UNIVERSITY OF CALIFORNIA, SAN DIEGO

Risso's and Pacific White-sided Dolphins in the Southern California Bight:
Using Echolocation Clicks to Study Dolphin Ecology

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

by

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The dissertation of Melissa Sue Soldevilla is approved, and it is acceptable in quality and form for publication on microfilm:

Chair

University of California, San Diego

2008

DEDICATION

This thesis is dedicated to my son, Kai Soldevilla, for greeting me with a bright smile every morning and reminding me of all the joy that exists in the world when we treat it with care and protect the life within it.

> You're in charge of the last of the truffula seeds.
> And truffula trees are what everyone needs!
> Plant a new truffula. Treat it with care.
> Give it clean water, and feed it fresh air.
> Grow a forest. Protect it from axes that hack.
> Then the Lorax, and all of his friends may come back.
> **Dr. Seuss**, *The Lorax*

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Starting a new family while pursuing graduate studies presents its own unique challenges and triumphs. Mario Soldevilla has bee an amazing husband helping me to meet and surpass every challenge and celebrate every triumph. He deserves extra special thanks for putting up with me and always taking such wonderful care of our family under any circumstances I threw at him. Both Kai and Mario have been a wonderful grounding source as well as a source of inspiration and fun and they mean all the world to me. Additionally, I've been blessed with an amazing extended family who have provided support and love through all of my endeavors. My parents have always encouraged my determination and drive while helping me to find a way to achieve my dreams. My sister has always believed in me which kept me going when times were rough. My in-laws took me in right from the start and provided a home away from home and a new perspective on the world for which I will always be grateful. A special thanks is due to my mother-in-law who made sure a clean home was never a worry and was quick to hop on a plane anytime we needed a helping hand and heart.

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ABSTRACT OF THE DISSERTATION

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This dissertation examines the efficacy of using passive acoustic monitoring of dolphin echolocation clicks to study ecological questions about spatial and temporal distribution patterns and the influence of environmental variability on dolphin activity. First, the groundwork is laid by examining echolocation clicks recorded from concurrent visual and acoustic surveys and testing whether species-specific features exist in the spectral content of clicks recorded in the presence of five delphinid species: short-beaked common dolphins (*Delphinus delphis*), long-beaked common dolphins (*Delphinus capensis*), bottlenose dolphins (*Tursiops truncatus*), Risso's dolphins (*Grampus griseus*), and Pacific white-sided dolphins (*Lagenorhynchus obliquidens*). Unique spectral banding patterns are discovered only for Risso’s and Pacific white-sided dolphins and two distinct click types are found for Pacific white-sided dolphins. Next, autonomous recordings from six sites are analyzed for the presence of Pacific white-sided and Risso’s dolphin click bouts and diel, seasonal, and interannual variability in click activity are described. Risso’s dolphins are more vocally active during the night which I suggest is related to foraging on diel vertically migrating squid. Seasonal and interannual variability in Risso’s dolphin call activity are high. Comparisons of diel, seasonal and spatial variability of the two Pacific white-sided click types are made and the two click types are shown to exhibit differences in usage patterns. This comparison reveals a southern and northern distribution pattern between the click types adding support to the hypothesis that the two click types represent the two morphologically and genetically distinct populations which overlap in the study area. Finally, the ability to predict variability in click activity is examined with respect to the environment by building generalized additive models. Remotely-sensed environmental variables are modeled with respect to current time and time-lagged data to examine questions about the underlying oceanographic processes which may lead to dolphin occurrence. The inclusion of time-lagged environmental data can improve predictive models and allows a realistic time frame for conservation and management mitigation efforts. Passive acoustic monitoring of echolocation clicks has revealed patterns in diel activity and seasonal movements of Risso’s and Pacific white-sided dolphins and shows promise for improved predictive habitat models.

