular AB	6/30/02	A only	14	87.3 (1.2)	85.0 (1.2)	15.2 (2.2)			17-23	159.4 (2.9)	172.6 (2.9)
		A pair	11	87.7 (1.4)	85.1 (0.7)	17.8 (2.0)	48.5 (0.0)	1261 (690)	20-26	158.7 (4.1)	171.8 (4.1)
		B pair	13	50.8 (0.9)	45.9 (0.3)	16.0 (0.8)			3-9	163.4 (3.2)	177.0 (3.3)
D	9/26/03	AM/ FM	10	45.4 (7.6)	45.0 (9.1)	2.2 (0.8)	14 (11)		1-6	171.1 (2.6)	180.2 (5.3)
		D	12	70.6 (15.7)	34.8 (10.7)	2.7 (0.9)			2-5	172.8 (2.6)	188.6 (9.5)
D	9/28/03	D	5	77.2 (17.7)	43.7 (12.8)	0.9 (0.5)	1656 (379)		1-2	168.7 (7.3)	NA
D	7/28/04	D	39	79.3 (14.4)	39.5 (9.3)	1.5 (0.5)	-		1-2	167.8 (3.5)	NA

Table 2.5. Summary of behavioral correlates for each call type. “Other calls” refers to the presence of additional calls heard from the focal animal. Coordination “within” refers to observed organization within the group, while “between” is observed coordination between the focal animal and others who do not appear to be directly associated with the focal animal. The number in parentheses in N is the number of known sex individuals producing that call type. Function has been assessed based on our observation presented in this paper and the concordance with observations presented in other published reports of calling whale behavior.

	Call Type			
	Song AB	**Singular A/B**	**D**	**HV**
N	5 (4)	3 (1)	(3)	(1)
Sex	Male	Male	Male & Female	Male
Behavior	Traveling	Feeding, Traveling, Milling	Feeding	Feeding
Group Size	1	2-3	1+	1
Other Calls?	No	No	AM/FM	D
Coordination Within/Between	No/No	Yes/?	Yes/?	No/?
Function	Reproduction	Reproduction/ Territory defense?	Social/Contact (food associated)	Social/ Aggression?

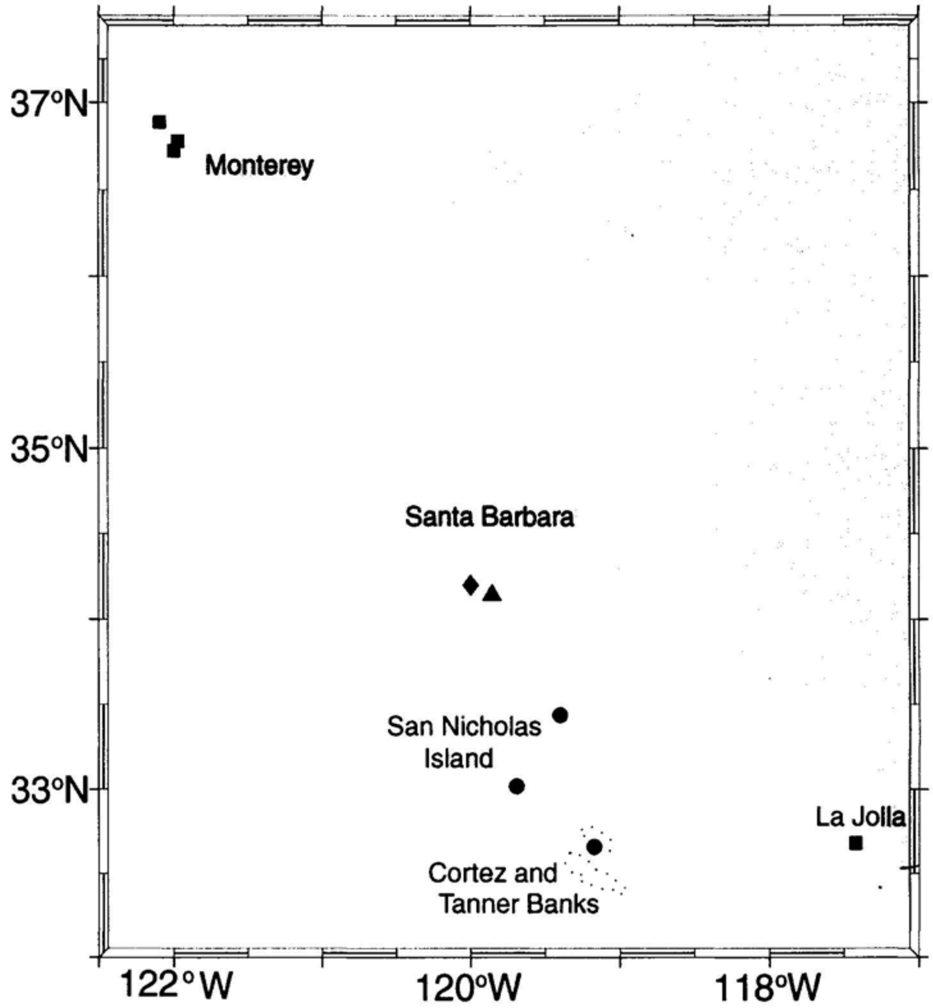

Figure 2.1. Blue whale study area off central and southern California. Symbols indicate the position of a tag deployment which recorded calls (■ = BProbe, ♦ = Crittercam, and ▲ = DTag), or the location of a skin sample of a calling whale (●).

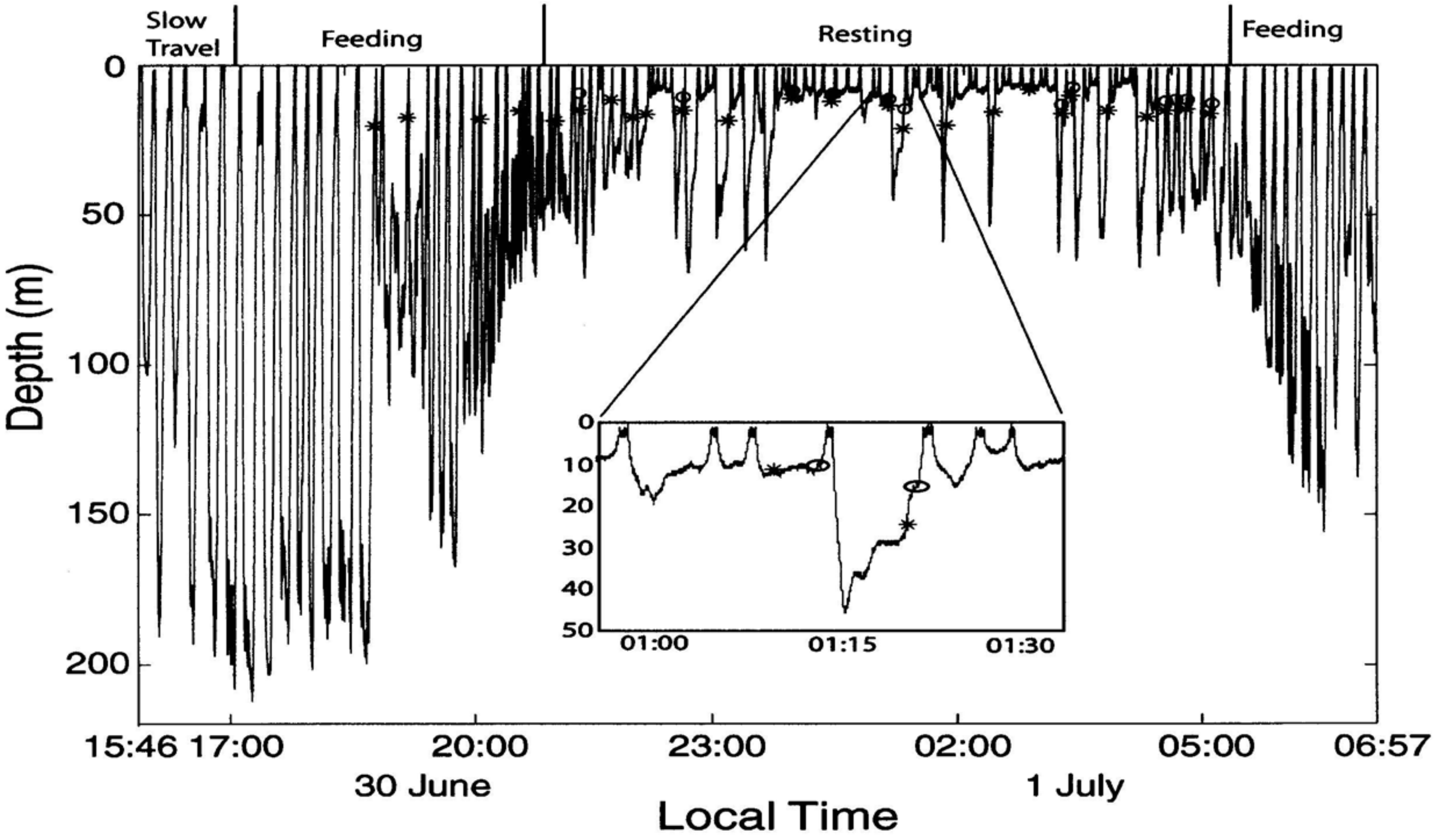

Figure 2.2. Dive profile of calling whale on June 30, 2002 tagged near La Jolla, CA. The depth and time at which A (*) and B (○) calls were received at the tag are indicated. The tagged whale's general behavior is annotated along the upper axis. Periods of feeding track the vertical migration of the whale's euphausiid prey and are evidenced by vertical lunges at depth (Croll *et al.* 1998). The period between sunset and sunrise is highlighted with grey shading. The inset shows detail of two dives including A and B calls. The tagged whale was male and paired with a pregnant female.

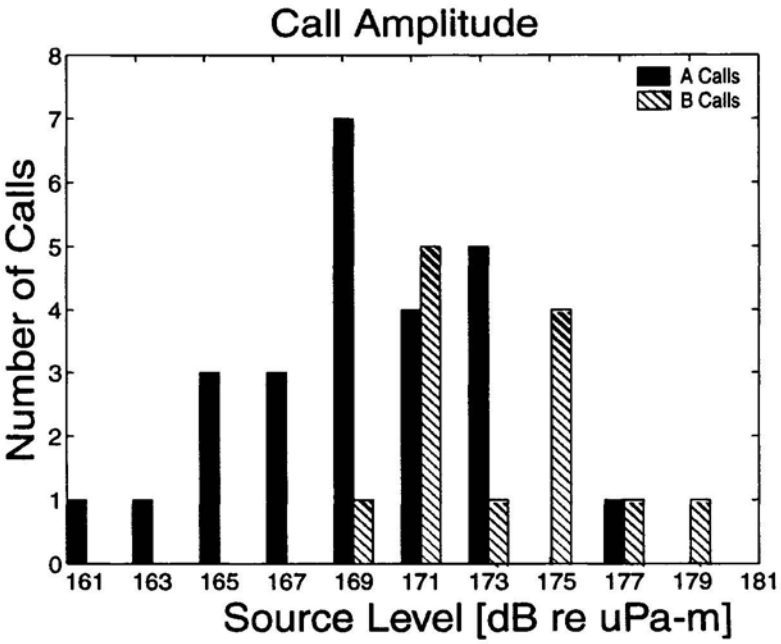

Figure 2.3. June 30, 2002 source level estimates for each call type estimated from received levels recorded on the tag including spherical spreading losses and Lloyd mirror interference.

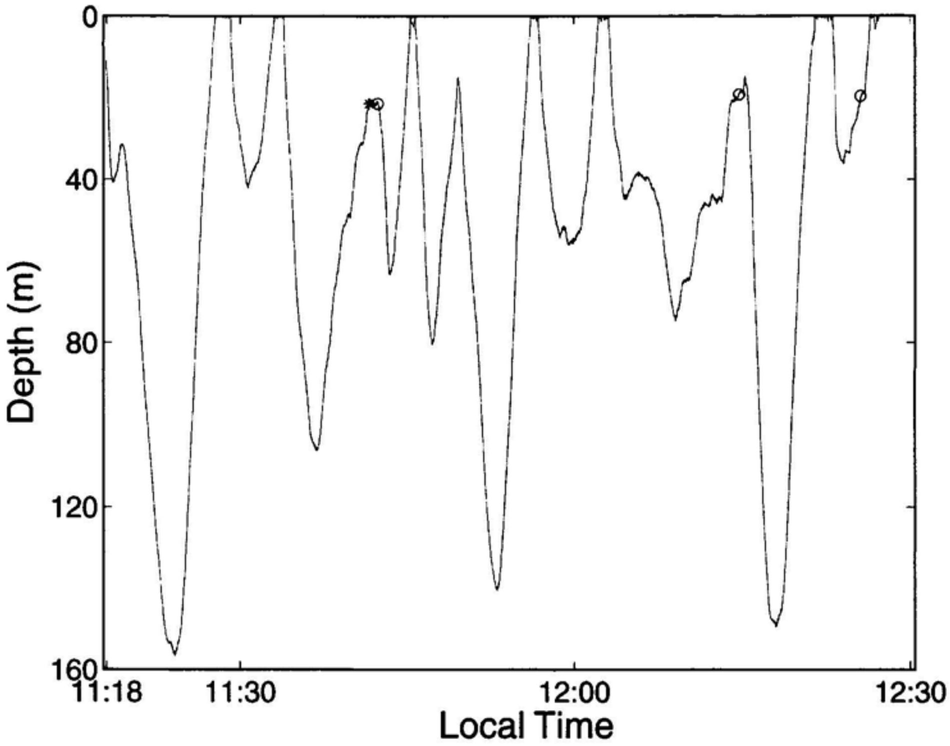

Figure 2.4. Dive profile for calling whale tagged on June 24, 2002, in the Santa Barbara Channel. The depth and time at which A (*) and B (o) calls were produced are marked. The tagged whale was male, and was paired with a female blue whale.

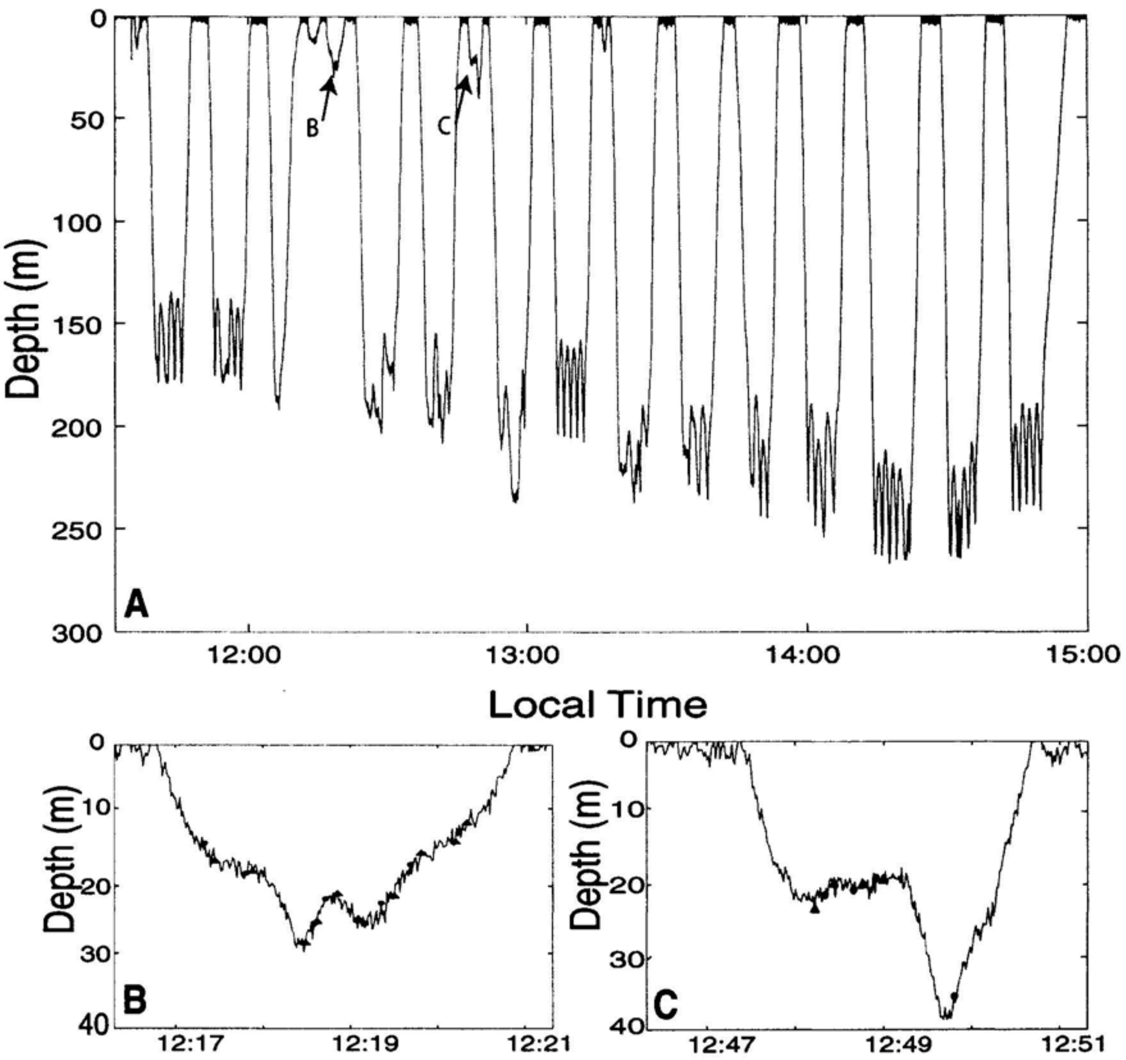

Figure 2.5. Dive profile for tagged D and variable calling whale on September 26, 2003 in Monterey Bay. A) Overall dive profile indicating vertical lunging feeding behavior, punctuated by two anomalously shorter, shallower dives containing calls (labeled B and C corresponding to panels below). B) and C) provide depth and timing of D calls (▲) and highly variable AM and FM calls (●).

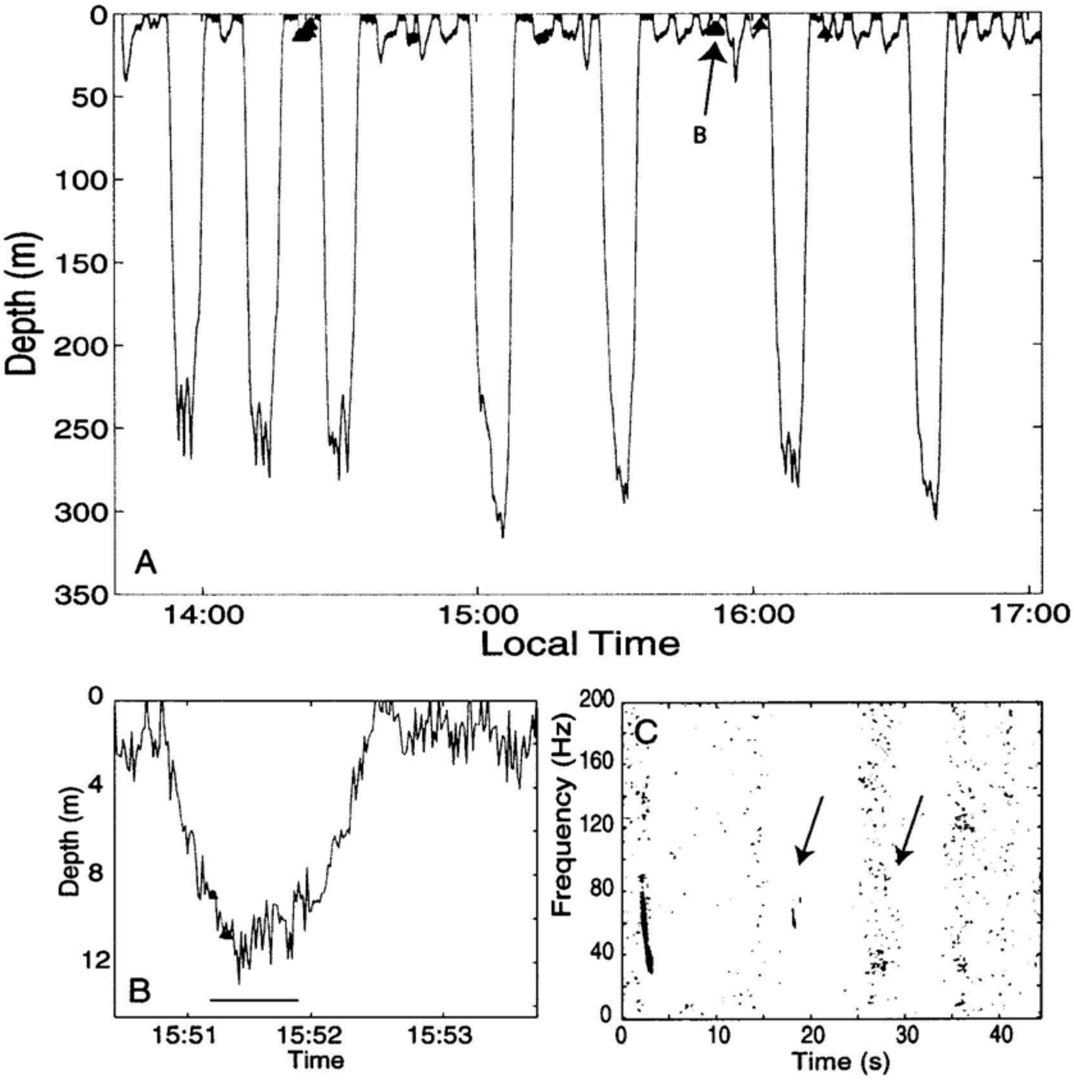

Figure 2.6. Dive profile for tagged whale of pair observed September 28, 2003 in Monterey Bay. A) Overall dive profile of tagged female with times of medium and high SNR D calls noted by ▲. One calling dive is shown in greater detail (B) in which there are likely counter-calls between the whales in the pair. High and medium SNR calls are noted as ▲, and the horizontal line indicates the time period shown in panel C. C) Spectrogram showing counter-calls heard during B), with high SNR call likely produced by tagged female, and low SNR calls (indicated by arrows) likely produced by the untagged male in the pair.