CHAPTER 1

INTRODUCTION

"The considerable difference between the sounds we heard in the presence of [numerous odontocete species] encourages us to hope that these underwater calls may be sufficiently characteristic to be helpful in distinguishing cetaceans at sea. Such listening probably will have to be carried into the supersonic range"

Schevill & Lawrence 1949

The Southern California Bight (SCB) is a region of rich ecological diversity that supports a wide variety of cetacean species. Cetaceans are top predators in this ecosystem and protected by federal laws. The SCB has abundant natural resources and many of the unique features that make it an ideal habitat for cetaceans also make it an ideal location for many human recreational and commercial activities, some of which may have negative impacts on cetaceans. The SCB is home to two major gillnet fisheries which are known to kill cetaceans through incidental entanglement (Julian and Beeson, 1998). Los Angeles and Long Beach harbors are major shipping ports and a large amount of traffic passes through the shipping lane between the California Coast and the Northern Channel Islands. Ship strikes and shipping noise are potential threats to many cetacean species. Over 25 offshore oil platforms are distributed along the southern California coastline (McCrary et al., 2003). Oil spills from offshore drilling and marine tankers are a potential threat to cetaceans (Loughlin et al., 1996). San Diego Harbor and the offshore San Clemente Island are home to active naval bases and are the location of numerous naval activities, including active sonar training operations which have been linked to the strandings of beaked whales (Evans and England, 2001). To comply with federal laws and minimize the impact of anthropogenic activities on cetaceans, a basic knowledge of their abundance, distribution, behavior and movement patterns is necessary.

While cetaceans offshore of southern California are some of the best studied cetaceans in the world, large gaps in basic knowledge of their ecology remain. This is in part due to the difficulties inherent in studying these patchily distributed animals over wide areas of the ocean from ship and aerial based surveys and in part due to the great variability in their responses to oceanographic variability. Ship-based visual surveys (e.g. Forney and Barlow, 1998) are limited in spatial and seasonal coverage, the conditions they can survey under, and by cost considerations. Most studies are limited to nearshore areas that are more easily accessible, to seasons in which weather conditions are mild, and to daytime when light is available for surveying. Aerial surveys are able to cover greater areas and rougher conditions expanding their range and seasonal coverage, but they are extremely dangerous and have been limited to studies of endangered species for which no better method is available. Both methods perform poorly at detecting long-duration diving cetaceans. In terms of oceanographic variability, the development of habitat models offer promise for distinguishing between changes in abundance and changes in distribution on seasonal and interannual timescales.

Passive acoustic monitoring can overcome some of the difficulties inherent to visual surveys; however, this method also comes with its own unique challenges. Sound travels great distances underwater and cetaceans have adapted to take advantage of this fact. Passive acoustic monitoring takes advantage of the abundant vocalizations produced by marine mammals. Recordings can be made concurrently with ship-based visual surveys to enhance cetacean detections. Additionally, autonomous recording packages can be deployed at remote locations and record continuously through day and night, across seasons and years at low expense. This offers a tremendous increase in the ability to sample animals 24 hours a day and across seasons when rough weather and darkness preclude the use of visual surveys. Long-duration divers are often sampled better with acoustics than visual surveys (Barlow and Taylor, 2005). However, for acoustic methods to be useful to study distribution and abundance: 1) vocalizations need to be classifiable at least to the species level, 2) behavioral patterns of vocalization need to be known, 3) animals should be localizable to understand detection probability, and 4) propagation conditions and potential masking sources should be understood.

Many baleen whale calls are highly stereotyped and, for these, acoustic species classification methods are reliable (e.g. fin whales, *Balaenoptera physalus*, (McDonald et al., 1995); blue whales, *Balaenoptera musculus*, (Thompson et al., 1996; Stafford et al., 1999); minke whales, *Balaenoptera acutorostrata*, (Rankin and Barlow, 2005)). Calls of most odontocete species are much more variable, and include tonal whistles, broadband echolocation clicks and burst-pulsed calls. Only those species with highly distinct calls, such as sperm whales (*Physeter macrocephela)*, some beaked whales, and some populations of killer whales (*Orcinus orca*), are currently acoustically classifiable (Ford, 1989; Goold and Jones, 1995; Madsen et al., 2005a; Zimmer et al., 2005). Delphinids have been particularly challenging as most research has been limited to lower frequencies (<24 kHz), the region that contains whistles which are often as variable between species as they are within species. Most research into dolphin echolocation has focused on its function in biosonar applications and the few studies that have investigated species specificity have shown little promise (e.g. Nakamura and Akamatsu, 2003); however much of this work has focused on a limited number of click features from captive animals and have only included echolocation clicks recorded on-axis, i.e. along the main axis of the directional beam pattern. Recent advances in passive acoustic monitoring technology allow continuous recording up to 100 kHz, extending acoustics into the frequency range of echolocation clicks. Now is an excellent time to revisit Schevill and Lawrence's (1949) hypothesis that states that extending recordings into the supersonic range may reveal species specific differences between delphinid calls.

The overarching goals of this dissertation are to determine whether high-frequency echolocation clicks contain species-specific information that will enable researchers to distinguish them in long-term autonomous recordings and to examine spatial and temporal variability in dolphin occurrence from autonomous recordings in the SCB. Additionally, predictive habitat models are developed that correlate dolphin occurrence with environmental variability to investigate the ecology and seasonal movement patterns of dolphins for use in mitigation of potential impacts of anthropogenic resource use off Southern California.

BACKGROUND

Odontocete call descriptions

Beginning with the first recordings of underwater sounds of beluga whales (*Delphinapterus leucas*) almost sixty years ago (Schevill and Lawrence, 1949), researchers have tried to describe the variety of sounds produced by odontocetes and their behavioral contexts. Initial studies based call descriptions on aural representations and included such expressive names as barks, squeals, screams, buzzes, squawks, chirps, rasps, blats, and yelps (Wood, 1953; Pryor et al., 1965; Schevill et al., 1966; Caldwell and Caldwell, 1968; Caldwell et al., 1969; Watkins and Schevill, 1972; Norris et al., 1994). Later studies aimed to quantify and consolidate the variety of call types and today calls are divided into three major subdivisions: narrow-band whistles, broadband echolocation clicks and broadband pulsed calls (Richardson et al., 1995). While the precise distinctions between these call types are somewhat arbitrary (Murray et al., 1998), they remain useful classifications.

Whistles are lower frequency tonal sounds, with fundamental frequencies generally ranging between 1-25 kHz (Richardson et al., 1995), although whistles of some species have been reported as high as 40 kHz (Oswald et al., 2004). Not all species of odontocetes produce whistles, with notable exceptions including sperm whales, porpoise species and members of the Cephalorhynchus genus. (Herman and Tavolga, 1980). Whistles are thought to function in social interactions (Herzing, 2000; Lammers et al., 2003), and their function as contact calls, “signature” whistles or part of a variable repertoire has been a controversial topic over the last decade (Caldwell et al., 1990; McCowan and Reiss, 1995; Janik and Slater, 1998; Janik, 1999; Smolker and Pepper, 1999; McCowan and Reiss, 2001; Fripp, 2005; Janik et al., 2006). Due to the ease of recording this call type with commercially available recording devices, whistles have received the most attention in studies of species-specificity (Steiner, 1981; Wang et al., 1995; Rendell et al., 1999; Oswald et al., 2003; Oswald et al., 2004). Species with particularly distinctive whistles have shown high classification successes while others remain a challenge (Oswald et al., 2007).

Studies of pulsed calls have been limited, possibly because their high variability causes difficulties in defining and categorizing them (Murray et al., 1998). One definition for these click types are broadband (5-150 kHz) click trains with interclick intervals less than 5 ms, the lower extent of human auditory temporal perception, which leads humans to hear them differently as illustrated by descriptive terms such as screams, squeals and moans (Murray et al., 1998). Among the best studied of these calls are those produced by killer whales, denoted “discrete calls”, which can be classified to species and matrilineal subgroup (Ford, 1989). Pulsed calls have been described as having a social function, particularly in species that do not whistle (Dawson, 1991), but they may also be involved in echolocation. Unique temporal patterns have been described in the burst-pulsed calls of northern right whale dolphins (*Lissodelphis borealis*) (Rankin et al., 2007). Limited effort has been put into species classification of this call type (e.g. Roch et al., 2007).