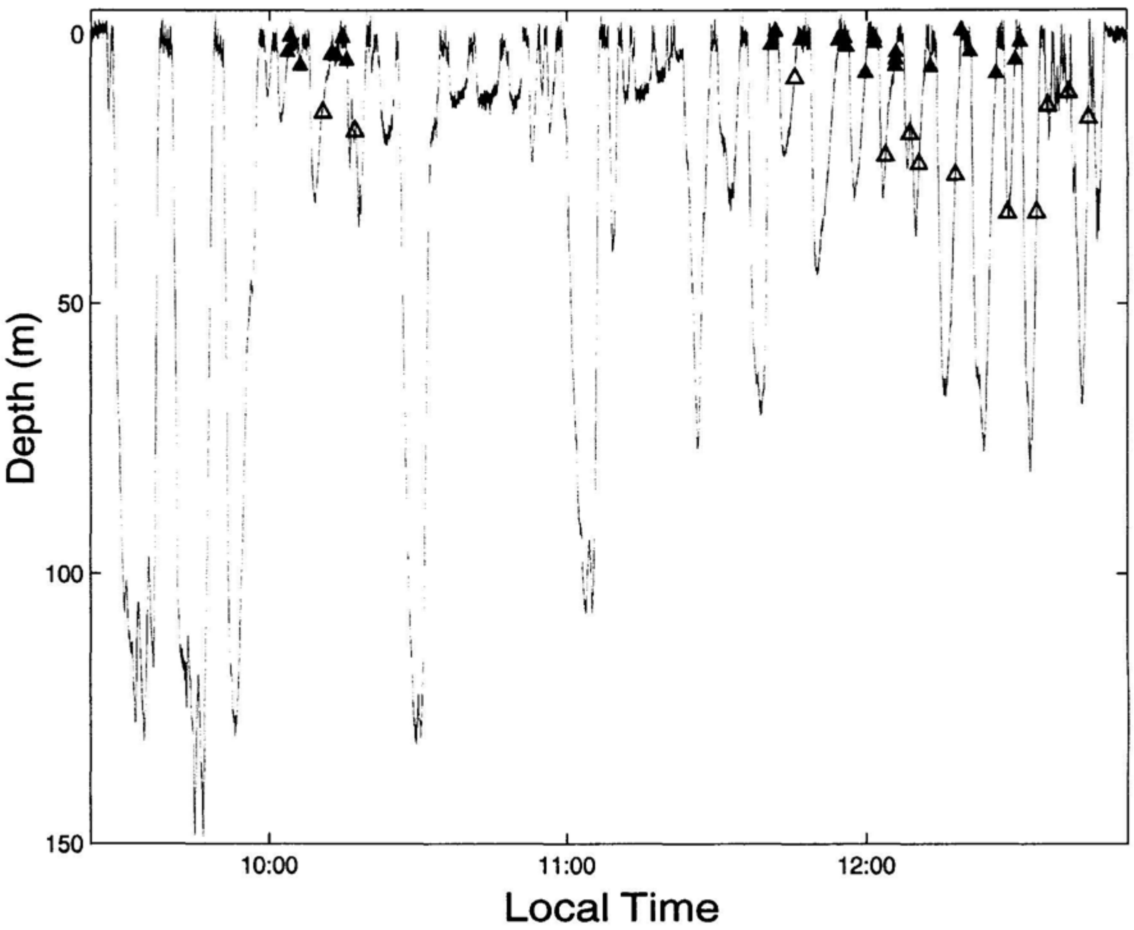

Figure 2.7. Dive profile for tagged whale of a pair observed July 28, 2004 in Monterey Bay. It is likely that calls were produced by both whales in the pair, with those occurring shallow (▲ < 6 m) produced by the non-tagged whale, and those deep (Δ >10 m) by the tagged animal because of the difference in received level and estimated source level.

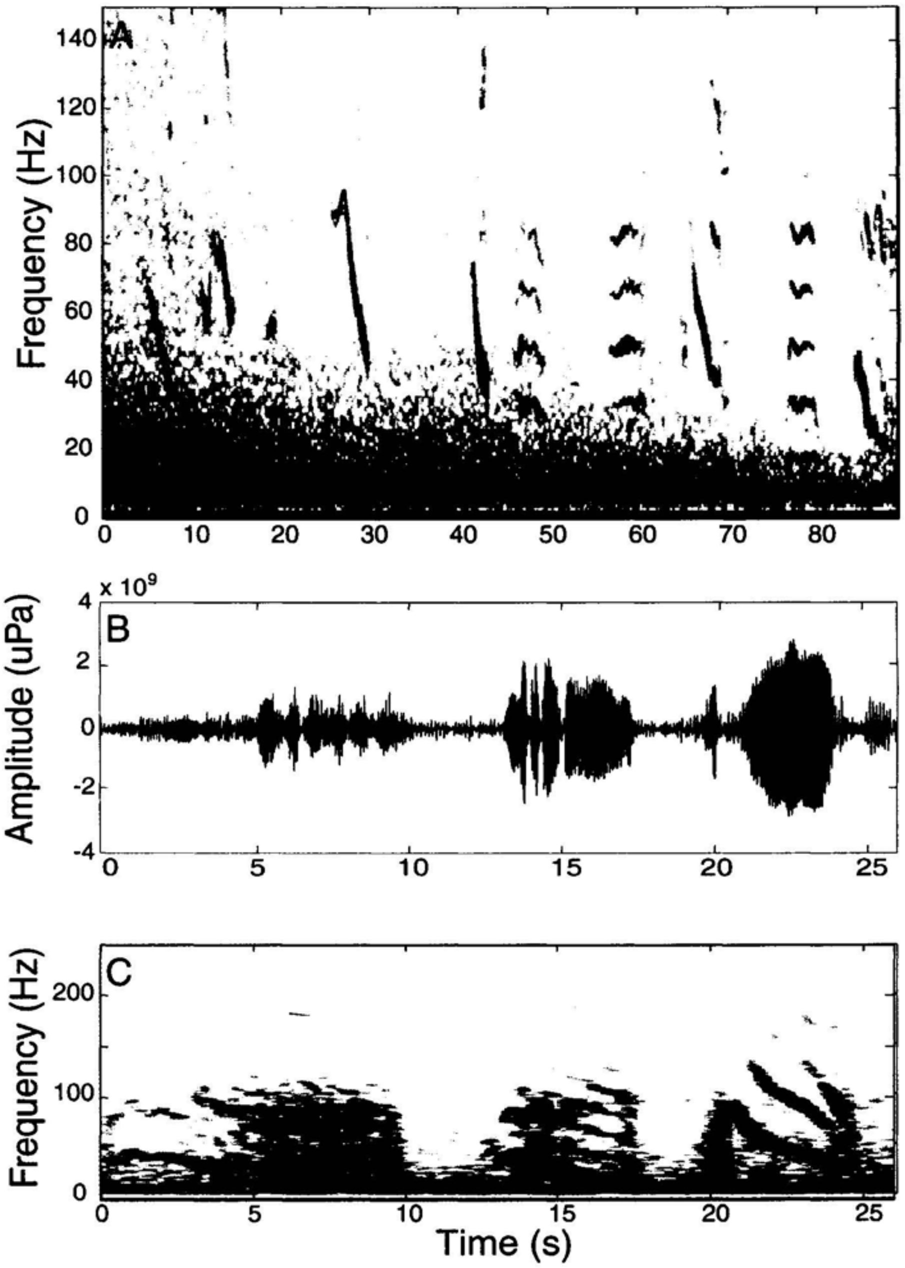

Figure 2.8. A) Spectrogram of D and highly variable tonal calls recorded by the tag on September 26, 2003 in Monterey Bay. D calls are quite variable with different starting and ending frequencies for each call. Tonal calls are frequency modulated, and similar in frequency content to traditional B calls, but are of shorter duration. B) Time series and C) spectrogram of three sequential AM and FM calls from the same tag deployment.

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The text of Chapter Two, in full, has been submitted for publication to the journal Animal Behaviour. The dissertation author was the primary researcher and the co-authors listed in this manuscript supervised the research which forms the basis for this chapter.

CHAPTER 3

Temporal and Spatial Pattern in Blue and Fin Whale Call Occurrence in the Southern California Bight

Abstract

The seasonal, annual, and daily patterns of two blue whale call types (B and D) and fin whale calls were monitored at five sites at Cortez and Tanner Banks from 2000 to 2004. Blue whale B calls were separated into song (i.e., patterned calls) and single calls based on the consistency of call intervals. While patterned series of fin whale calls were evident, automated sorting of calls into patterned and single call categories was not possible due to the variability in call phrasing among animals and seasons. Blue whale D calls were present from April to November, preceding song and single B calls recorded from June to January. The number of days each call type was recorded increased from 2001 to 2003. Fin whale calls were recorded year-round, with a primary peak in call occurrence from August to December. Smaller increases in fin whale calling occurred in winter and spring though the timing of these peaks varied annually. Diel variation in calling was evident with the predominant patterns consisting of increased blue whale song and single B calls at dawn, night and dusk, increased blue whale D calls during the day, and more fin whale calls at dawn. This pattern was annually variable with some years showing no diel variation in calling. Spatial variability in the detection of some call types was evident in the magnitude of the seasonal signal and the presence of a diel calling pattern. Temporal and spatial variability in call occurrence is related to several

factors, including environmental conditions, whale behavior, and acoustic transmission characteristics. Estimating the variability in calling on temporal and spatial scales (i.e., behavioral ecology) is key to the development of tools to use calling to derive indices of abundance.

Introduction

Blue (*Balaenoptera musculus*) and fin (*B. physalus*) whales produce low frequency, stereotypical sounds. Monitoring the occurrence of these calls allows for the description of these species distribution and migrations (eg. Thompson and Friedl 1982, Moore *et al.* 1998, Stafford *et al.* 1998, Watkins *et al.* 2000, Stafford *et al.* 2001, Burtenshaw *et al.* 2004). Using calls to evaluate population size and health has been limited, however, by our lack of understanding of calling behavior. Most previous work on the distribution of vocal blue and fin whales has focused on the presence and geographic distribution of a single call type without attention to the occurrence of other calls in the species repertoire. However, it is not known if these easily detectable call types are a robust indicator of the overall presence and distribution of these species, or if other calls would provide a more accurate assessment of the population in some regions or seasons. If some calls are associated with feeding and others with reproduction as Chapter 2 suggests, it is likely that each call type will have a different pattern of occurrence depending on the availability of prey, the local population density, and at different times of year. Attention to the variability in the occurrence of call types, and on small temporal and spatial scales, will provide a more complete picture of blue and fin whale distribution, habitat use, and the potential development of acoustic monitoring for population assessment.

Northeast Pacific blue whales migrate annually between productive summer feeding grounds off California and lower latitude breeding grounds near Mexico (Calambokidis *et al.* 1990, Reilly and Thayer 1990) and Costa Rica (Mate *et al.* 1999, Stafford *et al.* 2001). This migratory pattern, determined in large part through photo-identification and satellite tracking of whales among regions, is supported by acoustic records of calling throughout the range (Stafford et al. 2001). The seasonality of blue whales in Southern California feeding areas has been described from ship and aerial surveys, indicating that blue whales are present in the highest concentrations in the summer, with dwindling numbers into the fall and winter (Forney and Barlow 1998, Larkman and Veit 1998, Carretta *et al.* 2000). Along the coast of North America, the greatest amount of calling occurs off southern and central California in the summer and fall (Burtenshaw et al. 2004), spatially coincident with the large number of animals visually sighted in this region (Calambokidis and Barlow, 2004).

Little is known about the migration behavior of North Pacific fin whales. They are known to occur in all months off the coast of California (Forney and Barlow 1998, Carretta *et al.* 2000), with increases in abundance during the summer. Year-round acoustic observations from several different locations indicate that fin whales are heard in all months off Oregon, Washington, and British Columbia, with seasonal increases in the fall and winter (Moore *et al.* 1998, Watkins *et al.* 2000), similar to seasonal call patterns off Hawaii (Thompson and Friedl 1982, McDonald and Fox 1999). There have been no long-term studies of fin whale acoustic presence in the Southern California region, with only incidental recordings of their presence in the summer and fall (eg. Clark and Fristrup 1997, Croll *et al.* 2001, McDonald *et al.* 2001).

While studies have described the occurrence of calls over broad spatial scales, little attention has been paid to the small scale variability in blue and fin whale calling. In particular, call types other than those most easily detectable have generally been ignored. From August, 2000 to February, 2004, we collected continuous acoustic data at Cortez and Tanner Banks in the Southern California Bight to evaluate: 1) how the occurrence of calls varies on annual, seasonal, and daily time scales, 2) how call reception varies spatially, and 3) if blue and fin whale calling patterns are related. Recent advances in automatic signal detection have allowed us to examine differences in the patterns of three styles of blue whale calling (song, singular B, and D calls) and fin whale calling. While the overall seasonality of blue and fin whale calls remains stable over the four year time series, annual, daily, and spatial patterns of call reception are evident both within and between species. Our findings underscore the need to understand the ecological role of calling for these species.

Blue and Fin Whale Calls

Blue whales are known to produce at least four different sound types. Type A and B calls (Thompson *et al.* 1996) are long duration (~20 s), low frequency (16 Hz), harmonically rich sounds which can occur together in an alternating series of A and B calls (Rivers 1997, Stafford *et al.* 1998), termed song (McDonald et al., in press) (Figure 3.1a), or as individual calls (Chapter 2). Most acoustic descriptions of blue whale distribution and seasonality are based on A and B calls, while the distinction between song or singular is overlooked. These calls have also been shown to occur most commonly during dusk, night, and dawn (Wiggins *et al.* 2005, Stafford *et al.* 2005). A third call type known as the D call was originally described by Thompson et al. (1996), as a down-sweeping (90 Hz – 25Hz), short duration (1-4 s) call (Figure 3.1b). Finally, a fourth class of highly variable amplitude (AM) and frequency modulated (FM) calls have been observed (Thode *et al.* 2000, Chapter 2). Type A calls and highly variable AM and FM calls were not monitored during this study.

Observations using focal animal tracking and acoustic recording tags (described in Chapter 2) have indicated that song and single A and B calls likely have different behavioral contexts. In summary, song A and B calls are most commonly heard from traveling solitary males, and may be involved in reproduction. Single A and B calls have been recorded from males in pairs and groups engaged in a variety of behaviors including traveling and feeding. Type D calls are heard from both sexes and occur as counter-calls among feeding blue whales and in short sequences from individual whales.

Although capable of producing several low frequency call types, fin whales most commonly produce short duration (~1 s), low frequency down-sweeps (35-18 Hz) (Figure 3.2c). These signals were first identified in the North Atlantic as a fin whale call by Schevill et al. (1964) and have since have been attributed to fin whales worldwide. Some fin whale populations may be distinguished by their song, or consistent patterns in their intercall interval, although no characteristic interval has yet been identified for the eastern North Pacific population (Hatch and Clark 2004). Fin whale songs are produced by males, which may be stationary (Watkins *et al.* 1987, Croll *et al.* 2002) or traveling (McDonald and Fox 1999). Fin whale calls may also occur in call-counter-call sequences among traveling individuals (McDonald *et al.* 1995, Wiggins *et al.* 2004).

Methods

Acoustic Data Collection

Except for the period 5 February to 15 April 2002, 1,215 d (3,120 instrument-d) of continuous acoustic data were recorded at Cortez and Tanner Banks from 20 August, 2000 to 20 February, 2004, using Acoustic Recording Packages (ARPs) and Ocean Bottom Seismometers (OBSs). Recorders were positioned at one to four sites around the banks (Table 3.1). The banks are approximately 180 km west of San Diego, California, in the southern portion of the Southern California Bight (Figure 3.2), and rise to within 100 m of the sea surface. Several species of cetacean, including blue and fin whales feed near the banks. Cruises were conducted every two to six months to service the recorders, consisting of battery and data disk replacement and instrument site changes.

ARPs are bottom-mounted data logging systems with a 16-bit A/D converter, 36 GB of storage capacity, a hydrophone tethered 10m above the seafloor, a release system, ballast weights, and flotation (Wiggins 2003). From August 2000 to June 2002 the hydrophones had an amplified sensitivity of -154 dB re: Vrms/μPa with a low-end roll-off of 5 Hz. In July 2002, the hydrophones were replaced with a lower electronic noise version with a sensitivity of -157 dB re: Vrms/μPa. Data were collected with a sample rate of either 500 or 1000 samples/sec, resulting in an effective bandwidth between 5 and 250 or 5 and 500 Hz respectively. The sample rate was chosen based on the desired deployment duration and instrument recording capacity. The maximum recording duration at 500 Hz sampling rate was 400 d.

During two periods, from June to July 2002, and November, 2003 to February, 2004, Ocean Bottom Seismometers (OBSs) were used while ARPs were removed from the area for hydrophone replacement or for relocation to other regions. Although OBSs were designed for monitoring seismic sounds, they also record the low-frequency sounds of blue and fin whales (McDonald *et al.* 1995). Bottom-mounted OBSs are similar to ARPs; the primary differences between these systems is the reduced maximum sampling rate (128 Hz) of the OBSs, resulting in an effective bandwidth of 1-60 Hz (Sauter *et al.* 1990).

Data Processing

Following instrument retrieval, the acoustic data were downloaded to processing computers and examined for the presence of blue and fin whale calls using the software program *Ishmael* (Mellinger 2002). Initially the data were checked by a human analyst prior to the use of an automatic detection algorithm to record the occurrence of calls. *Ishmael* provides three separate methods of automatic call detection: energy summation, spectrogram correlation, and waveform matched-filtering. Each of these methods was tested for accuracy at detecting blue and fin whale calls using a data-set previously scanned by an analyst. The goal was to minimize the number of missed calls and false detections (incorrect classification).

Spectrogram correlation was found to be the best detection method for blue whale B and fin whale 20 Hz call types with fewer false detections than the energy summation method and fewer missed detections than the matched-filter method. Spectrogram correlation detects calls by cross-correlating a synthetic time-frequency kernel representing a whale call, with the acoustic spectral data. The result is a detection function which indicates the likelihood a matching call is present (Mellinger and Clark

1997, 2000). This detection function must exceed a user specified threshold for a specified period of time before the call is recognized. After detection, a segment of the acoustic data containing the detected call is saved to computer disk. The threshold, the time above threshold (duration the detection function must exceed the threshold), and the detection neighborhood (minimum time between detection events) were iteratively adjusted until the rate of false detection was less than 3%. A trade-off exists between the number of false-detections and the number of missed calls, increasing the missed call rate to approximately 20%. Approximately 1000 detections per month were randomly chosen from each site to verify that the false detection rate remained at or below 3%.

The characteristics of the detection kernel for blue whale and the fin whale calls are shown in Table 3.2. The blue whale B call third harmonic was chosen because its signal-to-noise ratio (SNR) is typically better than the fundamental and other harmonics. The A call was not chosen for analysis because its pulsed character, and generally lower SNR, reduced its detection rate relative to B calls when using either spectrogram correlation or energy summation. Annual shifts in the frequency content of the blue whale B call (J. Hildebrand, personal communication) were accommodated by annually adjusting the kernel. Spectrogram equalization was used to reduce the effect of time-varying ambient noise on call detection rate. Spectrogram equalization is a form of automatic gain control which subtracts the time averaged spectral level in each frequency bin from the spectrogram resulting in more consistent background noise levels through time. This type of signal conditioning is particularly useful for detecting nearly tonal calls, such as blue whale B calls, during periods of high shipping noise.

Blue whale D calls are highly variable in sweep rate and frequency content. These characteristics make it difficult to design a time-frequency kernel which can reliably detect this call type. As an alternative to automatic detection, D calls were picked by an analyst from one randomly chosen day per week at each site throughout the monitoring period. The analyst used Matlab code, written to quickly examine large sections of data and log the time of each call. The total number of days in which D calls were heard per season was extrapolated from the number of monitored days containing calls.

Extraction of Calling Patterns

Following automatic detection of blue whale B and fin whale calls, intercall intervals were computed from the detection times in an effort to separate blue and fin whale song from calls occurring without a consistent temporal pattern (single calls). For the purposes of this paper, song is defined as a sequence of stereotypical calls or phrases occurring in a repeated pattern, similar to the definition of McDonald *et al.* (in press). Conversely, single calls are those occurring irregularly, without a recognizable pattern or as calling among individuals. The interval between each call and all other calls within 200 s was computed to identify consistently occurring intervals representative of song sequences. Song intervals were independently computed by an analyst using a subset of the detections and then compared with the intervals derived automatically. When constant song intervals were identified and confirmed by an analyst, the song intervals were used to sort call detections into song and single categories for evaluation of calling patterns unique to each call type.