The last call type are broadband clicks (5-150 kHz), short duration pulses that have been demonstrated to be used in echolocation across numerous species (e.g. Kellogg, 1958; Caldwell and Caldwell, 1971; Evans, 1973; Kamminga and Wiersma, 1981; Au, 1993). The most striking differences in echolocation clicks occur between families. For example, beaked whale clicks are longer duration and exhibit a frequency upsweep (Madsen et al., 2005b; Zimmer et al., 2005), porpoise clicks are longer duration, narrowband polycyclic pulses (Kamminga et al., 1996), while delphinid clicks are typically shorter duration, oligocyclic broadband pulses (Au, 1993). Sperm whales, however, have clicks that fall into opposite frequency extremes (Weilgart, 1990; Madsen et al., 2005a). Clicks have been well studied for use in biosonar and a set of standard click measurements are usually described in the literature, including duration, interclick interval, peak frequency, central frequency, -3 dB, -10 dB and RMS bandwidths and Q-value (Au, 1993).

Behavioral studies

Knowledge of usage patterns of different call types and their relation to behavior is important for understanding and interpreting autonomous acoustic recordings. Studies examining these relationships range across a variety of species, and a summary of the general findings is presented here. Daily activity patterns of the Hawaiian spinner dolphins (*Stenella longirostris*) are among the most thoroughly described of all delphinids (Norris et al. 1994). Spinner dolphins exhibit a stereotypical diel behavioral pattern that involves night-time foraging on the deep scattering layer, movement into protected bays after dawn, a 4-5 hour period of morning rest, followed by active behaviors including aerial behavior and zig-zag swimming in the afternoon before the dolphins head offshore to forage again just before sunset. Spinner dolphins are vocally active whenever they are physically active, with rest periods being a time of unusual silence. Rates of sounds production vary with daily activities. Rates of all call types (whistles, screams, burst-pulses, clicks) were greater during night, foraging and traveling activities (Brownlee, 1983). A study of Atlantic spotted dolphins (*Stenella frontalis*) and bottlenose dolphins (*Tursiops truncatus*) (Herzing, 1996) indicates that most echolocation activity, including razor buzzes, echolocation with rostrum in sand and echolocation with overlapping trills and upswept whistles, were all associated with foraging/feeding behavior, though another click behavior, genital buzzes, were involved in social interactions. Nowacek (2005) found higher rates of echolocation and “pops” during foraging than non-foraging behaviors in bottlenose dolphins off Florida. Similarly, Dos Santos and Almada (2004) and Jones and Sayigh (2002) found that small groups of bottlenose dolphins had increased rates of echolocation during foraging behaviors, but also found decreasing click rates with increasing numbers of animals and suggest that eavesdropping may be important. In a study of Pacific humpback dolphins (*Sousa chinensis*), Van Parijs and Corkeron (2001) found that 76% of click trains occurred during foraging behaviors, while 16% and 7% occurred during socializing and traveling, respectively. Dolphins were generally quiet during travel and milling behaviors. Overall, these studies indicate that the highest rates and occurrence of dolphin echolocation behavior occurs in conjunction with foraging behaviors, however, they are also important during social and traveling behaviors. Resting behavior is a time of low acoustic activity.

DISSERTATION OUTLINE

The first goal of this dissertation is to investigate the potential to identify echolocation clicks to the species level. Chapter two, entitled “Classification of Risso’s and Pacific white-sided dolphins using spectral properties of echolocation clicks” describes the results of this study. Through simultaneous ship-based visual and acoustic surveys, recordings were made of five species of dolphins: long-beaked common dolphin (*Delphinus capensis*), short-beaked common dolphin (*D. delphis*), Risso’s dolphin (*Grampus griseus*), Pacific white-sided dolphin (*Lagenorhynchus obliquidens*), and bottlenose dolphin. Detailed spectral analyses are carried out to examine whether consistent features are present within a species clicks that are distinct between the five species. Unique patterns of spectral peak and notch frequencies are discovered for two of the five species, Risso’s and Pacific white-sided dolphins, which are consistent across schools and distinct between species. Additionally evidence for two distinct click types is presented for Pacific white-sided dolphins. This species and sub-species specificity of echolocation clicks enables us to identify Risso's and Pacific white-sided dolphin echolocation click bouts in autonomously recorded data.

Once clicks can be identified to species, temporal and spatial trends in acoustic activity can be examined. In Chapter three, entitled "Spatial and Temporal Patterns of Risso's Dolphin (*Grampus griseus*) Echolocation Click Activity in the Southern California Bight," two and a half years of data are analyzed from automonous recorders located at six sites throughout the Southern California Bight to investigate trends in diel and seasonal calling activity. Risso's dolphin echolocation activity occurs significantly more during the night than during the day throughout the SCB indicating a consistent behavioral trend which I hypothesize to represent nighttime foraging on diel-vertically migrating squid. No significant trend in seasonal calling activity was found as interannual and site variability was as great as that found among seasons.

The presence of two distinct click types produced by Pacific white-sided dolphins was an unexpected finding. I try to unravel the significance of these two click types in chapter four, entitled "Comparison of Spatial and Temporal Patterns of Echolocation Click Activity for Two Click Types Produced by Pacific White-sided Dolphins (*Lagenorhynchus obliquidens*) in the Southern California Bight." By examining how spatial patterns and diel and seasonal trends of occurrence vary between the two click types, I consider the implications of differences in variation on several hypotheses to determine what the distinct click types may represent.

Finally I examine whether the seasonal, annual and site variability in occurrence of click activity of Risso's and Pacific white-sided dolphins can be explained by variability in the environment. In chapter five, entitled "Habitat Modeling Using Passive Acoustic Recordings: Risso's Dolphin (*Grampus griseus*) and Pacific White-sided Dolphin (*Lagenorhynchus obliquidens*) Click Bout Occurrence in the Southern California Bight," I investigate the power of time-lagged remotely-sensed oceanographic data to predict delphinid acoustic activity using generalized additive models. The incorporation of a time lag into the environmental data allows investigation of the dynamic processes which lead to productivity at high trophic levels and has encouraging implications for mitigation of anthropogenic impacts.

Each of the following chapters is intended to stand alone as a publishable unit, and the reader may encounter some redundancy in the introduction and methods for each chapter. Chapter 2, entitled "Classification of Risso's and Pacific white-sided dolphins using spectral properties of echolocation clicks" has been published in the Journal of the Acoustical Society of America and is presented as part of this dissertation with acknowledgement to the co-authors in the study.

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CHAPTER 2

CLASSIFICATION OF RISSO'S AND PACIFIC WHITE-SIDED DOLPHINS USING SPECTRAL PROPERTIES OF ECHOLOCATION CLICKS

ABSTRACT

The spectral and temporal properties of echolocation clicks and the use of clicks for species classification are investigated for five species of free-ranging dolphins found offshore of southern California: short-beaked common (*Delphinus delphis*), long-beaked common (*D. capensis*), Risso's (*Grampus griseus*), Pacific white-sided (*Lagenorhynchus obliquidens*), and bottlenose (*Tursiops truncatus*) dolphins. Spectral properties are compared among the five species and unique spectral peak and notch patterns are described for two species. Spectral peak mean values from Pacific white-sided dolphin clicks are 22.2, 26.6, 33.7 and 37.3 kHz and from Risso's dolphins are 22.4, 25.5, 30.5, and 38.8 kHz. Spectral notch mean values from Pacific white-sided dolphin clicks are 19.0, 24.5 and 29.7 kHz and from Risso's dolphins are 19.6, 27.7, and 35.9 kHz. ANOVA analyses indicate that spectral peaks and notches within the frequency band 24-35 kHz are distinct between the two species and exhibit low variation within each species. Post-hoc tests divide Pacific white-sided dolphin recordings into two distinct subsets containing different click types which are hypothesized to represent the different populations which occur within the region. Bottlenose and common dolphin clicks do not show consistent patterns of spectral peaks or notches within the frequency band examined (1-100 kHz).