The occurrence of each blue and fin whale call type was examined for annual, seasonal, daily, and spatial pattern. The mean daily calling rate, measured as the number of call detections per day, was tested for significant deviations among years, and across simultaneously sampled sites. Mean hourly calling rate was used to test for significant changes in calling among four sun-phases: dawn, day, dusk, and night. Annual, daily, and spatial changes were tested using a non-parametric analysis of variance, the Kruskal-Wallis test. This test was chosen because of the heterogeneity of variances among sampled units. Annual variations in calling rate were tested by pooling data across sites. Data collected at simultaneously sampled sites were combined into a single daily detection rate normalized by the number of contributing sites. The pooled daily calling rates were then tested for significant departures from the median value each year. The start date of each year is offset from 1 January to account for overflow in the blue whale migratory season into the next calendar year. Each year is defined here as 1 March to 28 February. Significant departures from the median values were tested for the direction of the difference using a Multiple Comparison test (Zar 1999).

Differences in calling through the day were examined by sorting calls into dawn, day, dusk, and night bins, the periods of which were derived from the United States Naval Astronomical Application Department for San Diego, California. This sorting procedure is described in more detail in Wiggins *et al*. (2005). The number of calls occurring in each sun-phase per day was normalized by the length of the phase in hours. The daily mean among sun-phases was then subtracted from each phase.

Finally, spatial calling patterns at Cortez and Tanner Banks were examined by sorting detections for each site. Periods for comparison were chosen based on the longest continuous periods within a calling season when more than two instruments were sampling the region. Detection distance is expected to vary among sites due to: 1) the complex bathymetry of the region, 2) variability in average noise levels, and 3) variability of call source levels. These differences in detection distance among sites are not known, and, therefore, no quantitative corrections were applied. Before statistically testing for differences among sites the seasonal changes in call rate were removed from the data by computing the mean number of calls among sites for each day and subtracting that value from the call counts at each site. The mean-adjusted number of calls occurring per day at each site was then statistically tested for annual and daily changes in calling.

Results

The detection of blue and fin whale calls was variable on several temporal and spatial scales. Two blue whale B call intervals were identified through the sorting of call intervals: 48 s for consecutive B calls (BBB), and 128 s for B calls with an interspersed A call (BAB). Song calls were the most common blue whale call type, with an average of 27,582 calls occurring per site per year. The annual call detection rate for other blue whale call types was 12,872 single B calls per site, and 16,573 D calls per site. Patterned sequences of fin whale calls were occasionally present (eg. Figure 3.3); however, patterned call intervals were highly variable among whales and through time, preventing automated separation of single calls from potential patterned segments. We have chosen not to describe these patterned sequences from fin whales as song, as the sequences displayed a high degree of variability both within and between whales. Most patterned phrases were observed by the analyst in winter, though it is not possible to determine if patterned calls may have also been present during periods of high calling in summer and fall. There were on average 137,136 fin whale calls per site annually.

Temporal Variability: Annual, Seasonal, Diel

The average seasonal occurrence for each blue whale call type is shown in Figure 3.4a. Blue whale D calls were initially detected in April and May and continued through November. Blue whale B calls occurred later in the summer and fall, from June to January. Single B calls represent a higher proportion of the total number of B calls detected at the beginning (June-July) and end (November–January) of the calling season. Both song and single B call types peaked in September with a daily detection rate of 409 song calls and 146 single calls.

Fin whale calls were recorded in all months of the year, with peak detection in September and October (Figure 3.4b). The average daily detection rate was 2,000-2,500 calls during this peak. The lowest daily call detection rates occurred in the late winter and spring, with detection rates ranging from approximately 250 calls in early March to 750 calls in April.

Although a seasonal signal is apparent for both species, year-to-year variations in blue and fin whale call detections were also evident (Figure 3.5). The number of days in which blue whale calls were detected increased from one year to the next (Table 3.3); however, there was no significant annual change in the daily call rate for any blue whale call type (Table 3.4). The extended calling season of blue whales from 2001 to 2003 was due to the increasingly early arrival of D calls in the spring and the progressively later departure of B calls in the winter (Figure 3.5a). In contrast, fin whale calls were detected every day of the year (Table 3.3), and daily call rates were variable among years (Table 3.4) with the highest daily call rates occurring in 2002. The seasonality of fin whale calling changed slightly each year with an increase in fin whale call detection between November and January after a relative drop in detections in the late fall. The timing of this winter calling peak shifted annually such that the bi-modal fall and winter seasonal pattern evident in Figure 3.5b is not apparent when all years are pooled (Figure 3.4b). The number and choice of monitoring locations changed from one year to the next (Figure 3.4c), potentially influencing call detections for both species. Sites were not continuously monitored for the entire study, and the overall picture of blue and fin call whale presence described above is an average from the five monitored sites.

The hourly call detection rate was compared among dawn, day, dusk, and night periods for each year of monitoring effort. A diel pattern of calling was evident for some call types in some years (Table 3.6). In general, blue whale D calls were most common during the day, while song and single B calls peaked between dusk and dawn. Fin whale calling was most common at dawn. Strong diel patterns generally persisted for two to five days from June through August, with increasingly longer periods later in the summer and fall. Interspersed between periods with the predominant diel arrangement of calls were times with opposite or no daily pattern.

Spatial Variability

Significant spatial variability in call detection rates was evident indicating preferential use of some areas. Variability among sites was evaluated for two simultaneously monitored periods, from 20 June to 25 October 2001, and 16 April to 4

November 2003. The number of calls detected per day averaged into one week bins is shown in the left column of Figures 3.6-3.9. In 2001, all three sites had the greatest D call detection rate early in July, with decreasing detections through October. Song and single B call detection increased from June through October. During this period, the detection rate of blue whale single B calls was significantly different among sites (Table 3.5), while other blue whale call types did not exhibit significant spatial variability. The significantly low call rates at southeast Tanner Bank (site 2) relative to the other sites (Table 3.5) is primarily due to low detection rate at that site in July and August. Fin whale detection rates varied significantly among sites (Table 3.5) due in part to the duration of the calling peak at each site (Figure 3.7 a-c). Most fin whale calling occurred at north-west Cortez Bank (site 5) throughout the concurrent monitoring period.

Somewhat different from the spatial patterns observed in 2001, all call types showed significant spatial variation in 2003 (Table 3.5). Blue whale D calls were significantly more abundant at southeast Tanner Bank (site 2) than at northeast Cortez Bank (site 5), with very few early season calls at northeast Cortez Bank (site 5) (Figure 3.8a-c). The highest number of blue whale song calls and the greatest proportion of song to single calls occurred at north Tanner Bank (site 1). Fin whale calls were significantly more common at both Tanner Bank sites (sites 1 and 2) than at northeast Cortez Bank (site 5). This difference in fin whale detection is due to the generally lower detection rate and lack of spring peak at Cortez Bank (site 5) (Figure 3.9a-c), representing a shift in fin whale distribution from 2001.

Spatial variability in the diel call patterns described above reveal greater complexity in daily call production rates. The hourly occurrence of calls was computed for each site during the two periods of concurrent monitoring. The hourly occurrence of calls, rather than the summary of calls into sun phase bins, is shown in the right column of Figures 3.6-3.9 to allow for a more detailed examination of the variability in calling among sites and throughout the day. The occurrence of calls in each sun-phase was also computed and tested. In 2001, the daily occurrence of blue whale song and single B calls described above was the same as that observed at sites 2 and 3. Site 5 showed significant changes in calling only between night and day. The occurrence of blue D calls was not significant among sites; however, visual inspection of the hourly occurrence of calls indicates a trend toward increased calling in the morning and late afternoon at all sites. Although the spatially pooled data from 2001 indicated no diel variation in the occurrence of fin whale calls in 2001, site 3 showed significantly higher calling rates at dawn (Figure 3.7d).

The diel call patterns observed from 16 April to 4 November 2003 were quite different from those seen during 2001. The distribution of blue whale song and single calling was not significant for any site among dawn, day, dusk and night periods. The primary difference from 2001 was the relatively high levels of song during the day at the Tanner Bank sites (sites 1 and 2). A significant increase in the occurrence of D calls during the day can also be attributed primarily to the Tanner Banks sites (sites 1 and 2). In contrast to 2001, fin whale calling was significantly different among sun phases at all sites with the highest detections occurring at dawn (Table 3.6). Hourly counts for each site (Figure 3.9d-f) indicate calling occurred in two peaks, one from dusk to midnight, and the other from early morning through dawn.

Discussion

Blue and fin whale calling rates at Cortez and Tanner Banks are variable on several temporal and spatial scales. Blue whales calls were heard in this area predominantly from June to November, with slight variations in the timing of the arrival and departure of some call types. Fin whales were heard year-round, with a peak in call production during fall, coincident with the peak of blue whale B call production. However, the patterns of blue and fin whales calling are more variable than this summary suggests. On the largest scales, attention to the occurrence of different blue whale calls indicate a longer seasonal presence than has been observed from visual surveys (Forney and Barlow 1998, Carretta *et al.* 2000) or by monitoring of B calling alone (Burtenshaw *et al.* 2004, Wiggins *et al.* 2005). Annual variability in the timing and magnitude of winter and spring fin whale call peaks may indicate plasticity in the migratory patterns of this species. On smaller scales, calling rates for all blue and fin whale call types are variable throughout the day and these diel patterns change annually. In addition, significant variability in the distribution of calling whales throughout this relatively small study area has implications for the development of habitat models or the derivation of estimates of abundance by impacting the perceived pattern of calling through choice of a single monitoring site. The observed patterns in blue and fin whale calling may depend on many environmental and behavioral factors, including acoustic propagation, oceanographic productivity and prey availability, and the behaviors of each species including the potential interactions between them.

Large Scale Patterns: Blue Whale Seasonality and Abundance

Our observations of blue whale calls at Cortez and Tanner Banks generally agree with the patterns of calling observed by previous studies, with two notable exceptions. First, by monitoring the presence of D calls, we observed an earlier arrival of blue whales into the Bight than was previously documented. Visual surveys indicate few to no whales in winter and spring (Forney and Barlow 1998, Larkman and Veit 1998, Carretta *et al.* 2000), and acoustic surveys of B calls show the arrival of blue whales in May or June (Burtenshaw *et al.* 2004, this study). The behavioral and environmental correlates of D call production described in Chapter 2 indicate that D calls are produced by and among feeding whales. This early season detection of D calls in the long-term acoustic records at Cortez and Tanner Banks probably indicate the arrival of feeding whales in the region, two to three months prior to the production of song and single B calls. Monitoring D calls throughout the blue whales' range may yield seasonal or geographic patterns of use not previously understood. The addition of D calls to acoustic surveys will be necessary to fully describe blue whale presence and evaluate productive habitat.

Second, by separating B calls into song and single categories, we observed that relatively fewer song calls occur in the beginning and end of the season. This finding will have implications for using B calls for population abundance estimates. Because whales producing single B calls make fewer calls than singing whales per unit time, the high proportion of single calls at the edges of the calling season suggest more whales are calling during those periods than would be accounted for if all calls were assumed to be part of song. The rate of single call production and the proportion of whales producing single calls will need to be accounted for when developing acoustic census methods based on this call type.

Large Scale Patterns: Fin Whale Migration

The seasonal occurrence of fin whale calls in the Southern California Bight has not been previously reported. Fin whale calls were heard year-round at Cortez and Tanner Banks with a consistent peak in calling from August to October. Calling also increased slightly in two peaks in the winter and spring, although the timing of these peaks shifted up to two months annually. The year-round occurrence of fin whales in the Bight is in agreement with visual surveys for fin whales, indicating higher abundance in the summer and lower numbers in the winter (Forney and Barlow 1998, Carretta *et al.* 2000). Fin whale calls have been observed elsewhere throughout the North Pacific (Northrop *et al.* 1967, Thompson and Friedl 1982, Moore *et al.* 1998, Watkins *et al.* 2000), with some sites indicating year-round acoustic presence.

Fin whales are known to use the same 20 Hz call type both in patterned sequences (Watkins *et al.* 1987, Clark *et al.* 2002, Hatch and Clark 2004), and as counter-calls among individuals (Thompson and Friedl 1982, McDonald *et al.* 1995, Wiggins *et al.* 2004). Evaluation of the acoustic data by an analyst indicated that while patterned phrases and counter-calls among individuals were both present year-round, counter-calls were more prevalent in the summer and patterned sequences were easily identified only in the winter. Although the large number of calls may have obscured some patterned phrases during summer and fall call peaks, the general occurrence of patterned calling in the winter agrees with other studies of fin whale calling in the North Pacific (Thompson and Friedl 1982, Watkins *et al.* 2000). In particular, patterned calls are observed from California (this study) to Hawaii in the winter (Thompson and Friedl 1982, McDonald and Fox 1999). Furthermore, it is apparent that there is some shift of patterned calls from these southern locations to locations near Oregon, Washington, British Columbia, and the Aleutian Islands through the summer and fall (Watkins *et al.* 2000), though it is not possible to determine if this movement represents a single dispersed population, or smaller populations with similar migratory movements. The recovery of fin whales marked in winter in Southern California off Oregon, British Columbia, and the Gulf of Alaska in summer supports this migration (Rice 1974). However, because calls are heard year-round, we cannot discount the possibility of a resident fin whale population within the Southern California region.

The summer/fall peak in fin whale calling at Cortez and Tanner Banks complicates the simple model of fin whale migration. The fall peak is thought to consist primarily of call-counter-calls, or calls occurring with irregular intervals, a call type often associated with feeding, socializing, and transiting animals (Watkins 1981, McDonald *et al.* 1995, Wiggins *et al.* 2004). Fin whales producing irregular call intervals have been observed throughout the North Pacific. Call-counter-calls occur year-round off British Columbia and the Emperor Seamounts, but show seasonal presence off Oregon, Washington, the Aleutian Islands (Moore *et al.* 1998), and Hawaii (Thompson and Friedl 1982). Fall peaks near Hawaii, and from California to Washington may be linked to the spring and summer peak near the Aleutians, suggesting a migratory path opposite to that described from patterned calls. Quantitative description of fin whale call intervals, in addition to genetic studies of population identity will be required before this complicated pattern of fin whale movements and seasonal presence at Cortez and Tanner Banks can be adequately addressed.

Interactions Between Blue and Fin Whales

In general, the distribution patterns of blue and fin whales are very similar. Their distribution does differ in some regions, such as the Antarctic, where blue whales are found close to the ice edge and fin whales further to the north (Mackintoch 1966, Širović *et al.* in prep). Blue whales are also abundant in the eastern tropical Pacific (ETP), where fin whales are quite rare (Wade and Gerrodette 1993). This study, and other reports of the abundance and distribution of blue and fin whales, have shown that both species occur in the Southern California Bight. In particular, both species are commonly found at Cortez and Tanner Banks. However, there are some subtle differences in the patterns of calling exhibited by each species which may indicate interactions between them. Our observations indicate that on average, fin whale calls are five times more abundant than blue whale calls, such that on nearly every day of the year there are more fin whale calls than blue whale calls at all sites. Recent estimates of blue and fin whale abundance off California, Oregon, and Washington (Barlow 2003, Calambokidis and Barlow 2004) indicate that while seasonally variable, the fin whale population is generally only approximately 10% larger than the blue whale population. While it is not possible to translate total call abundance to animal abundance from this dataset, this may indicate that fin whales are generally more common at Cortez and Tanner Banks than blue whales, or that fin whales are far more vocally active than blue whales.

Seasonally, as the peak in blue whale calls declines late in the fall, a winter peak in fin whale calling commences (Figure 3.4). The opposite pattern occurs in the spring with the decline in fin whale calling as blue whale D calls become abundant (Figures 3.4, 3.8, 3.9). It is clear that blue and fin whales do not follow the same migratory routes in the northeast Pacific. While the pattern of increasing and decreasing fin whale calling coincident with the departure and arrival of blue whale calling may represent avoidance by fin whales, they may also be indicative of independent migratory behaviors for each species.

Because it was not possible to locate calling whales during this study we cannot address the fine scale differences in blue and fin whale distribution. Among simultaneously monitored sites there is occasionally large overlap in blue and fin whale calling suggesting that there are adequate food resources within the local region to support aggregations of both species. During other periods there is little overlap, in particular at site 5 in 2003 (Figures 3.8 and 3.9). Some of the overlap may be explained through variation in detection distance among call types and sites. For example, large increases in blue whale song calling relative to D calls and fin whale calls may indicate longer-range propagation of this call type from the adjacent deep basins. In general blue and fin whales are co-occurring in this region during the summer and fall, with little evidence of interaction among the species during that time. Interactions between these species are important to define not only to understand the ecology of each species, but also to determine if their calling rates are related, complicating the use of calls for assessing population abundance.

Acoustic Propagation

The patterns of blue and fin whale calling observed here are dependant on physical (detection distance) and ecological (prey biomass, variability in migratory paths) factors. Although detection distance was not measured as part of this study, its potential influence must be acknowledged before other oceanographic and behavioral contributions to small scale calling patterns can be fully explored. Detection distance is dependant on four factors: 1) bathymetry, 2) transmission loss, 3) masking by ambient noise, and 4) the amplitude of the sounds produced. Cortez and Tanner Banks are wide, flat, shallow zones (100-200 m) along the western escarpment of the Santa Rosa-Cortes Ridge. They lie within a region of complex bathymetry, including the San Nicolas Basin to the east and a gradual deepening toward the Patton Escarpment to the west (Figure 3.2). Interaction of sound with the shallow and complex bathymetry can impact the detection range at each site. In particular, reflection of sound off the parallel Banks and inefficient transmission in very shallow water has likely reduced the detection distance at site 3 relative to the other sites. It is likely that the detection distances at sites 1, 2, 4 and 5 are greater as these sites are adjacent to deep basins, although they may also be affected by local shadowing of sound by the Banks and other bathymetric features.

Neither transmission loss nor ambient noise levels were explicitly examined as part of this study. However, some reports from the Cortez and Tanner Bank region are available providing insight into the impact of these factors. In deep water, acoustic intensity decreases with the square of distance. At Cortez and Tanner Banks, spherical spreading should theoretically apply only for the first 200-300m until the sound has traveled a distance roughly equal to the water depth. Beyond that range, transmission loss often becomes cylindrical, with amplitude decreasing with the cube of range. These simple relationships are complicated by the shape of the sound speed profile (determined by temperature, salinity, and pressure), and interaction with shallow bathymetry. Sound speed profiles (SSP) collected at Cortez and Tanner Banks and in nearby waters show a consistent downward refraction of acoustic rays (Richardson *et al.* 1995, Zoksimovski 2004). While refraction away from the surface leads to reduced detection distance for near-surface hydrophones, bottom-mounted sensors, like those used in this study, may actually experience an increase in detection distance as rays are reflected between the negative gradient in the sound speed profile and the seafloor. In addition, particularly steep sound speed gradients may result in direct path arrival of sound at distances between 4 km and 8 km depending on the depth of the source relative to the depth of the SSP gradient, resulting in transmission losses up to 15dB less than that predicted by spherical spreading (Zoksimovski 2004). The experiments of Zoksimovski were conducted at higher frequencies than those of blue and fin whale calls preventing specific conclusions about the magnitude of transmission loss on blue and fin whale signals. However, daily changes in sound speed at this site do indicate that detection distance will be impacted over short time scales (Zoksimovski 2004).

Seasonal and diel patterns in ambient noise have been examined at nearby San Clemente Island. Wenz (1961) found little variation in low-frequency ambient noise seasonally, with the greatest increases due to storms predominantly occurring during the winter months. Additionally, that study found diel variability in noise levels with the highest noise occurring at local midnight. Gradual increases in shipping since the 1960s have led to an overall increase in ambient noise levels (Andrew *et al.* 2002). However, the gradual increases in ambient noise from ships have likely not impacted the results of our study as shipping occurs at all hours of day and in all seasons.

Oceanographic Productivity and Prey Variability

The physical and biological oceanography of the California Current promote high prey biomass for blue and fin whales. Blue whale movement and distribution in the California Current is well correlated with zooplankton aggregations, particularly euphausiids (Schoenherr 1991, Croll *et al.* 1998, Fiedler *et al.* 1998). Fin whale prey associations have not been well studied in the Southern California Bight, although they are thought to be more opportunistic feeders than blue whales. In other regions of the North Pacific fin whales have been found feeding primarily on euphausiids, secondarily on copepods (Nemoto and Kasuya 1965, Kawamura 1980, Flinn *et al.* 2002), and in limited quantities on fish and cephalopods including herring, cod, smelt, pollock, sardine, rockfish, mackerel and squid (Kawamura 1980).

Euphausiids can be found in the Southern California Bight throughout the year, although the maximum population biomass is generally found in the summer and fall (Brinton 1976), coincident with the peak abundance of blue and fin whales in the region. The distribution and density of euphausiids is dependant on oceanographic conditions (Brinton 1981, Mackas 1995, Marinovic *et al.* 2002). Southward transport of nutrient-rich water in the California Current coupled with wind-driven coastal upwelling promotes euphausiid production. The strength of local upwelling influences the success of the spring cohort, yielding the summer and fall biomass (Brinton 1976) which will become prey for foraging blue and fin whales. Turbulent mixing promoted by the complex bathymetry of the Southern California Bight, including shelf breaks, island slopes, and seamounts, acts to further increase surface nutrient concentrations. These nutrients support dense aggregation of primary and secondary production (Fiedler *et al.* 1998), which support the creation of patches of high euphausiid biomass. Feeding whales aggregate in these patches (Croll *et al.* 1998).

Whether a single population, or a revolving presence of different populations, the occurrence of fin whales in the Bight year-round may be linked to their ability to take advantage of many prey types. The oceanography of the Southern California Bight promotes high seasonal biomass of several species of copepod and schooling fish. While euphausiid biomass is generally lower in the winter and spring winter, other prey species are more abundant during these seasons. Similarly, competition for euphausiid prey may lead to the spatial segregation of blue and fin whales observed during some periods, such that the flexibility in fin whale's diet may allow them to forage apart from euphausiid aggregations. However, lack of quantitative data on the prey preferences of fin whales in the Southern California region prevent specific conclusions on the relative distribution of blue and fin whales relative to prey resources.

The climatology of the California Current has changed in recent years. In 1999, a shift occurred bringing relatively cool, pigment-rich waters, yielding higher zooplankton biomass than had been observed since 1991 (Durazo *et al.* 2001, Schwing *et al.* 2002, Venrick *et al.* 2003). The increase in blue and fin whale prey may be related to some of the calling patterns described here. The observed increase in the number of days in which blue whale calls were recorded from 2001 to 2003 (Table 3.3) may be related to an increase in prey availability attracting foraging blue whales to the region. Blue whales are also known to feed off the Baja Peninsula in the spring (Rice 1974); however, zooplankton concentrations off Baja have been anomalously low since 2001 (Venrick et al. 2003). A lack of food resources off Baja may have brought blue whales north into the Southern California Bight where prey was abundant, earlier than is typically observed. The increasingly early arrival of D calling blue whales in 2002 and 2003 is likely indicative of the distribution of prey resources.

Differences in call detection among sites cannot be explained with the available oceanographic data, but are likely linked, in part, to the prey available. Euphausiid aggregations over abrupt topography have previously been observed in the northeast Pacific. These aggregations may be created by an increase in euphausiid productivity generated by topographically induced upwelling or by topographic blockage of the euphausiid's daily vertical migration (Genin 2005). The long residence time required for increased production created by localized upwelling to cascade through the local food web is unlikely over banks and seamounts (Genin and Boehlert 1985). In fact, high resolution remotely sensed ocean color in the Southern California Bight reveals no persistent or localized patches of chlorophyll above seamounts and banks (Palaez and McGowan 1986). Instead, topographic blockage (Issacs and Schwartzlose 1965) is thought to trap vertically migrating euphausiids above the shallow topography during the day. Such an increase in euphausiid biomass at Cortez and Tanner Banks might explain, for example, the relatively high number of D calls at site 3 in 2001. Local topographically induced eddies may entrain patches of high euphausiid biomass, and local patterns of advection may lead to higher euphausiid biomass near some sites. Aggregation of blue and fin whale prey at Cortez and Tanner Banks through this process may explain small scale variability in the occurrence of some call types (Figures 3.6-3.9), as increases in calling on the order of days or weeks may be influenced by the persistence of local prey aggregations.

Unfortunately, no oceanographic data are available which were collected on the same temporal and spatial scale as the acoustic data described here, complicating the direct association between environmental variability and the observed calling patterns. While satellite-derived oceanographic data has shown promise for relating calling whale distribution to oceanographic variability (Moore *et al.* 2002, Burtenshaw *et al.* 2004), the coherence between these satellite measured oceanographic variables and whale presence is not strong, likely due to the temporal and spatial disconnect between phytoplankton abundance and large euphausiid aggregations. In addition, satellites do not reliably provide small-scale (less than 10 km or one week duration) measurements, preventing their use in explaining the short time and space scale changes in calling whale presence we have observed at Cortez and Tanner Banks. Future studies of blue and fin whales, and other cetacean calling patterns should be designed to include environmental sampling. This may be accomplished by placing acoustic sensors at spatial scales compatible with existing sampling schemes (eg. CalCOFI), or may include integrated oceanographic sampling at smaller spatial scales.

Diel Call Patterns and Prey Availability

The diel patterns of blue whale call occurrence observed here and in the eastern tropical Pacific (Stafford *et al.* 2005) are probably linked to prey distribution and abundance. Significantly greater blue whale B calling at dusk, night and dawn than during the day was previously identified (Stafford *et al.* 2005, Wiggins *et al.* 2005). Both reports suggested that the occurrence of B calls is related to the diel vertical migration behavior of blue whale's euphausiid prey. Reanalysis of Wiggins *et al.* (2005) as part of this dataset indicate that both single and song B calls contribute to the diel signal. However, the strength of this pattern in 2001 is an anomaly. In 2002, only song calls were diurnally distributed, and in 2003 no diel pattern of B calling was observed. Evaluation of diel calling rates for type D calls shows variability in the production of that call type as well. Because D calls are produced by and among feeding whales, high call rates during the day, as described here, would indicate feeding occurs during this period. This is supported by studies of diving behavior indicating a drop-off in lunge diving at night (Croll *et al.* 1998, Chapter 2). Although this pattern is not significant in 2001 and 2002, it may be due to sample size limitations imposed by picking calls only once per week, yielding too much variability in calling to identify prominent calling patterns. While the production of some call may be related to prey availability, the relationship is complex and requires more directed study of the coherence between prey concentration and the production of calls.

The diel distribution of fin whale calls has not been widely studied. A single report from Midway Island in the central Pacific, indicates a doubling in fin whale patterned calling near local 4 PM and 8 PM (Northrop *et al.* 1967). Although a peak in calling after dusk was observed at Cortez and Tanner Banks in 2003, the general pattern is characterized by increased calling at dawn (Table 3.6). It is not possible to say with certainty how the pattern of call production observed in the Southern California Bight is related to the context of the calls because the occurrence of patterned and single calls could not be automatically identified. The songs of male fin whales are thought to be used to attract females to rich food resources (Croll *et al.* 2002), suggesting these calls would be most common in the hours in which feeding occurs. Analysis of stomach contents of fin whales in the North Atlantic have shown that feeding occurs primarily at night (Vikingsson 1997); although time-depth recorders deployed on fin whales in the Southern California Bight indicate they also feed during the day (Acevedo-Gutierrez *et al.* 2002). The local availability of prey through the day may vary among regions potentially explaining the opposite calling patterns and feeding patterns observed among regions.

Conclusions

Acoustic monitoring has been widely used to evaluate the presence of vocal cetaceans in regions and seasons inaccessible to visual surveys, and to describe the seasonal and geographic distribution of calling. Our multi-year study of blue and fin whale calling on several spatial and temporal scales provides insight into the benefits and limitations of acoustic monitoring. Visual surveys are common in the Southern California region. Comparing visual estimates of seasonal abundance with the seasonal patterns described here indicates that visual surveys alone do not completely describe the seasonal presence of blue whales. In addition, all blue whale B and D call types must be monitored to fully describe the seasonality and daily presence of blue whales. In contrast, fin whales are present and vocal year-round in the Bight. However, it is unclear whether this is indicative of a resident population, or a larger, widely ranging population periodically visiting the Southern California Bight. Smaller scale temporal and spatial patterns of calling are likely related to local oceanographic productivity, and to a smaller degree on acoustic propagation. Blue and fin whales appear to show preference for similar regions around Cortez and Tanner Banks seasonally. The spatial bias in the occurrence of some call types has implications for the use of autonomous recorders for deriving estimates of population abundance, as some sites may show anomalously low or high call rates depending on oceanographic productivity, the influence of acoustic propagation, and time of year.

Tables and Figures

Table 3.1. ARP and OBS site locations 20 August 2000 to 20 February 2004.

Site	Latitude (N)	Longitude (W)	Water Depth (m)
1	32 45.6	119 12.5	150
2	32 41.3	119 01.9	300
3	32 35.8	119 08.8	200
4	32 23.3	118 55.4	430
5	32 39.5	119 19.8	320

Table 3.2. Ishmael spectrogram correlation kernel parameters for blue whale B call and fin whale call detection.

	Year	Frequency Start (Hz)	Frequency End (Hz)	Time Start (s)	Time End (s)
Blue whale B call	2000	52.5	51	0	1.5
		51	49.2	1.5	3
		49.2	48.8	3	4.5
		48.8	48.4	4.5	10
	2001	52	50.5	0	1.5
		50.5	48.7	1.5	3
		48.7	48.3	3	4.5
		48.3	47.9	4.5	10
	2002	51.5	50	0	1.5
		50	48.2	1.5	3
		48.2	47.8	3	4.5
		47.8	47.2	4.5	10
	2003	51	50.5	0	1.5
		49.5	47.7	1.5	3
		47.7	47.3	3	4.5
		47.3	46.8	4.5	10
Fin whale	2000-03	35	20	0	0.8

Table 3.3. The number of days in which blue and fin whale calls were detected each year pooled among sites. Year is defined as March 1 – February 28 to allow for the extension of the blue whale calling season into the next calendar year. Data from 2000 were excluded since they did not represent an entire blue whale season. Blue D calls days are shown in parenthesis to indicate the extrapolated number of days based on the number of those actually picked over the year. There are only 294 days of acoustic monitoring effort in 2002-03.

Call Type	2001-02	2002-03	2003-04
Blue song B	202	242	256
Blue single B	200	238	255
Blue D	(207)	(211)	(241)
Fin (All)	365	294	365

Table 3.4. Kruskal-Wallis comparison of median daily calling rate per year across all sites. The number of days with calls (N), and the χ^2 values are given in addition to the probability of a significant difference (p) between medians. Significantly different medians ($p<0.05$) were tested for inter-annual relationships using the Multiple Comparison test (Multicompare). Year is defined as March 1 – February 28 to allow for overlap of blue whale calling season into the next calendar year. Blue whale D call rates are per week since data from only one day per week are available.

Call Type	N	χ^2	p	Multicompare
Blue D	39	1.76	0.416	
Blue song B	202	3.42	0.181	
Blue single B	254	0.3	0.862	
Fin	272	57.37	3.48E-13	2002 > 2001 = 2003

Table 3.5. Kruskal-Wallis comparison of median daily calling rate among sites for two periods with concurrent monitoring at three sites. The number of days with calls (N) is shown along with the χ^2 value, and the probability of a significant difference (p) between medians. Significantly different median values ($p<0.05$) were tested for inter-site differences using the Multiple Comparison test (Multicompare). Site locations are shown in Figure 3.2b.

Date	Call Type	N	χ^2	p	Multicompare
20 June – 25 October, 2001	Blue D	24	0.21	0.901	
	Blue song B	126	1.05	0.591	
	Blue single B	126	18.74	8.53E-05	S2 < S3 = S5
	Fin	126	18.24	0.0001	S3 < S5
16 April – 4 November, 2003	Blue D	41	6.23	0.044	S5 < S2
	Blue song B	171	9.99	0.0068	S5 < S1
	Blue single B	181	10.46	0.0054	S5 < S1
	Fin	200	24.22	5.49E-06	S5 < S1 = S2

Table 3.6. Kruskal-Wallis comparison of median hourly calling rate for each all type across sites in four daily bins: dawn, day, dusk, and night defined by nautical twilight. The number of days with calls (N) is shown along with the χ^2 value, and the probability of a significant difference (p) between medians. Significant differences in median values among the four daily periods were tested for specific differences using a Multiple Comparison test (Multicompare in table). Twilight, sunrise, and sunset times are from U.S. Navy Astronomical Data Tables.

Year	Call Type	N	χ^2	p	Multicompare
2001	Blue D	35	5.42	0.144	
	Blue song B	184	54.57	8.50E-12	Day < Dusk = Night < Dawn
	Blue single B	198	30.51	1.08E-06	Day < Dusk = Night = Dawn
	Fin	363	2.22	0.52	
2002	Blue D	29	3.24	0.357	
	Blue song B	202	9.54	0.023	
	Blue single B	239	0.9	0.825	
	Fin	285	31.53	6.56E-07	Dusk < Dawn = Day Night < Dawn
2003	Blue D	48	12.73	0.0053	Night < Day
	Blue song B	216	4.95	0.176	
	Blue single B	256	2.44	0.486	
	Fin	362	54.85	7.40E-12	Dusk < Day = Night < Dawn

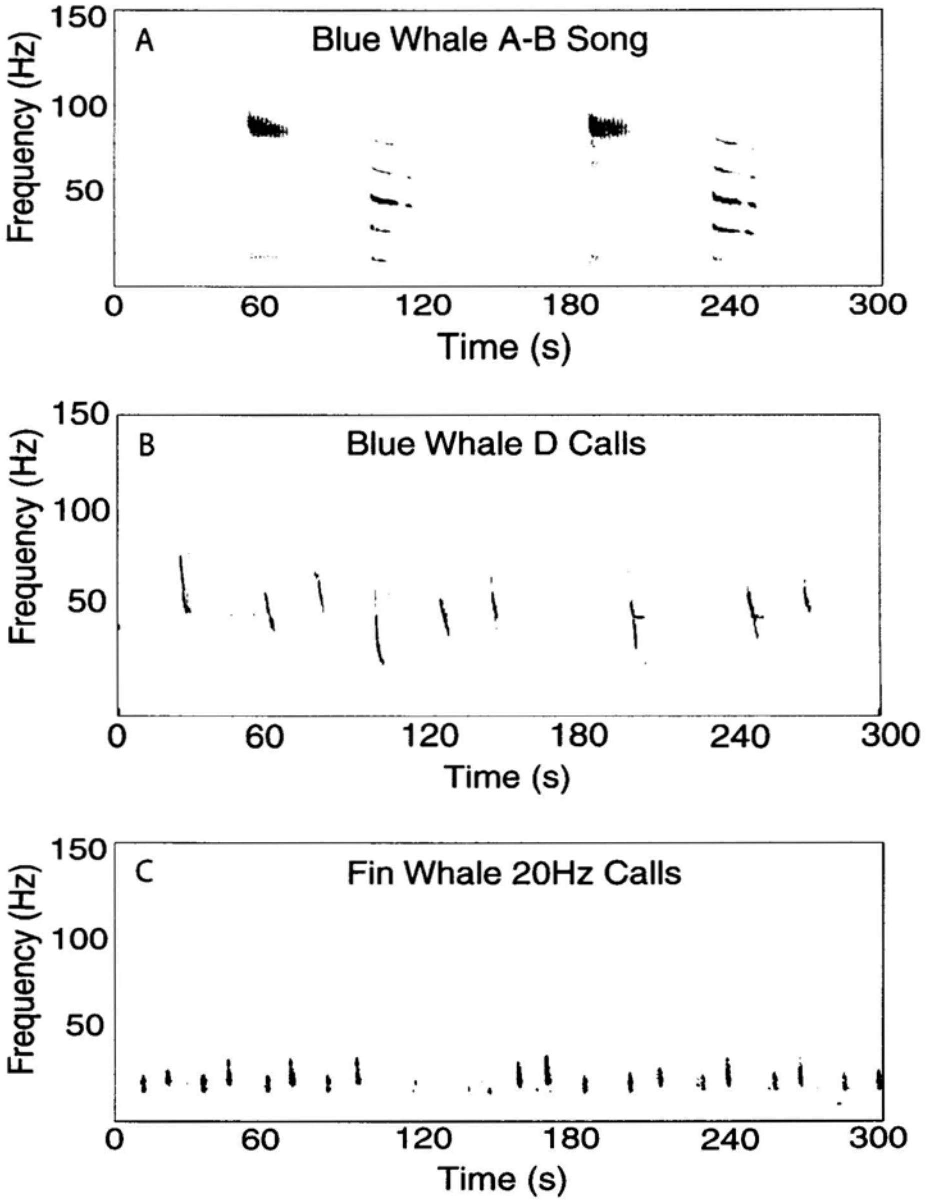


Figure 3.1. Northeast Pacific blue and fin whale call types detected in this study. A) Blue whale A and B calls organized into a song pattern. These calls may also occur singly, with frequency and duration characteristics identical to those represented here. B) Blue whale downswept D calls, indicating the large variability in frequency content and sweep rate. C) Fin whale 35-20Hz calls shown here in a call-counter-call sequence. These calls are also organized into song patterns as shown in Figure 3.3.

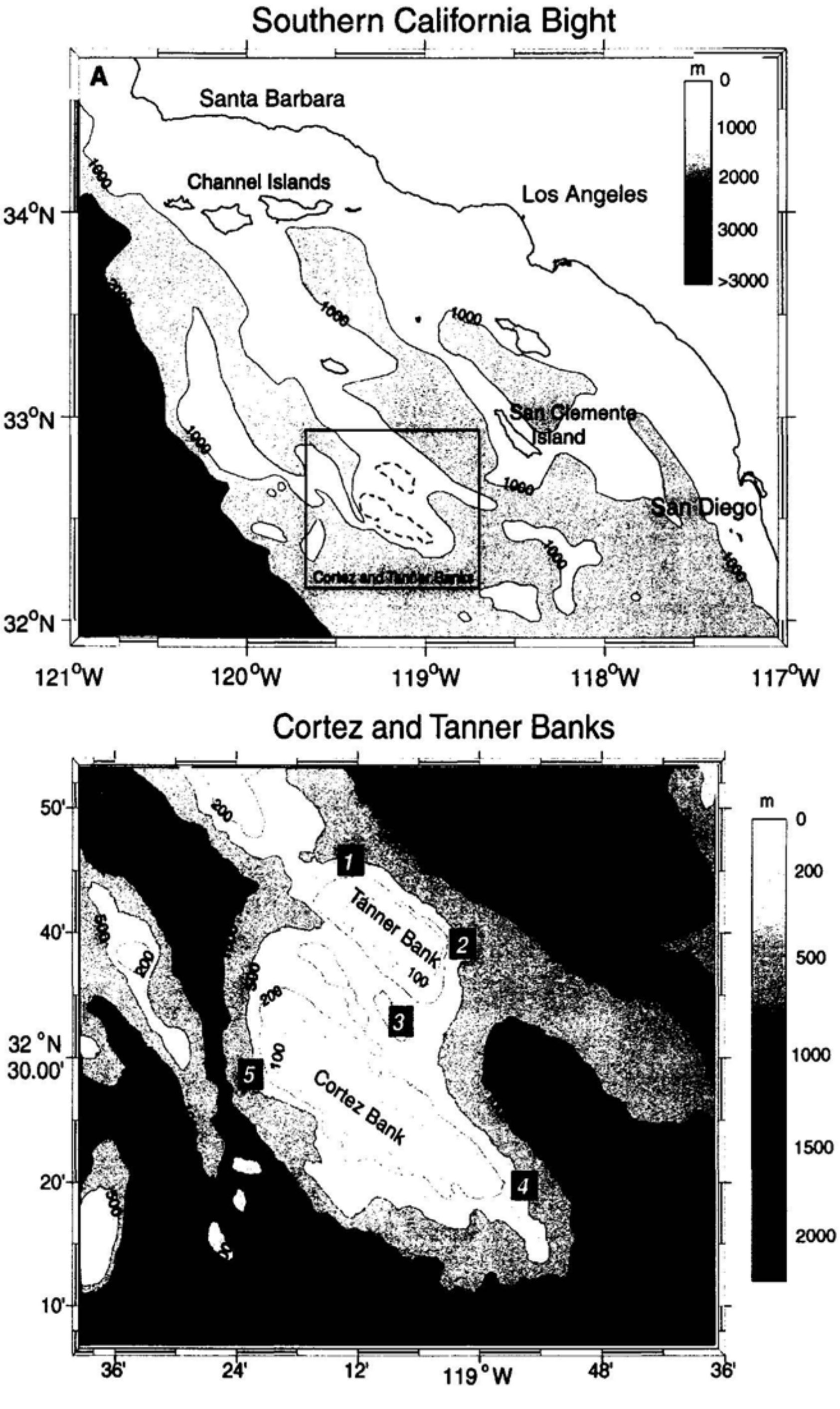


Figure 3.2. A) Southern California Bight bathymetry showing the Cortes and Tanner Banks study site. B) Cortes and Tanner Banks with monitoring locations noted as black lettered squares. Monitoring positions and depths are listed in Table 3.1.