INTRODUCTION

Accurate classification of recorded calls to species is needed for passive acoustic monitoring of wild cetaceans. Passive acoustic monitoring is increasingly being used for towed hydrophone line transect surveys (Barlow and Taylor, 2005) and for remote, long-term monitoring of populations using autonomous instruments (Mellinger et al., 2004; Sirovic et al., 2004; Oleson et al., 2007; Verfuss et al., 2007). Recent technological advances allow long-term recordings to reach higher bandwidths (Wiggins and Hildebrand, 2007), which prompts research into use of higher frequency calls for species classification. Odontocete species regularly emit high frequency clicks and burst-pulsed calls, in addition to lower frequency whistles (Richardson et al., 1995) and usage of these call types varies with behavioral state, geographic location and geometric spacing of conspecifics (Jones and Sayigh, 2002; Lammers et al., 2003; Nowacek, 2005). Advances have been made in classifying delphinid whistles to species (Oswald et al., 2003; Oswald et al., 2004), but little work has focused on classifying delphinid burst-pulses and clicks to species (Roch et al., 2007), particularly at frequencies greater than 24 kHz. While the clicks of porpoises, sperm whales and beaked whales are easily distinguishable from delphinid clicks based on time duration, interclick interval and peak frequency characteristics (Goold and Jones, 1995; Kamminga et al., 1996; Madsen et al., 2005; Zimmer et al., 2005), delphinid clicks thus far have remained unclassifiable at the species level.

Most echolocation click research to date has focused on the performance of sonar systems and only a few studies look for species-specific characteristics. Kamminga et al. (1996) show that four species of porpoises can be distinguished at the sub-family level by time duration and dominant frequency of their clicks. Akamatsu et al. (1998) compare peak frequency and duration characteristics of finless porpoise (*Neophocaena phocaenoides*), baiji (*Lipotes vexillifer*), and bottlenose dolphins (*Tursiops truncatus*) and find that finless porpoise can be distinguished from the two dolphins, but show overlap in duration and frequency between the two dolphin species with a tendency toward lower frequencies from baiji and higher frequencies from bottlenose dolphins. Nakamura and Akamatsu (2003) compare clicks from six captive odontocete species and find that harbor porpoise (*Phocoena phocoena*) and false killer whale (*Pseudorca crassidens*) clicks are distinguishable from four species of dolphin clicks based on click duration and peak frequency. The clicks of baiji, short-beaked common (*Delphinus delphis*), bottlenose, and Pacific white-sided (*Lagenorhynchus obliquidens*) dolphins can not be distinguished from each other with these characteristics (Nakamura and Akamatsu, 2003). To our knowledge, distinct species-specific differences have not been documented within delphinid clicks.

As a result of the focus on dolphin sonar system performance, most research effort has been directed at understanding clicks produced on-axis. However, on-axis clicks may not accurately represent the full ensemble of clicks that will be acquired during passive acoustic monitoring of free-range odontocetes. Au et al (1978) demonstrate significant distortion in the waveshape and spectral content of clicks as a function of beam angle. They establish that off-axis click durations are longer, typically due to multipaths of the initial click pulse, and suggest that the multipaths are due to reflections within the head, from the external environment, or a combination of the two. Internal reflections are dependent upon anatomy and may contain additional information; however, thus far, no study has examined whether the distorted spectra from off-axis clicks contain a species-specific signature. Clicks recorded during passive acoustic monitoring surveys will come from animals of unknown acoustic orientation; therefore detailed spectral descriptions of all recorded clicks are needed for wild dolphins, regardless of orientation.

Five species of dolphins are commonly observed in the waters offshore of southern California. Short-beaked common and long-beaked common (*D. capensis*) dolphins are small dolphins (160-210 cm and 190-240 cm, respectively) (Heyning and Perrin, 1994), typically sighted in offshore tropical and temperate waters in schools of hundreds to thousands of individuals (Evans, 1974; Polacheck, 1987; Selzer and Payne, 1988; Gaskin, 1992; Gowans and Whitehead, 1995). They were only recently recognized as separate species (Heyning and Perrin, 1994). Pacific white-sided dolphins are small dolphins (230-250 cm) (Walker et al., 1986) endemic to cold temperate North Pacific waters (Leatherwood et al., 1984; Green et al., 1992) and are observed in schools ranging between 10-1000 individuals (Leatherwood et al., 1984). The offshore population of bottlenose dolphins consists of medium-sized dolphins (290-310 cm) (Perrin and Reilly, 1984) that are typically sighted in medium-sized groups (1-30) (Shane, 1994) throughout tropical and temperate waters (Forney and Barlow, 1998). Risso's dolphins (*Grampus griseus*) are larger dolphins (400 cm) typically found in medium-sized groups (10-50) in tropical and temperate waters (Leatherwood et al., 1980; Kruse et al., 1999). Click feature measurements have been published for free-ranging Risso’s and bottlenose dolphins and for captive Pacific white-sided, common, Risso’s and bottlenose dolphins (Table 2.1).