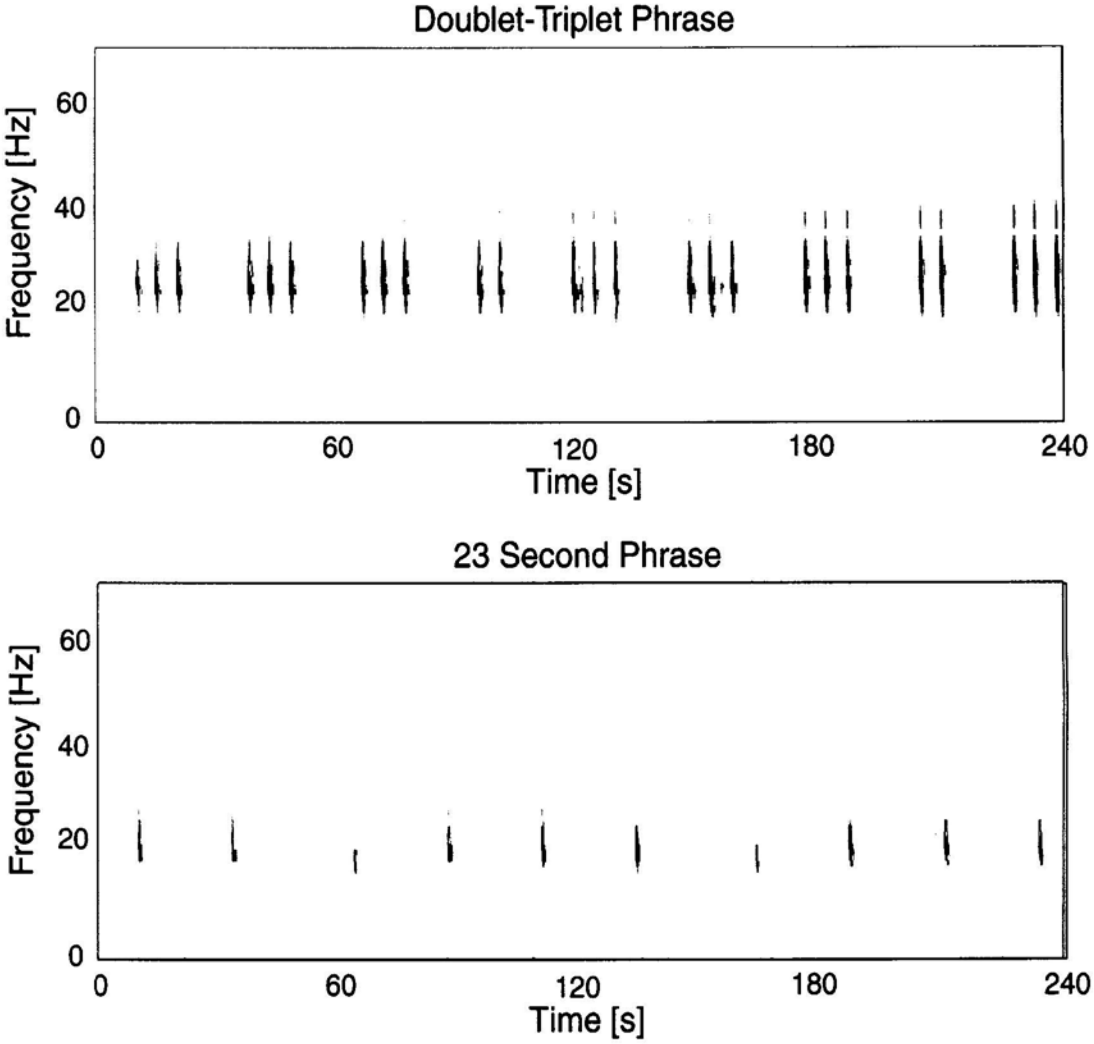


Figure 3.3. Examples of fin whale song observed at Cortes and Tanner banks. A) Doublet-triplet pattern found at site 3 in 2001. B) Consistent 23 s interval pulses with varying frequency content found at sites 2 and 3 in 2003 and 2004.

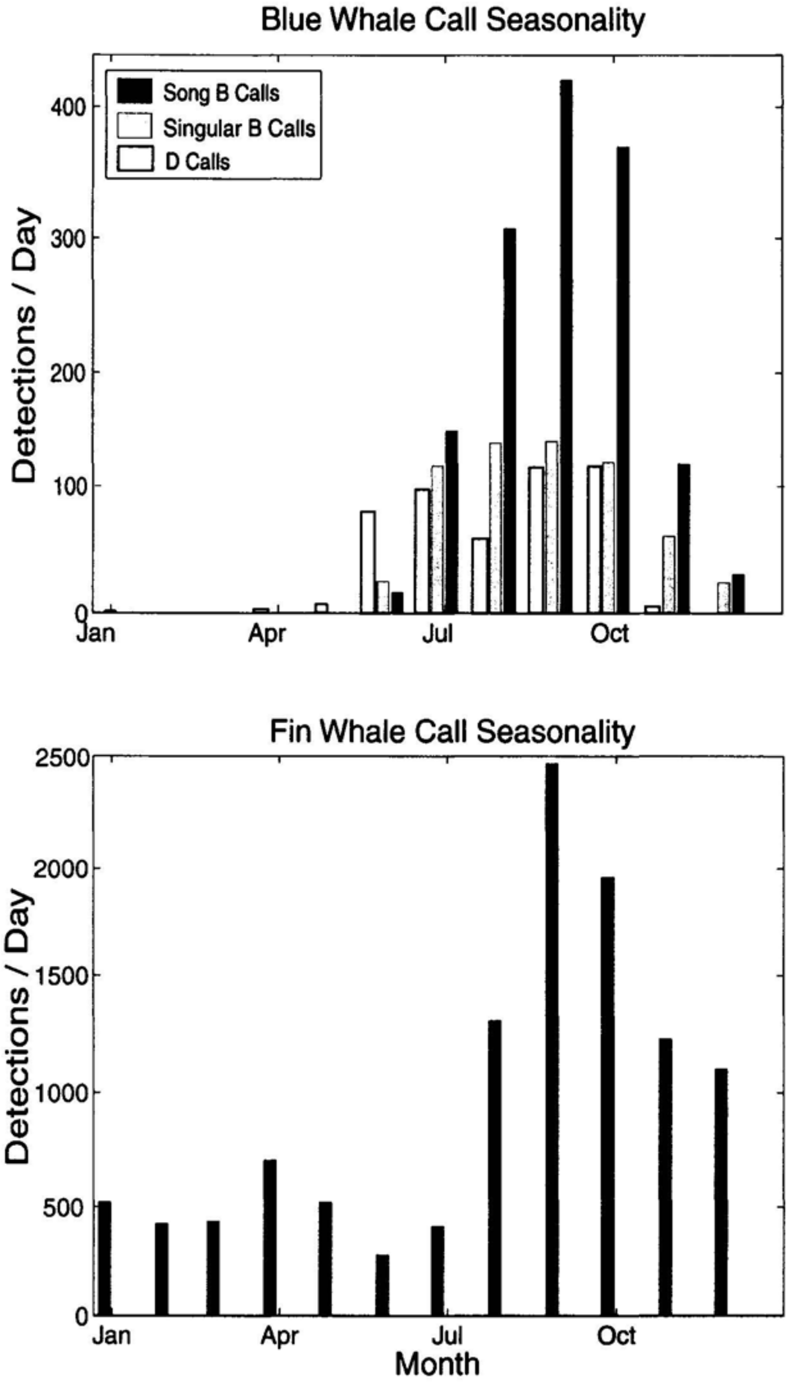


Figure 3.4. Seasonality of blue and fin whale average annual calling rates (detections per day) at Cortes and Tanner Banks in one month bins. A) Blue whale song, singular B, and D call seasonality. B) Fin whale annual call occurrence.

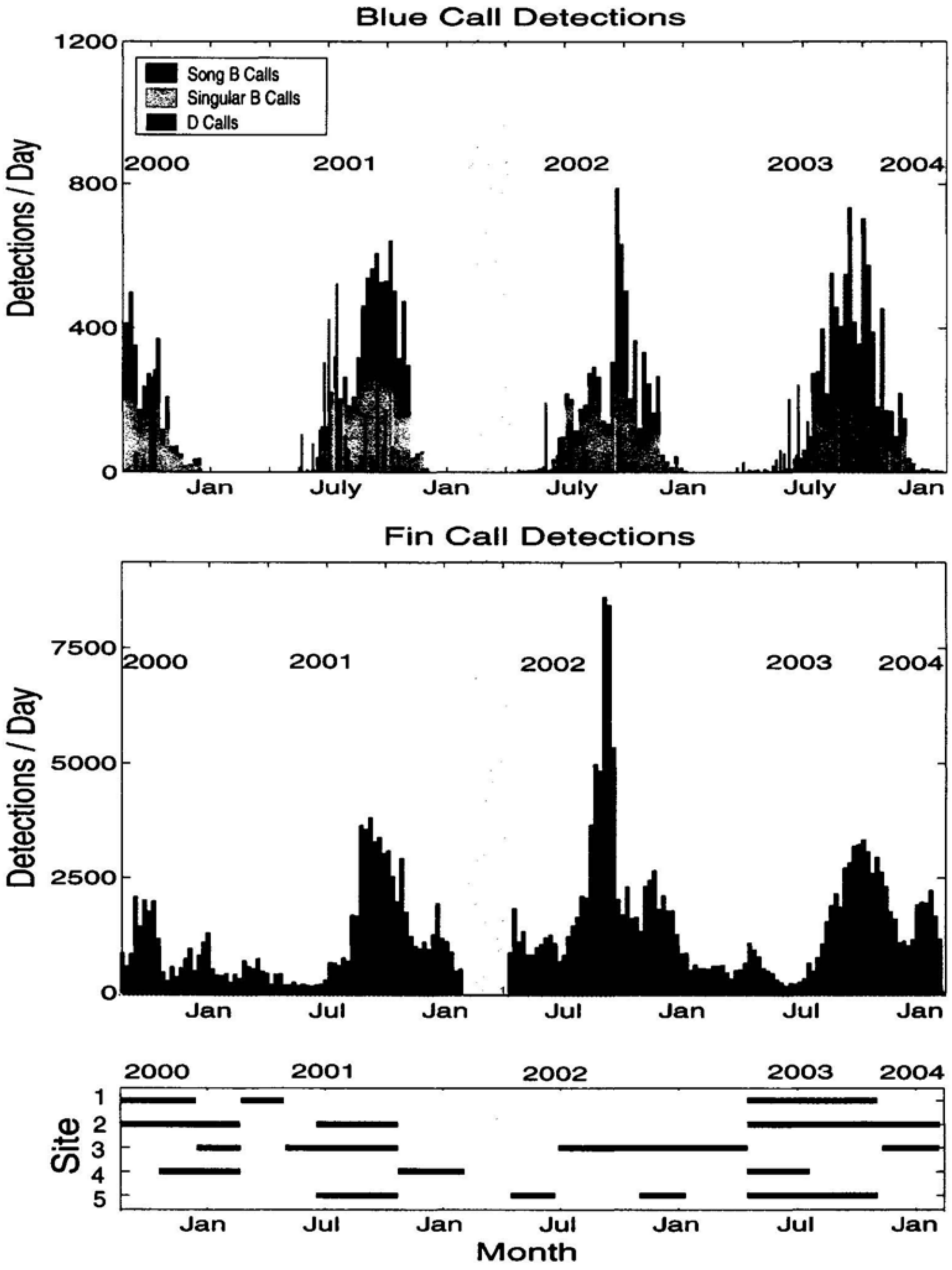
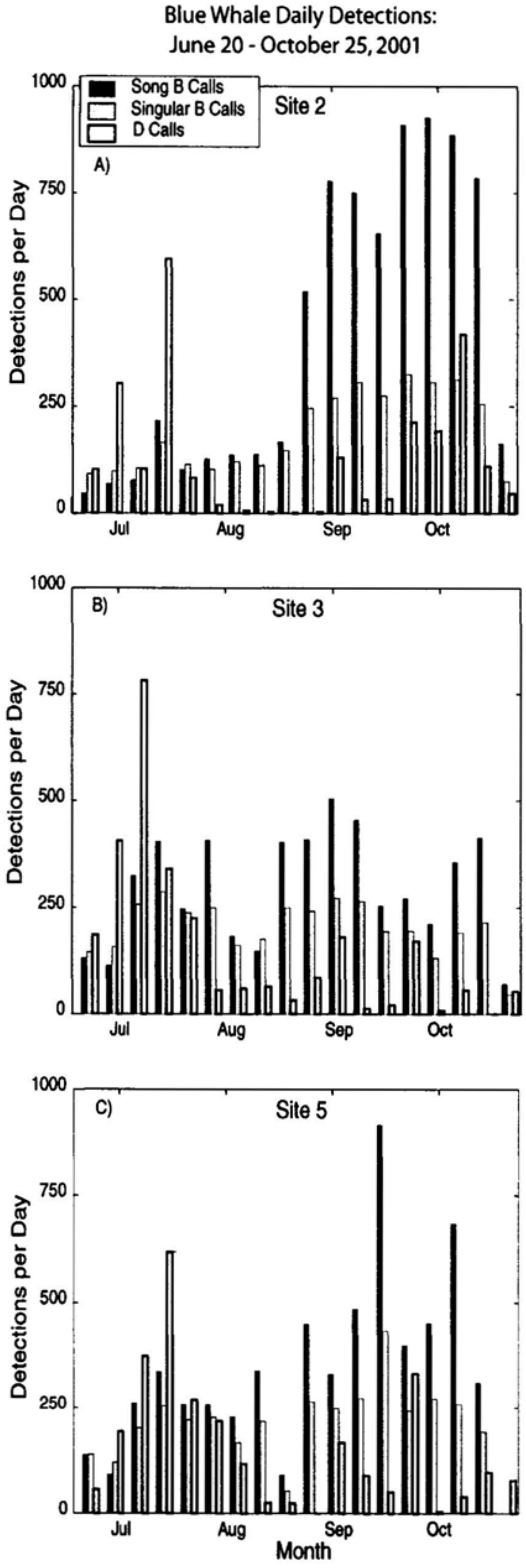
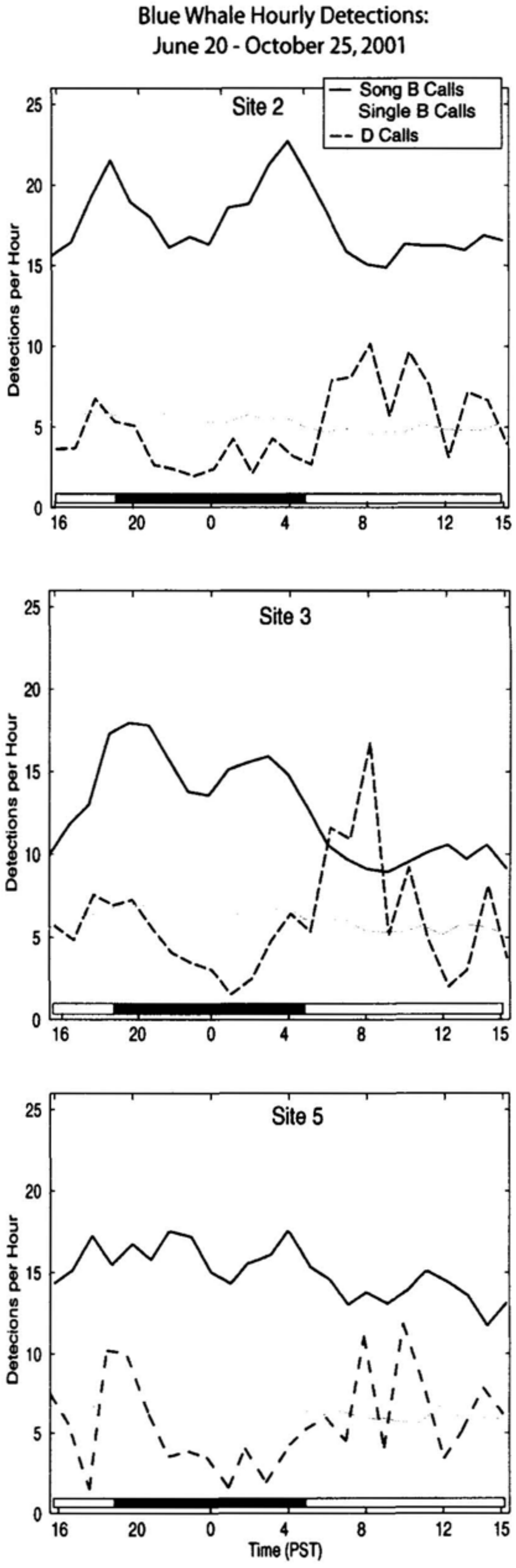


Figure 3.5. Blue and fin whale call detections from 20 August, 2000 to 20 February, 2004. A) Song and singular B calls, and D calls are indicated. B) Fin whale call occurrence. C) Sites monitored over the study period. Grey hatching indicates no were data available.

Figure 3.6. Blue whale calling rates (detections per day) at three sites from 20 June to 25 October, 2001 shown in one week bins. A-C) Daily call occurrence by blue whales at sites 2, 3 and 5. D-F) Diel occurrence for blue whale call types at sites 2, 3, and 5. Sun phase is indicated by the bar at the bottom of each panel, with white = daylight, black = night, and grey = dusk and dawn, respectively. Notice the pattern of preferred song production at dusk and dawn at sites 2 and 3 and preferred D call production during daylight hours at all sites. The hypothesis that the median hourly calling rate was the same among sun phases was rejected at all sites for song and singular call, similar to the 2001 pooled results in Table 3.6. The daily distribution of D calls was not significant at any site.



Blue Whale Daily Detections:
June 20 - October 25, 2001



Blue Whale Hourly Detections:
June 20 - October 25, 2001

Figure 3.7. Fin whale calling rates (detections per day) at three sites from 20 June to 25 October, 2001 shown in one week bins. A-C) Daily fin whale call occurrence at sites 2, 3, and 5. D-F) Diel occurrence for fin whale calls at sites 2, 3, and 5. Sun phase is indicated by the bar at the bottom of each panel, with white = daylight, black = night, and grey = dusk and dawn, respectively. The Kruskal-Wallis P-value for the hypothesis that the median hourly calling rate is the same among sun phases is shown adjacent to the curve for each site along the right margin of each figure. Only site 3 was significant with at night and dawn call detection rates significantly higher than day and dusk rates.

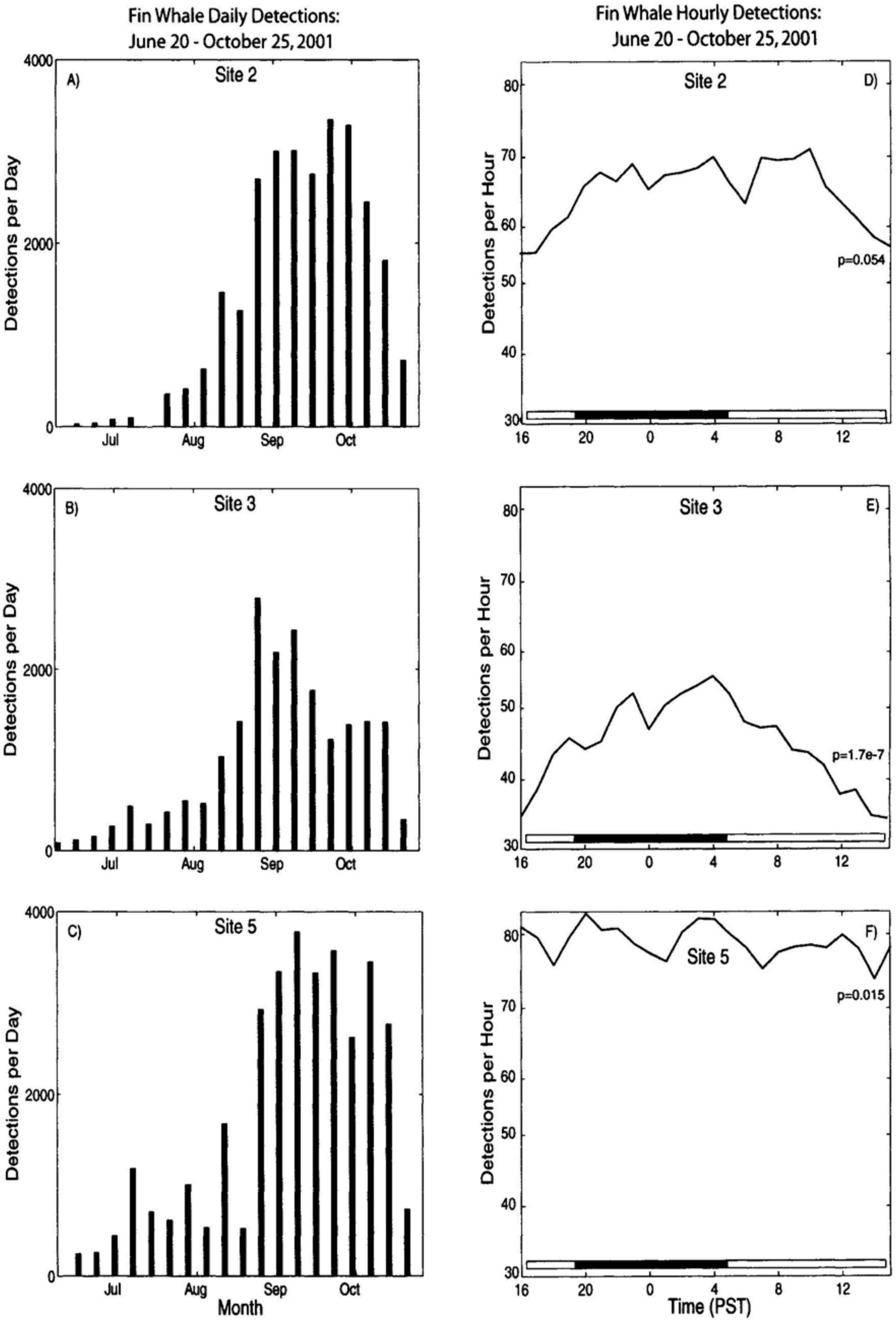

Fin Whale Daily Detections:
June 20 - October 25, 2001
Fin Whale Hourly Detections:
June 20 - October 25, 2001
A)
Site 2
Detections per Day
4000
2000
0
Jul
Aug
Sep
Oct
D)
Site 2
Detections per Hour
80
70
60
50
40
30
p=0.054
16
20
0
4
8
12
B)
Site 3
Detections per Day
4000
2000
0
Jul
Aug
Sep
Oct
E)
Site 3
Detections per Hour
80
70
60
50
40
30
p=1.7e-7
16
20
0
4
8
12
C)
Site 5
Detections per Day
4000
2000
0
Jul
Aug
Sep
Oct
Month
F)
Site 5
Detections per Hour
80
70
60
50
40
30
p=0.015
16
20
0
4
8
12
Time (PST)

Figure 3.8. Blue whale call rates (detections per day) at three sites from 16 April to 4 November, 2003 shown in one week bins. A-C) Daily call occurrence for each call type at sites 1, 2, and 5. D-F) Diel occurrence for blue whale call types at sites 1, 2, and 5. Sun phase is indicated by the bar at the bottom of each panel, with white = daylight, black = night, and grey = dusk and dawn, respectively. These daily patterns are different from those shown in Figure 3.6. The hypothesis that the median hourly calling rate was the same among sun phases was not rejected for any call type at any site.

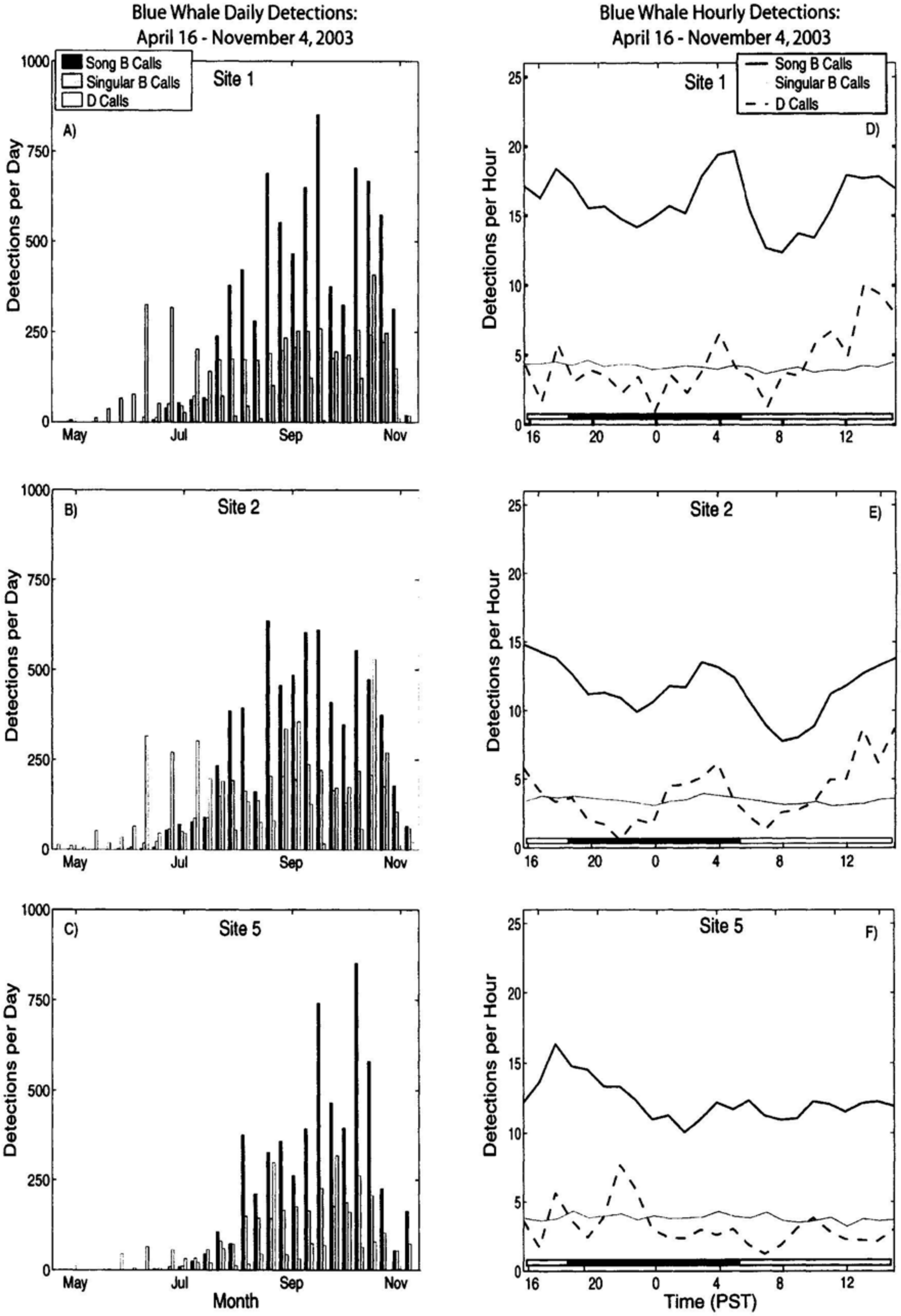
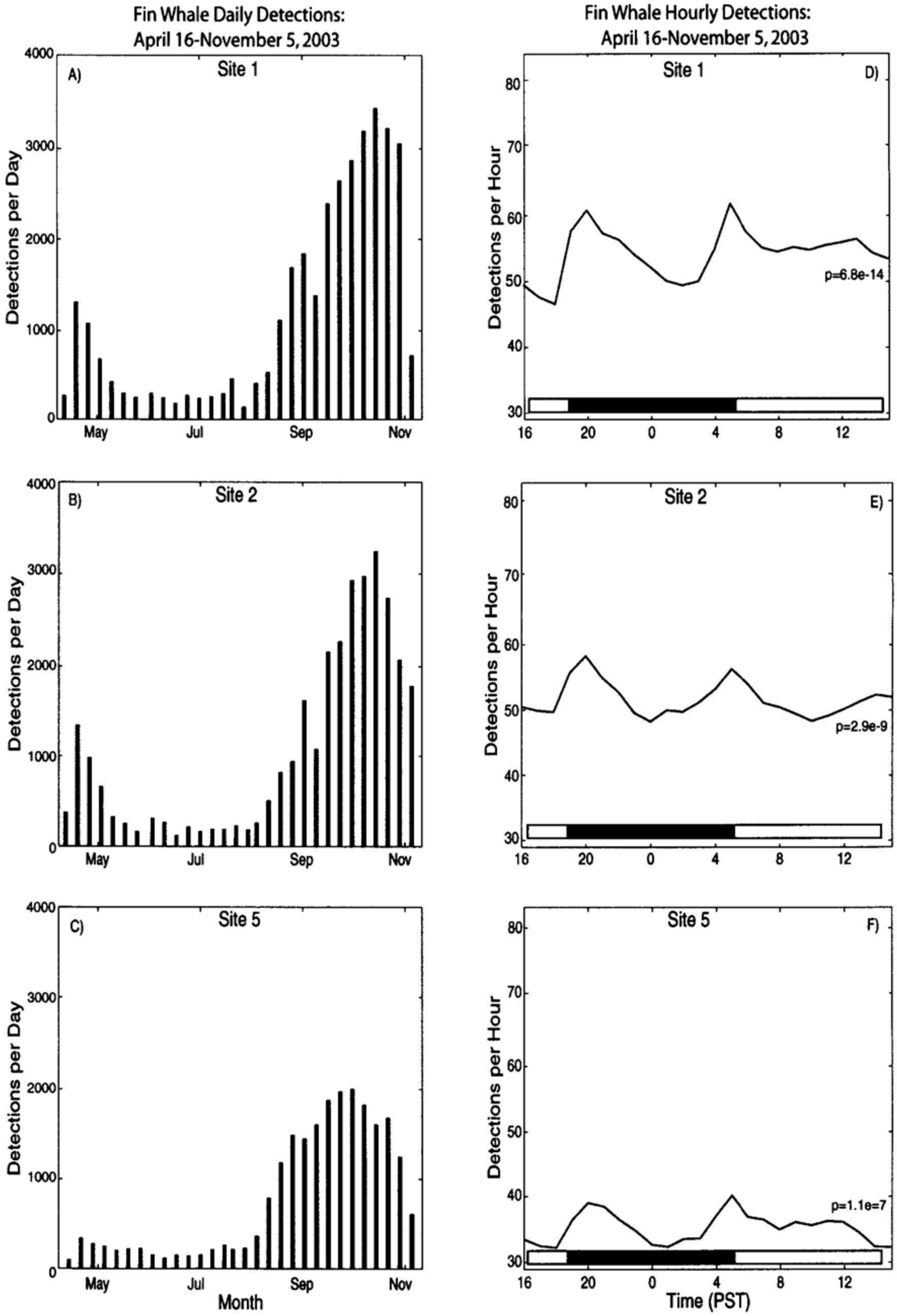

Blue Whale Daily Detections:
April 16 - November 4, 2003
Blue Whale Hourly Detections:
April 16 - November 4, 2003
Song B Calls
Singular B Calls
D Calls
Site 1
A)
B)
Site 2
C)
Site 5
D)
E)
F)
Detections per Day
0
250
500
750
1000
May
Jul
Sep
Nov
Month
Detections per Hour
0
5
10
15
20
25
16
20
0
4
8
12
Time (PST)

Figure 3.9. Fin whale calling rate (detection per day) at three sites from 16 April to 4 November, 2003 shown in one week bins. A-C) Daily call occurrence at sites 1, 2, and 5. D-F) Diel occurrence of fin whale calls at sites 1, 2, and 5. This pattern is different from that observed during 2001 (Figure 3.7). Sun phase is indicated by the bar at the bottom of each panel, with white = daylight, black = night, and grey = dusk and dawn, respectively. The Kruskal-Wallis P-value for the hypothesis that the median hourly calling rate is the same among sun phases is shown adjacent the curve for each site along the right margin of each figure. There was significantly greater calling at dusk and dawn then at day or night at all sites.


Fin Whale Daily Detections:
April 16-November 5, 2003
Fin Whale Hourly Detections:
April 16-November 5, 2003
A)
Site 1
D)
B)
Site 2
E)
C)
Site 5
F)
Detections per Day
0
1000
2000
3000
4000
May
Jul
Sep
Nov
Month
Detections per Hour
30
40
50
60
70
80
16
20
0
4
8
12
Time (PST)
p=6.8e-14
p=2.9e-9
p=1.1e=7

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CHAPTER 4

Blue Whale Visual and Acoustic Encounter Rates from Shipboard Surveys in the Southern California Bight

Abstract

Visual and acoustic surveys for blue whales (*Balaenoptera musculus*) were conducted in the Southern California Bight during bi-monthly cruises between April and November of 2000 through 2003 to evaluate the relationship between visual and acoustic detection rates. Surveys consisted of transit and stationary periods resulting in hourly visual and acoustic encounter rates in nine sub-regions of the Southern California Bight. Temporal and spatial variability in, and the relationships among, visual and acoustic encounter rates were evaluated using generalized additive models (GAMs). The results of the GAMs indicate that visual encounter rate is predicted by sub-region, month, transit state (transit or stationary), time of day, and year, AB caller acoustic encounter rates are predicted by month, transit state, and sub-region, and D caller acoustic encounter rates are predicted by month and the number of animals seen. The only common predictor in all three models was month, indicating a strong seasonal impact on encounter rate. However, comparison among models indicated that the seasonal peak of each encounter type was offset from the others, with D callers most frequent in June and July, visual encounters in July and August, and AB callers in August and September. Visual encounters were highest in regions known to be dense with krill, the blue whale's primary prey, while AB caller acoustic encounters did not occur more often in those areas, leading to significant

differences between visual and AB caller encounter rates in the Santa Barbara Channel (p = 0.0005), south of the Channel Islands (p = 0.015), and San Nicolas (p = 0.025) sub-regions. Dependence of one encounter type on another was seen only with D callers, where the number of whales heard D calling was related to the number of animals seen, suggesting these measures of whale occurrence are linked. A lack of correspondence between AB caller and visual encounter rates may be related to the traveling behavior of AB calling animals making them more difficult to see and the greater detection range of acoustic sensors detecting animals beyond visual range. These relationships should provide the basis for further studies of the coherence between visual and acoustic survey modes for blue whales.

Introduction

Cetacean abundance estimates are traditionally obtained through visual line-transect surveys (Buckland *et al.* 2001). During visual surveys, bias may arise if whales are not at the surface within view of the observer (availability bias) or if they are missed or not identified (perception bias). Therefore, abundance estimates derived from line-transect methods may be affected by the behavior of the animals surveyed. For example, feeding blue whales (*Balaenoptera musculus*) have longer surface intervals than traveling blue whales (Acevedo-Gutierrez *et al.* 2002), which increases the probability of visual detection. In addition, spatial and temporal biases in encounter rate exist for many species as animals aggregate near certain oceanographic features in different times of year (Forney and Barlow 1998, Forney 2000, Ferguson and Barlow 2001, Ferguson *et al.* in review). The production of low frequency calls by baleen whales, and the efficient propagation of sound over long distances make the use of passive acoustic monitoring a promising means for estimating whale abundance (Mellinger and Barlow 2003). In acoustic surveys, bias arises when whales do not vocalize within the detection range of the acoustic receiver (availability bias) or if the source of the vocalization is not identified (perception bias).

Dual-mode surveys, or those including simultaneous visual and acoustic observation, offer the ability to increase the probability of detection, by visually detecting quiet animals, and acoustically detecting vocal animals whose behavior may inhibit visual detection. The concurrent use of both survey types augments animal detection, and may yield quantitative relationships between the detection modes.

Dual-mode surveys for cetaceans are becoming more common, but show differences in the relationship between visual and acoustic detection rates across species. Dual-mode surveys for delphinids often have acoustic detection rates equal to or higher than visual sighting rates (Mellinger and Barlow 2003), with concurrent detection of groups in both modes (Thomas *et al.* 1986, Akamatsu *et al.* 2001). Surveys for sperm whales have indicated that acoustic detection rates are higher than visual detection rates (Leaper *et al.* 2000, Barlow and Taylor 2005). Concurrent visual and acoustic monitoring for baleen whales has generally been opportunistic, preventing quantitative comparison of visual and acoustic encounter rates. The two dual-mode surveys of large whales reported higher acoustic than visual encounter rates (Clark and Fristrup 1997, Swartz *et al.* 2003). Understanding the relationships between blue whale visual and acoustic encounter rates is necessary to evaluate the effectiveness of each survey type and to develop methods of abundance estimation based on both detection modes.

As long-term, fixed-point acoustic surveys become more common, there is growing interest in developing tools to analyze the patterns of call occurrence for abundance estimates. The specific statistical parameters required to estimate abundance from fixed-point surveys will be different from those developed for mobile visual surveys (McDonald and Fox 1999, Buckland *et al.* 2001) as animals may be within the survey region for several hours or days, vocalizing for all or part of that time. However, an understanding of the relationship between the number of whales or calls heard and the number of whales seen will be useful for interpreting detection patterns. Fixed-point acoustic surveys provide valuable information on species presence, but behavioral context of calls and variability in call rates complicate the statistical treatment of call occurrence for abundance estimation. Thus, calibration of acoustic detection rates from dual-mode surveys may provide a measure of the efficiency of autonomous acoustic surveys for abundance estimation.

Northeast Pacific blue whale call characteristics are well known and easy to identify. In the northeast Pacific blue whales make at least four types of calls. Long-duration, low-frequency type A and B calls are produced by males (Chapter 2) and occur in long stereotypical sequences (Rivers 1997, Stafford *et al.* 2001), classified as song (McDonald *et al.* in press) or as single calls (Chapter 2). Down-swept, type D calls (Thompson *et al.* 1996) are highly variable in sweep rate and frequency content and are produced by both sexes (Chapter 2). Other highly variable amplitude (AM) and frequency-modulated (FM) calls have also been heard (Thode *et al.* 2000, Chapter 2).

We compiled hourly counts of visually-encountered and acoustically-encountered blue whales from dual-mode surveys conducted in the Southern California Bight to evaluate the spatial and temporal variability within and among encounter types. Acoustic encounters included blue whales producing AB song calls or D calls. Using generalized additive models (GAMs), we evaluated the dependence of encounter rates on spatial and temporal variables (eg., month, year, time of day, sub-region) and identified the most significant sources of their variability. Our findings provide direction for future studies of the relationship between acoustic and visual encounter rates and the development of optimal methods of assessing blue and other baleen whale distribution and abundance.

Methods

Field Methods

Shipboard surveys for blue whales were conducted bi-monthly, from April through November, between 2000 and 2003 aboard the *R/V Robert Gordon Sproul*. Each cruise lasted four to ten days. The cruises combined multiple tasks, including instrument servicing, photo-identification, tissue sampling, tagging studies, and a dual-mode visual and acoustic survey. The ship's path was determined by 1) the need to service instrumentation in certain regions (Cortez and Tanner Banks) and 2) the presumed or known distribution of blue whales based on recent sighting reports. For these reasons, track lines were not determined prior to sailing nor were they equally distributed throughout the study area.

A team of observers maintained a watch for blue whales during most daylight hours. During transit periods, two observers scanned ahead to abeam of the ship using 7x50 power binoculars and un-aided eyes. A third observer also scanned for whales and recorded sightings and weather conditions (visibility, Beaufort sea state) every 30 minutes or when conditions changed. The direction and distance to each marine mammal sighting was noted using the ship's gyro and reticule binoculars. Observers rotated through the three watch positions, followed by a 60-90 minute break. When blue whales were sighted, the ship was commonly diverted to their position for photo-ID and biopsy with effort shifted from transit to stationary mode. Individual blue whales were tracked when the ship was stationary by monitoring dive intervals and surface positions. Occasionally, large aggregations of whales prevented visual tracking of individuals. During those periods, observers conducted five or ten minute scans and counted only unique surfacings. These scans were repeated every twenty to thirty minutes and scan counts were averaged for each hour.

Acoustic monitoring for calling blue whales occurred during daylight hours using DIrectional Fixing and Ranging (DIFAR) sonobuoys (SSQ-53B or 53D), capable of monitoring sounds ranging from 10 to 4000 Hz. The sonobuoy receiving and recording system has been described in detail elsewhere (McDonald *et al.* 2001, Swartz *et al.* 2003), and consists of a ship-mounted receiving antenna, calibrated ICOM-R100 radio receivers, and recording to digital audio tape or to hard disk. Acoustic signals were monitored at sea using the software *Ishmael* (Mellinger 2002). When a call was detected in the spectrographic display, the call was extracted and the bearing to the sound source was estimated using the DIFAR directional components (McDonald 2004). Blue whales producing AB song calls were easily tracked over time through the continuity of received call levels, the similarity of bearing angles, and the consistent timing of song sequences. The number of whales producing D calls was estimated by counting the number of unique bearing angles occurring in each hour. Since type D calls are produced intermittently and are known to occur as counter-calls between closely spaced animals (Chapter 2), the estimated numbers of whales producing this call type are likely underestimated. Occasionally calls were missed during processing for bearing angle, preventing us from counting individual calls. We ignored the contribution of blue whales producing infrequent A and/or B calls, as it was difficult to distinguish these calls from song A and B calls, although there may have been significantly more animals producing infrequent AB calls than song calls (Chapter 2).

Sometimes individual blue whales were both visually and acoustically detected following a cue from one survey mode. When a cue from one mode resulted in detection in the other mode, the second detection was not included in the analysis. Concurrent observations were only included if they were independently detected through both modes.

Analytical Methods

Blue whale visual and acoustic counts were summarized hourly and were associated with other variables describing the ship's speed, the geographic location, the start time of each hour, and the sighting conditions during that hour. Because the speed of the ship may impact the visual detectability of blue whales, transit distances during each hour were estimated using the straight-line distance between hourly start and end points. Transit distances less than 5 nmi were categorized as "stationary" and those greater than 5 nmi as "transit". Periods of concurrent monitoring less than one hour were excluded from the analysis. The blue whale sighting rate was summarized according to the number of individual whales seen, irrespective of group size. Blue whale acoustic encounter rate was summarized as the number of whales producing each call type (AB song or D). Time of day (in Pacific Daylight Time), month, decimal month (month + day/length of month) and year were associated with each hourly segment. Spatial variability in the encounter rate was evaluated by subdividing the Southern California Bight in two ways; first into north-south regions delineated at 33.5^0 N, and second, into nine sub-regions (Figure 4.1). These sub-regions were defined subjectively based on the continuity of bathymetry, islands, and the distribution of effort. Both subdivisions were available as regional categories during model selection.

Blue whale encounter rates were modeled using non-parametric generalized additive models (GAMs) since the relationship among explanatory variables were not known. GAMs are extensions of generalized linear models (GLMs), such that the additive predictors need not be constrained to linear functions, and may instead include non-parametric smooth functions of the predictors. The link function $g(\mu)$ of a GAM, similar to that of a GLM, relates the mean of the response variable given the predictor variables, $\mu=E(Y|X_1,\ldots,X_p)$, to the additive predictor:

$$g(\mu) = \alpha + \sum_{j=1}^{p} f_j(X_j)$$

(Hastie and Tibshirani 1990). Counts of sightings or acoustic detections per hour approximate a Poisson distribution. Therefore, encounter rate was modeled using a quasi-likelihood error distribution with variance proportional to the mean and logarithmic link function.

Three generalized additive models of blue whale encounter rate were built based on the hourly survey data: visual encounters, AB caller acoustic encounters, and D caller acoustic encounters. The model set was built to take advantage of the full extent of the survey data, including stationary periods in high blue whale density regions. The models were built based on the spatial, temporal, and survey variables described in Table 4.1. A null model for each detection type was built based solely on the mean value of the response variable. The null model was then used in the forward-backward step-wise selection procedure implemented by the software *S-Plus*. This procedure evaluated the improvement of model fit with the addition of each predictor variable. The forward-backward step-wise selection procedure allows several forms of individual predictors. For example, during model selection the super-variable "Region" was evaluated as the north-south division, the 9-way subdivision, or not present in the model. In this way, continuous and ordinal variables could be classified with various smoothing spline fits, allowing the model to choose among several forms of a particular predictor to produce a best fit model. Initial models were developed using only smoothing splines and linear fits for each continuous predictor variable. The degrees of freedom for the smoothing splines were limited to three allowing for non-linear effects while restricting unrealistic detail in the shape of the function. Akaike's Information Criterion (AIC) was used to determine the best fit model at each step (Akaike 1973).