This study describes echolocation clicks for five species of dolphins from the southern California region. This is the first study to describe recordings from free-ranging short-beaked common, long-beaked common and Pacific white-sided dolphins.

We describe the spectral content of echolocation clicks with emphasis on spectral peaks and notches and show that two species of dolphins have a unique peak and notch structure. We quantify the intra- and inter-specific frequency variation of these peaks and establish that they represent invariant and distinctive features as required for species specificity (Emlen, 1972; Nelson, 1989) thereby demonstrating their value for species classification in passive acoustic monitoring. Finally, we examine long-term autonomous recordings and quantify the number of click bouts that exhibit the described spectral patterns.

MATERIALS AND METHODS

Study area & survey platforms

Our study area encompassed the region offshore of southern California extending from 32°42’ N, 117°10’ W along the coast to 35°5’ N, 120°47’ W and offshore to 29°51’ N, 123°35’ W and 33°23’ N, 124°19’ W (Figure 2.1). Recordings were obtained in the southern California neritic and pelagic waters between November 2004 and April 2007 (Figure 2.1). Data were analyzed from multiple surveys: California Cooperative of Oceanic Fisheries Investigations (CalCOFI) oceanographic surveys, San Clemente Island (SCI) small boat operations, Scripps Institution of Oceanography (SIO) instrumentation servicing cruises on the R/V Robert Gordon Sproul, and FLoating Instrument Platform (FLIP, Fisher and Spiess, 1963) moored observations (see Table 2.2 for survey and instrumentation details).

The durations of dolphin school recordings obtained from the four studies varied due to differing survey goals. Recording sessions from CalCOFI surveys were typically of short duration because the ship could not deviate from its course to spend time with detected animals. During SIO instrumentation surveys and SCI field operations, the vessel was held stationary as animals swam past and recordings lasted as long as the animals stayed near the boat. Continuous acoustic recordings were obtained from the moored research platform FLIP resulting in recording sessions that last the duration that animals were audible at the FLIP hydrophone array. Data from these recordings were used only when the animals were within 1 km of FLIP as determined by visual observations.

Experienced marine mammal visual observers conducted the visual observation component of this project. Marine mammal detections and species identifications were made by a set number of observers using hand held binoculars, supplemented with 25X binoculars on some platforms. Sighting information included: location of group or animal, initial distance and angle from research vessel, group size, presence of calves, and general behavior. Additionally, weather and sea state data were recorded to account for missed animals due to poor sighting conditions. Acoustic recordings from all surveys were used only for schools that were determined to be single species. If an additional species was detected within 3 km, or if this could not be determined due to sea states greater than Beaufort 3, the recording was not used. Following Oswald et al.'s (2003) whistle study, we consider 3 km a conservative distance for species identification of clicks. Published studies indicate that whistles and echolocation clicks are not detectable beyond about 1 km (Richardson et al., 1995; Philpott et al., 2007), while we find that they are rarely audible beyond 3 km. Differentiation between short-beaked and long-beaked common dolphins is challenging in certain areas off California. In this study, data was used only when the visual identification by species was unambiguous.