Reduction of models to parametric forms is advantageous for the quantitative explanation of encounter rate. Non-parametric spline fits of predictor variables cannot be quantitatively interpreted. When the original stepwise selection procedure chose non-parametric fits of predictor variables, a special form of ANOVA, or Analysis of Deviance, for GAM objects was implemented within *S-Plus*. The deviance is analagous to the residual sum of squares for generalized likelihood models, and therefore may be used to assess goodness-of-fit and to compare models. The contribution of the non-parametric portion of each predictor was tested versus a linear parameterization. A non-significant result for a particular predictor variable indicates that the variable could be parametric without significant loss of explanatory power. The scope of non-parametric predictors with insignificant p(F)-values (<0.05) were re-parameterized using polynomial or exponential terms and the model selection process run again. Significant changes in overall model fit using the re-parameterized predictors were tested using an Analysis of Deviance between models. Non-significant results indicate that the fit was not altered by the re-parameterization.

AIC has a tendency to over-fit models, so the contribution of each predictor in the model was tested using a final Analysis of Deviance among model predictors. The significance of each predictor was examined by adding predictors one at a time to the model and sequentially testing for changes in model fit through calculation of a likelihood score. When a predictor did not significantly contribute to the model fit, the least significant predictor was eliminated, and the reminder of the predictors tested again. This iterative process continued until all remaining predictors were significant contributors to the model. Final encounter rate models were inverted to the scale of the response to allow for comparison among models.

Results

Effort

A total of 368 effort hours included 157 hours with visual encounters, 185 hours of AB caller encounters, and 106 hours of D caller encounters. This effort was not evenly distributed temporally or spatially. There were no blue whale detections in April;

therefore, that month was not included in the models. The spatial and temporal distribution of effort and hourly counts of visual and acoustic detections are shown for June-July, August, and October-November in Figure 4.2. Most effort occurred in August, with the least in October and November. Effort decreased from 2000 to 2003, with less effort in the northern regions of the study area in 2003. Daily effort peaked at noon and then decreased to 19:00, with a bias toward stationary effort in the afternoon.

Sighting Rate Model

The visual encounter rate model indicates significant temporal and spatial variability in the encounter rate, with an average of 2.33 animals per hour. The significant explanatory variables were sub-region, hourly start time, decimal month, year, and transit (Table 4.2, Figure 4.3). Decimal month was described as a nonparametric spline fit. More whales were seen during stationary periods than during transit periods, as expected since stationary periods were typically initiated for detailed studies of whales. Sightings increased from June to August, then decreased through November. Animals were seen more often in the Santa Barbara Channel, south of the Channel Islands, and in the San Nicolas regions relative to the rest of the study area. Sighting rates decreased between 2002 and 2003, due in part to reduced effort in regions of high sighting probability in those years. Sighting rate increased moderately with time of day, also an artifact of the distribution of effort.

AB Caller Acoustic Encounter Rate Model

AB caller encounter rates were also temporally and spatially variable, with an average encounter rate of 0.72 animals per hour. The encounter rate of singing blue whales based on model selection was explained by decimal month, transit, and sub-region variables (Table 4.2, Figure 4.4). Singing blue whales were more common in the early fall with fewer detections in June and November. The probability of detecting a singing blue whale was modestly higher in stationary mode, since stationary mode was commonly initiated when several calling blue whales were detected acoustically. Spatial variability was evident with the highest encounter rates (>1 animal per hour) occurring in the San Nicolas and SW San Nicolas regions, followed by the Butterfly Bank, Cortez and Tanner Banks, and Inshore regions.

Since sub-region was an important predictor for the AB caller and sighting rate models, the difference in the encounter rate between the detection types was tested for significance using a bootstrap test for the equality of means for each sub-region. The achieved significance level (ASL) of each test, equivalent to the p-value (Efron and Tibshirani 1998), is shown for each sub-region in Figure 4.6. The probability of visually encountering a blue whale was significantly greater than the probability of acoustically encountering an AB calling whale in the Santa Barbara Channel (SBC), South Channel Islands, and San Nicolas regions of the study area. More similar visual and AB caller encounter rates occurred in the central and south-eastern regions of the Southern California Bight and Pt. Arguelo.

D Caller Acoustic Encounter Rate Model

Variability in the average acoustic encounter rate for D callers of 0.46 animals per hour was explained by seasonal changes in encounter rate and a dependence on sighting rates (Table 4.2, Figure 4.5). D callers were encountered in the highest numbers in June, with sharply decreasing numbers into the late summer and fall. The number of D callers was related to the number of animals seen per hour (Figure 4.7). The encounter rate of D callers is likely biased downward due to the assignment of calls on similar bearings to a single caller.

Discussion

Seasonality

Seasonal variation in blue whale encounter rates is expected. Blue whales are migratory and spend only a portion of the year in the Southern California Bight before returning to lower latitude breeding grounds (Calambokidis *et al.* 1990, Mate *et al.* 1999). The temporal offset among the three different encounter types (visual, AB caller and D caller) indicates that a single detection mode may not adequately survey the entire blue whale population seasonality. This finding is similar to the seasonal shift observed between B and D calls using autonomous acoustic recorders (Chapter 3).

Seasonal differences in blue whale call types, suggested by our models, may be related to the foraging and reproductive behaviors. Each blue whale call type (AB song calls, AB single calls, and D calls) is associated with a different behavioral and environmental context. The two call types examined here, AB song and D calls, are the most distinctive in their behavioral context. Feeding whales of both sexes produce D calls (Chapter 2). Foraging animals migrate into the Southern California Bight early in the summer. Type D calls associated with foraging should be the most predominant call type during the early summer as suggested by our models (Figure 4.8). During fall, the breeding season approaches, and production of calls associated with mating should increase. AB song calls are heard from male blue whales (Chapter 2, McDonald *et al.* 2001) that are commonly traveling (Chapter 2, Thode *et al.* 2000, Watkins *et al.* 2000, McDonald *et al.* 2001, Clark and Ellison 2004) and probably function as a mating display. While AB calls can be heard year-round (Stafford *et al.* 2001), the fall increase in AB callers relative to visual sightings indicates that the proportion of AB callers increases in fall.

Seasonal differences in visual and acoustic detection have implications for interpretation of blue whale abundance surveys. D caller encounters and visual encounters share a June peak, with declining encounters into the fall. Other visual surveys for blue whales indicate a summer peak in their abundance in the Southern California Bight (Forney and Barlow 1998, Larkman and Veit 1998, Carretta *et al.* 2000). The increased proportion of AB callers in the fall and winter indicates more animals are traveling, rather than feeding or milling, increasing the proportion of animals potentially missed by visual surveys. If the goal of the survey is to derive a single estimate of abundance, AB callers will likely be accounted for earlier in the season. However, if the goal is derive seasonal estimates of abundance, acoustic monitoring for AB callers will be necessary, particularly in the fall and winter.

Spatial Variability

The significant spatial variability observed for visual encounters and AB caller encounters (Figure 4.6) is likely indicative of the dynamic oceanography in the Bight. Large aggregations of blue whales are consistently observed in the northern portion of the study area. The distribution of blue whales within the region is determined in part by their attraction to areas of predictably high prey density (Croll *et al.* 1998), such as the northern Channel Islands. High prey density is sustained by levels of high primary productivity downstream from coastal upwelling centers. This productivity may also explain the elevated visual detection rates in the Cortez and Tanner Banks and Butterfly Bank regions, as the dynamic bathymetry in those regions may encourage high euphausiid densities.

The Cortez and Tanner Banks and Butterfly Bank sub-regions are among the highest in AB caller acoustic encounters, along with the San Nicolas and SW San Nicolas regions. Several effort hours have only acoustic detections, while others have only visual detections (Figure 4.2). Hours with both visual and acoustic detections represent detections of different groups, with the animals that are seen independent of those that are heard. The coherence between the visual and acoustic encounter rates in the Cortez and Tanner Banks and Butterfly Bank regions suggest that these areas may represent portions of the Bight important to both feeding and traveling whales. In these regions, concurrent visual and acoustic monitoring may be important, as the two methods are nearly completely complimentary, sampling separate but equal proportions of the local population.

Calibration of Acoustic Surveys

Acoustic and visual survey detection rates have different detection range limitations. Acoustic detection range is dependant on physical and biological features, such as water temperature, bathymetry, ambient noise, and the directionality and amplitude of produced calls. Acoustic survey methods offer the ability to detect vocal cetaceans when they are not available to visual methods due to darkness, poor weather, or availability of animals at the sea surface. Visual detection range is dependant on sea state and weather, and the visibility of animals at the surface. Acoustic detection distances can be tens of km or greater for baleen whales (McDonald 2004), whereas visual survey detection distances are generally on the order of a few km.

Exact calculation of acoustic detection distance requires one to know either the amplitude of the call and acoustic transmission properties of the water column, or to have enough sensors for localization of a calling whale. Neither of these conditions was met during our survey. On two occasions when blue whales were initially encountered acoustically, leading to eventual visual identification, the whales were found up to 10km from the first acoustic detection. This distance is outside of visual detection range. The temperate waters of the Southern California Bight are generally downward refracting (Richardson *et al.* 1995, Clark and Fristrup 1997), and the bathymetry of the Bight is complex, likely limiting detection distances from near-surface hydrophones to tens of km or less. Acoustic detection distance is also likely to vary among survey regions and seasons. Comparison among regions and seasons may be impacted by changes in detection distance. These difficulties in estimating acoustic detection distance will be problematic for most surveys using sonobuoys for the detection of whales.

Our blue whale encounter rate models (Table 4.2) indicate that each encounter mode (visual, AB caller, D caller) is predicted by a unique combination of spatial, temporal, and behavioral factors. The seasonal dependence in all three encounter types and the spatial variability in visual and AB caller encounters complicate the relationship between visual and acoustic encounter rates. Our encounter rate models found that the proportion of animals producing AB calls increases during the season and that the number of AB callers is not predicted by the number of animals seen. This suggests that this commonly reported and widely studied call type is, in general, not a good indicator of overall whale density. In contrast, the encounter rate of D callers closely tracked visual encounters seasonally and spatially, with D caller encounter rate ultimately predicted by the number of animals seen. Similar behaviors and environmental features govern the distribution and detectability of whales that are seen and whales that are heard D calling.

The presence of D callers is a better indicator of blue whale distribution and abundance than AB callers; however, the variability in sweep rate and frequency content of D calls produced by a single animal complicate the distinction of nearby whales by frequency and amplitude characters. By counting only unique bearings, rather than individual calls, we have eliminated the possibility of counting two or more calling whales on a similar bearing. The relationship between D callers and visual sightings does appear to show an upper limit to the number of callers that may be identified. More research is required on the potential for a density-dependant relationship between D calling and the number of animals present; however, it does appear that counting D calls, as opposed to counting D callers, may be a more robust means of estimating the number of animals in a region.

The distinct spatial and temporal detection of AB callers versus visual encounters indicates that neither visual nor acoustic surveys uniformly survey blue whale presence (Figure 4.2). Blue whales are commonly heard on ship surveys during which they are rarely seen (Clark and Fristrup 1997, Rankin *et al.* in press, Širović *et al.* in prep, this study), potentially yielding estimates of the number of animals missed by visual surveys alone. The utility of acoustics for detecting vocal cetaceans has been proven many times (Mellinger and Barlow 2003). The question is: are encounters of AB calling whales useful for estimating abundance? AB calling is an unpredictable behavior and represents only males of the population. However, it is clear that acoustic monitoring for this call type does account for a portion of the population generally not surveyed visually. Nonetheless, relatively low encounter rates compared to visual surveys, and the nearly complete independence between those animals that are seen and heard suggest that acoustic surveys alone will not be an effective for estimating abundance.

Limitations of the Survey Design

The inclusion of the 'year' and 'time-of-day' predictors in the visual encounter rate model are likely not indicative of a real decrease in the use of the Southern California Bight from 2000 to 2003 or of an increased sightability of blue whales later in the day. While the algorithms of the generalized additive model are designed to remove the dependence of the response variable on each of the predictors in turn, the dependencies in highly confounded data may be difficult to deal with fully. For example, the largest aggregations of blue whales were found in the Santa Barbara Channel (SBC), south of the Channel Islands (S. Channel Is.), and San Nicolas Island (San Nic.) sub-regions.

However, in 2003, no regions north of San Nicolas were surveyed due to the necessity to keep the ship in the southerly regions to aid in other studies. As a result, overall encounter rates fell from 2000 to 2003 during this survey, while in fact, the blue whale population is thought to be increasing (Calambokidis and Barlow 2004), potentially due to inter-annual variability in habitat use. Similarly, an increase in detection rates throughout the day is related to the common transition to a stationary survey mode later in the day. It is likely that the lack of an evenly distributed sample, annually and daily, has led to the inclusion of these variables in the prediction of visual encounter rate. A systematic survey would likely not show this dependence on time of day or year.

The shipboard survey described here was not systematic. While our results may vary significantly from systematic surveys of blue whale abundance and distribution in the Bight, these results do provide some insight into the utility of acoustic surveys for the detection of blue whales during ship-based surveys, and for evaluating the results of autonomous acoustic records. The relationship between visual and acoustic detection rates is important to establish if acoustic surveys, either mobile or autonomous, are going to be a robust means for estimating cetacean abundance. Many surveys have shown that acoustic monitoring is a valuable addition to a survey, despite the inability to incorporate acoustic detections into the estimate of abundance. Statistical techniques to estimate abundance based on visual surveys are well understood; however, the modifications necessary to estimate abundance from acoustic surveys have not yet been developed. Further study on the acoustic behavior of blue whales should help us better understand the patterns observed here and make quantitative connections between visual and acoustic encounter rates.

Tables and Figures

Table 4.1. Predictor variables available during stepwise construction of visual and acoustic encounter rate models. Type cat = categorical, cnt = continuous, int = integer. Some predictor variables were grouped for model selection. A region group included NSregion and Sub-region, and a Month group included decMonth and Month. The variables used in each model are indicated by an "X".

Variable name	Description	Type	Values	Sighting GAM	AB caller GAM	D caller GAM
transit	Ship transiting? (1 =>5nmi/hr)	cat	{0, 1}	X	X	X
NSregion	1 = north of 33.5^{0}N 0 = south of 33.5^{0}N	cat	{N, S}	X	X	X
Sub-region	Nine subdivisions of Southern California Bight study area	cat	{Pt.Arguelo, SBC, S.Channel Is., San Nic., SW San Nic., San Clemente, Cortez Bank, Butterfly Bank, Inshore}	X	X	X
Month	Month of each effort day	int	[6, 7,…, 11]	X	X	X
decMonth	Month + day/length(month) for each effort day	cnt	(6.63, 11.13)	X	X	X
Year	Year of each effort day	int	[2000, 2001, 2002, 2003]	X	X	X
Stime	Start time of each effort hour	cnt	(6:00, 20:00)	X	X	X
Beaufort	Average Beaufort sea state during hour	int	[0, 1,…, 6]	X		
Visibility	Average observer visibility in nm during each hour	cnt	(0.25, 12)	X		
Animals	Number of animals seen per hour	int	[0, 1,…, 25]		X	X

Table 4.2. Final model parameters for visual and acoustic encounter rate models. The contribution of each variable to model fit may be evaluated by the change in deviance (Δ Deviance) with the addition of that predictor variable. The number of degrees of freedom, deviance, and the AIC of the null model are presented in parentheses to indicate model selection starting values. The change in AIC (Δ AIC) represents the increase in model fit versus the addition of degrees of freedom (Δ df) at each step of model selection.

Model	**Δ df**	**Δ Deviance**	**Δ AIC**	**F Value**	**Prob. (F)**
AB caller model					
Null model	(368)	(242.899)	(410.245)		
+ poly(decMonth,2)	2	-31.274	-43.7827	30.724	<0.0001
+ transit	1	-18.557	-25.2665	42.532	<0.0001
+ Subregion	8	-13.216	-16.1306	2.825	0.0047
D caller model					
Null model	(368)	(253.827)	(464.308)		
+ poly(Month,2)	2	-35.055	-86.6801	34.893	<0.0001
+ Animals^0.5	1	-35.562	-49.1002	70.795	<0.0001
Sighting model					
Null model	(368)	(6871.664)	(2167.24)		
+ Subregion	8	-2116.256	-648.997	21.514	<0.0001
+ Stime	1	-138.739	-46.743	11.284	0.0009
+ s(decMonth,3)	1	-40.024	-49.446	3.255	0.0721
+ Year	1	-55.707	-86.031	4.531	0.0340
+ transit	2.99	-168.262	-0.714	4.563	0.0038

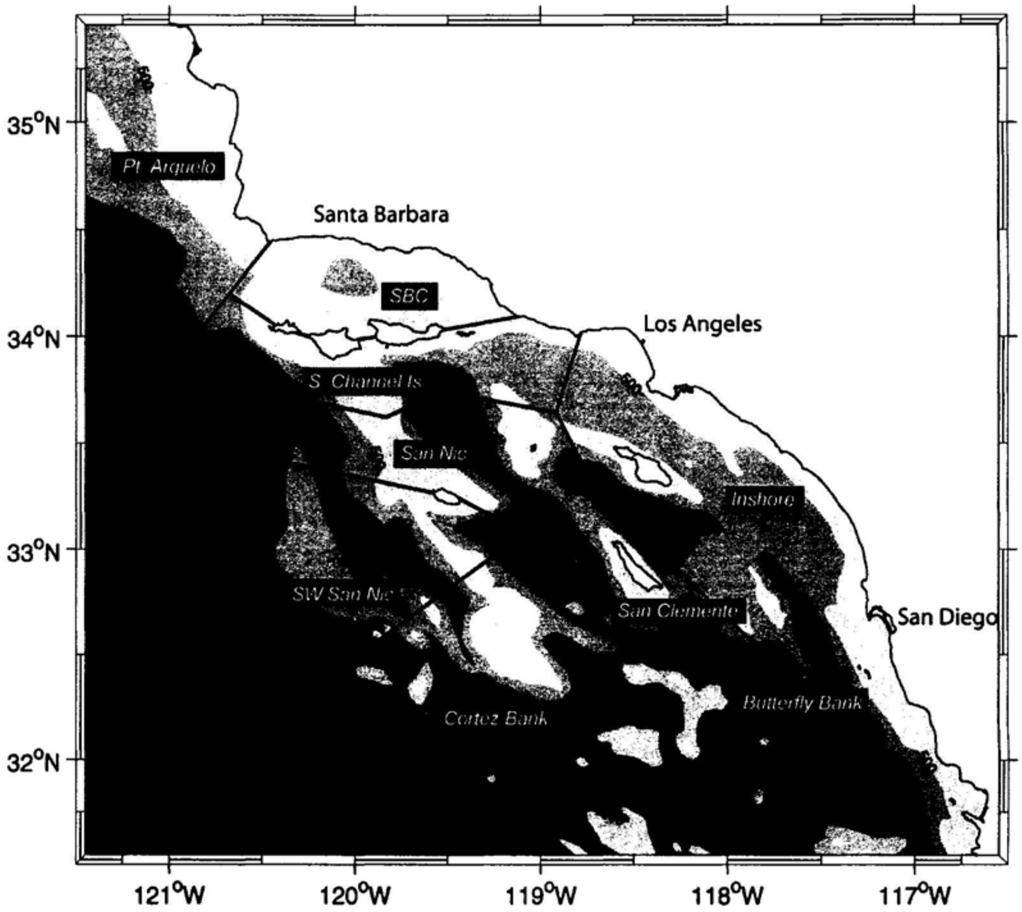

Figure 4.1. Southern California Bight study area. The nine subjectively defined sub-regions are shown overlaid on the bathymetric contours of the Bight. A north-south division (not shown) at 33.5^{0}N was also available during model selection. That division was not chosen in any of the encounter rate models. SBC = Santa Barbara Channel.

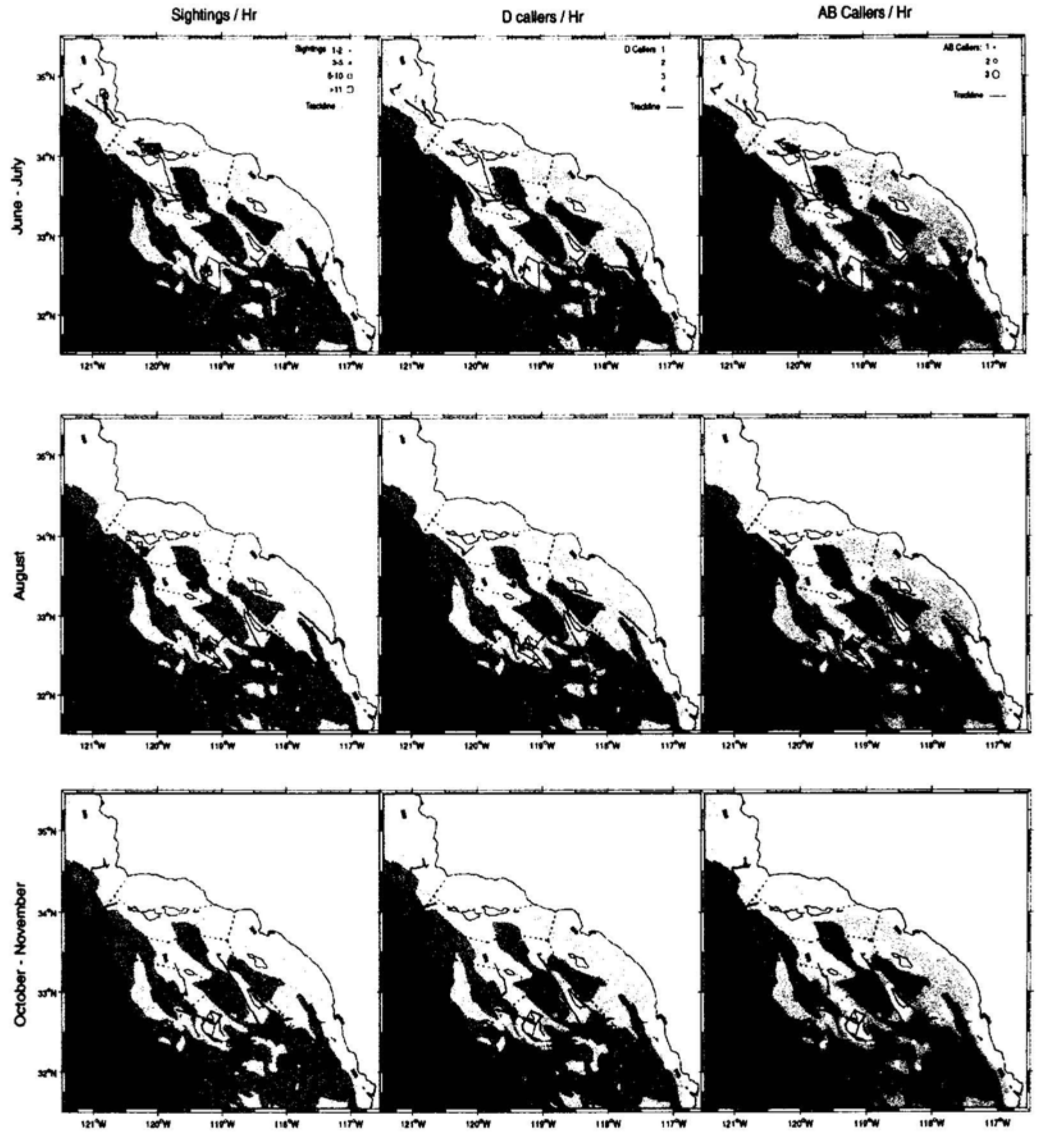

Figure 4.2. Visual and acoustic blue whale encounters from 2000 to 2003 organized in rows by month, and in columns by detection type. Rows (top to bottom): June-July, August, and October-November. Columns (left to right): Sightings/hr (green), D callers/hr (yellow), AB callers/hr (red). The number of animals encountered through each survey method is represented on the maps sized according to the number of whales counted, as shown in the legend in the top row. Track lines for the entire survey are shown as black lines. Sub-region divisions are shown by dotted black lines. Refer to Figure 4.1 for the name of each sub-region.

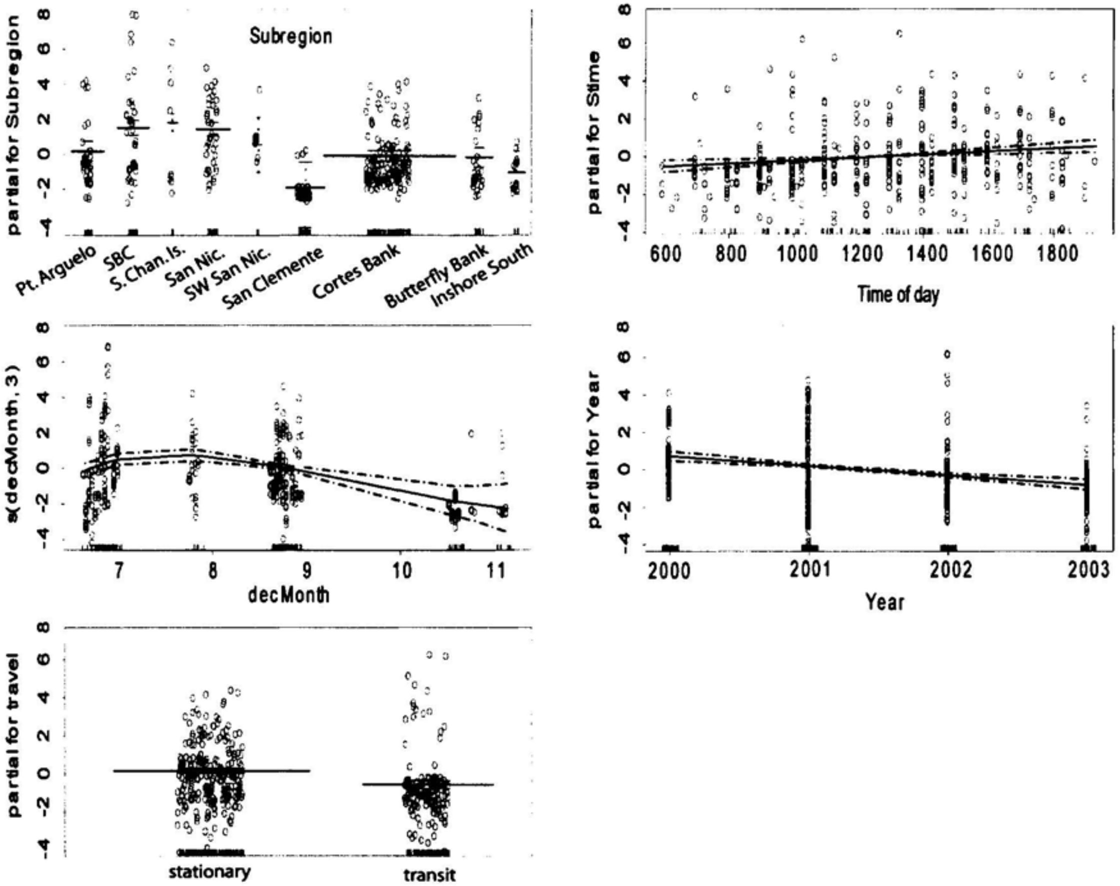

Figure 4.3. The mean-adjusted partial fit of each predictor variable for the visual encounter rate model. The plots show the average of the partial fit (-), the standard error of the fit (·--·), and the partial residuals (o). The vertical lines along the x-axis indicate the number of observations at each value of the predictor variable. The survey was considered stationary when the ship traveled less than 5 nmi/hr.

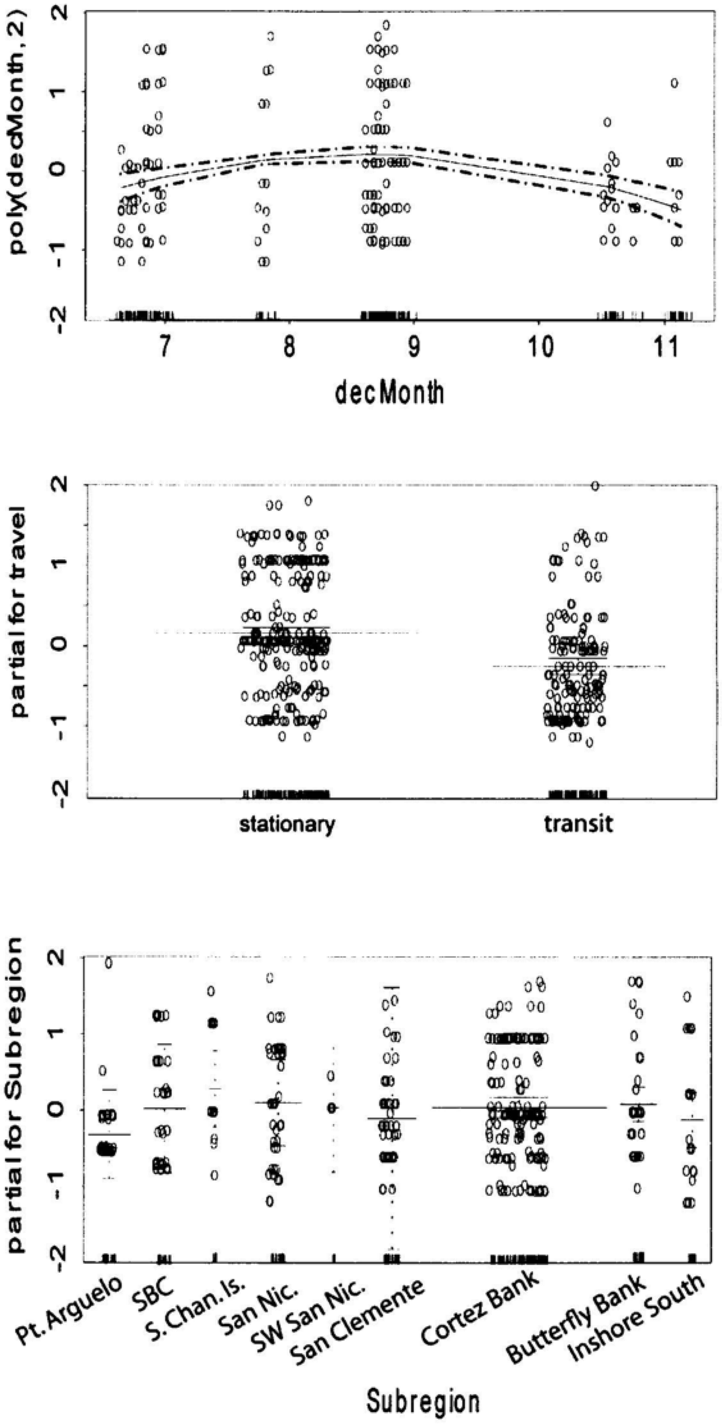

Figure 4.4. The mean-adjusted partial fit of each predictor variable for the AB caller acoustic encounter rate model. The plots show the average of the partial fit (-), the standard error of the fit (·-·), and the partial residuals (o). The vertical lines along the x-axis indicate the number of observations at each value of the predictor variable. The survey was considered stationary when the ship traveled less than 5 nmi/hr.

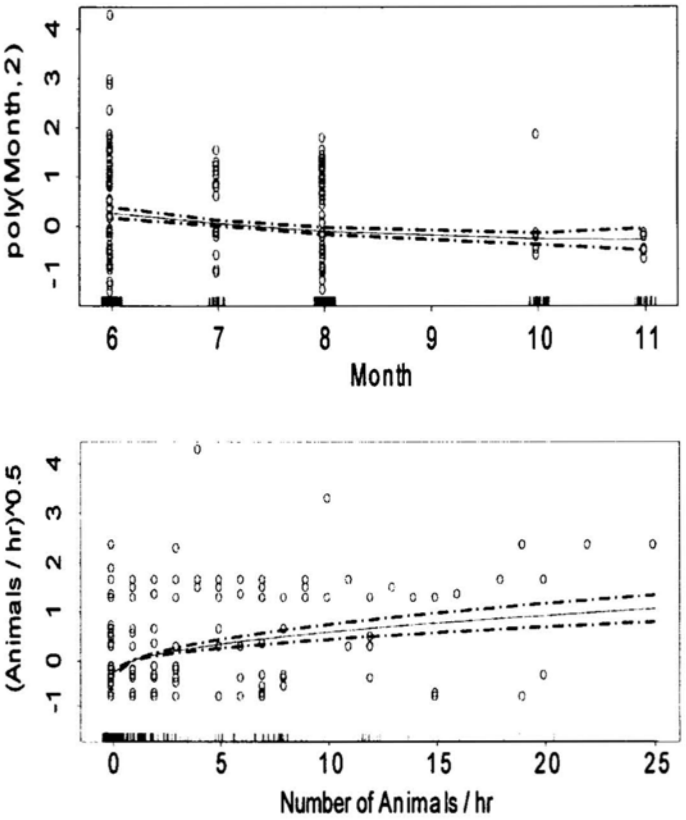

Figure 4.5. The mean-adjusted partial fit of each predictor variable for the D caller acoustic encounter rate model. The plots show the average of the partial fit (-), the standard error of the fit (·-·), and the partial residuals (o). The vertical lines along the x-axis indicate the number of observations at each value of the predictor variable.

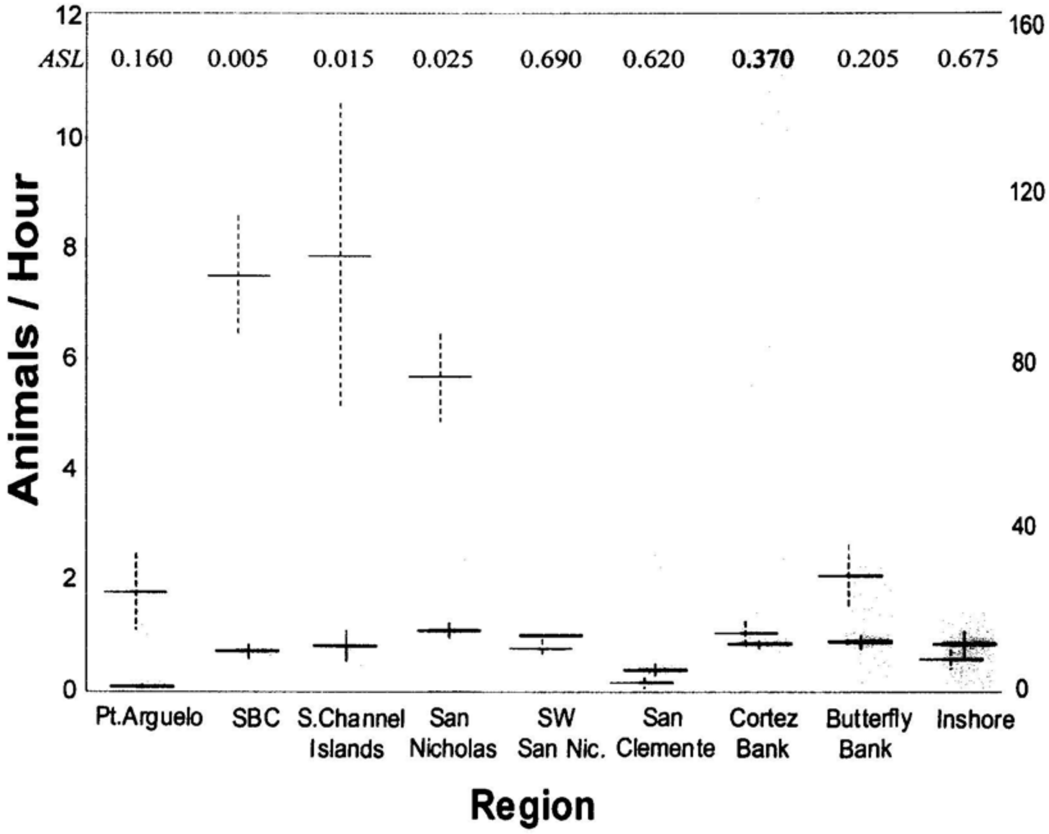

Figure 4.6. Visual and AB caller acoustic encounter rates for each of sub-region. Sub-region was chosen as a significant predictor of encounter rate for both models. The mean and bootstrap standard errors (SE), based on 200 bootstrap samples of the predicted values, are given for each encounter type in each sub-region. Encounter rates are indicated in the figure as follows: visual mean = grey line, visual SE = dotted line, acoustic mean and SE = black lines. The number of effort hours in each sub-region is shown by the grey bars and indicated along the right axis. The null hypothesis that the visual encounter rate was equal to the AB caller acoustic encounter rate in each sub-region was tested using a bootstrap test of the equality of means (Efron and Tibshirani 1998), a bootstrap analog to the Student's t-test (Efron and Tibshirani 1998). The achieved significance level (ASL), an approximation to the p-value, is shown along the top axis for each region.

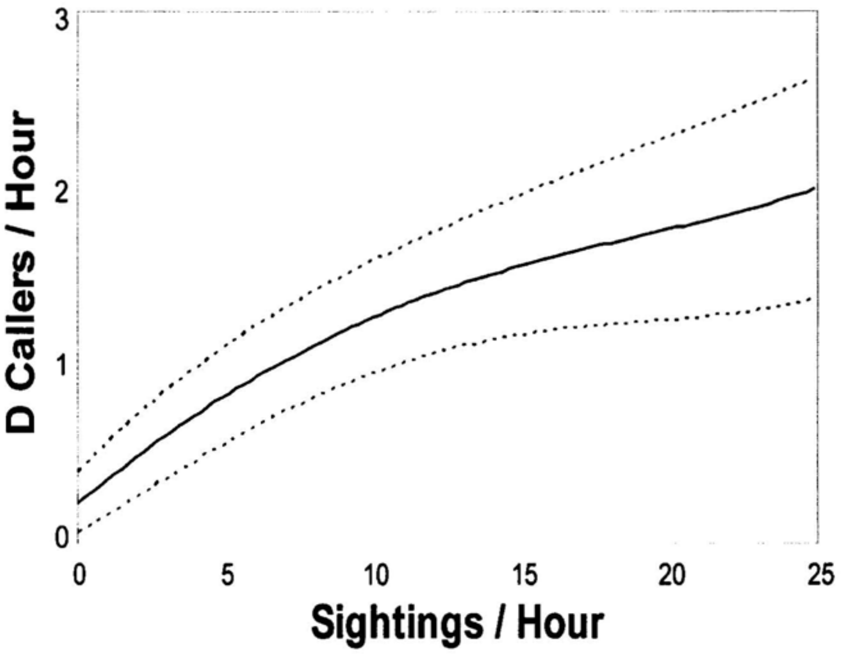

Figure 4.7. D caller acoustic encounter rate was predicted by the number of blue whales seen per hour. This relationship is likely an underestimate due to the inability to count all animals producing D calls when animals occurred on similar bearings.

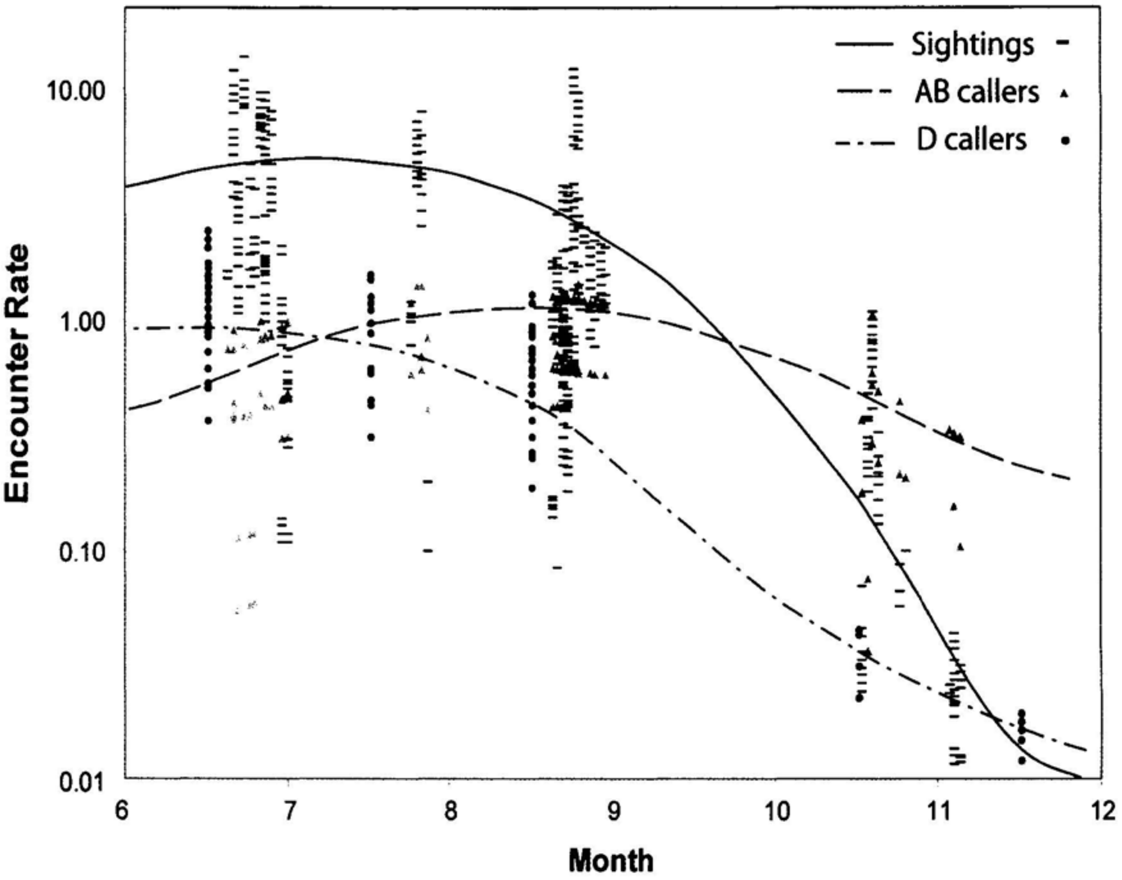

Figure 4.8. Visual and acoustic encounter rate (animals/hr) model predictions by Month. Point-wise predictions for each model type are shown as symbols indicated in the legend in the upper right corner. Point-wise predictions are based on the best-fit model with the variability in predicted values each month based on the range of the other input variables included in the model (Table 4.2). The smoothed average prediction for each model is shown by the line indicated in the legend. The line results from the inversion of the model coefficients using the specific link function. Note the log scale of the y-axis.

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The text of Chapter 4, in full, is in preparation for submission to the Journal of Cetacean Research and Management. The dissertation author was the primary researcher and the co-authors listed in this manuscript supervised the research which forms the basis of the chapter.