Acoustic sensors and digitization

The acoustic sensors used on the different surveys consist of a variety of hydrophone and pre-amplifier configurations (Table 2.2). Two types of omni-directional, spherical hydrophones were used: ITC 1042 hydrophones (International Transducer Corp., Santa Barbara, CA, USA) and HS150 hydrophones (Sonar Research & Development Ltd, Beverley, UK). These hydrophones exhibit a flat frequency response (+/- 3 dB) from 1-100 kHz. The hydrophones were connected to one of three custom-built pre-amplifier and band-pass filter electronic circuit boards: R100A, R100C and R300. The circuit boards were designed to whiten the ambient ocean noise which results in a non-linear frequency response that provides greater gain at higher frequencies where ambient noise levels are lower and sound attenuation is higher. The response increased 20 dB in amplitude from 10 kHz to peak at 90 kHz. The differing frequency responses of the various systems were compensated for during analysis using spectral means subtraction, as described in section II C. Hydrophones and circuit boards were suspended in 2.5-5 cm diameter oil-filled hoses to provide good acoustic coupling to the seawater. Towed hydrophone arrays were weighted with 9 kg of lead wire wrapped around the tow cable ahead of the hydrophone assembly so that the array was towed between 10-30m depth.

The analog signals from the hydrophone circuit boards were converted digitally and recorded with one of two systems: MOTU audio interface and recording software or a Fostex recorder. The MOTU 896HD firewire audio interface (Mark of the Unicorn, Cambridge, MA, USA) is capable of sampling 8 channels at 192 kHz with 24 bit samples. Each channel therefore had a Nyquist frequency of 96 kHz. Gain on the MOTU is adjustable with trim knob controllers and has a light emitting diode read-out of the signal amplitude. The knobs were adjusted to minimize clipping while maximizing signal strength and settings were noted. Signals were recorded directly to a computer hard-disk drive using the sound analysis and recording software Ishmael (Mellinger, 2001), with the instrumentation gain set to either -80 or -100 dB. The MOTU/Ishmael system has a flat frequency response (+/- 0.05 dB) from 1-90 kHz. The Fostex FR2 field memory recorder (Fostex America, Foster Electric, USA, Inc., Gardena, CA) is capable of sampling 2 channels at 192 kHz with 24 bit samples, yielding a Nyquist frequency of 96 kHz, and has a flat frequency response (+/- 3 dB) from 20Hz to 80 kHz. Signals were recorded directly to an 8 GB Compact Flash memory card (Transcend Information, Inc., Los Angeles, CA). The recordings were subsequently downloaded onto hard-disk drives.

Signal analysis

Signal analysis was performed with customized routines using MATLAB (Mathworks, Natick, MA). Start and end times of clicks were automatically located using a two-step approach. In the first step, a click detection algorithm was implemented on all acoustic data to locate potential click candidates in the frequency domain. Spectra were calculated on 5.33 ms of data using a 1024-point Fast Fourier Transform (FFT) with 50% overlap and a Hann window. Spectral-means-subtraction was performed on each spectrum by subtracting the mean of the spectral vectors of the surrounding 3 seconds of data. Individual spectra were selected as click candidates if a minimum percentage of frequency bins exceeded a minimum threshold within the bandwidth range of interest. Values for minimum percentage, threshold and bandwidth were set as 12.5%, 13 dB and 15-95 kHz, respectively. For each click candidate, start and end times were defined to be 7.5 ms before and after the click to provide noise for use in spectral-means-subtraction in the second step. Overlapping click candidates were merged. These automatic detections were subsequently scanned by a trained analyst and false detections and burst-pulse calls were removed. Clicks within burst-pulse calls may exhibit species-specificity; however their analysis is beyond the scope of this study.

In the second step, a finer resolution click detection algorithm was implemented on the data output from step one to search for the start and end point of each click in the time domain. To remove any noise caused by water flow around the towed hydrophone, the signal was high-pass filtered with the -3dB point at 3 kHz using a finite impulse response filter. The Teager energy operator (Kaiser, 1990), a measure which provides nearly instantaneous energy tracking by using only three consecutive signal samples, was calculated for the clicks obtained in the first step. The Teager energy operator of a discrete time signal is defined as:

$$\Psi[\mathrm{x}(n)] = \mathrm{x}^2(n) - \mathrm{x}(n+1)\,\mathrm{x}(n-1) \qquad (1)$$

where n denotes the sample number. Kandia and Stylaniou (2006) demonstrate the utility of the Teager energy operator for detection of sperm whale regular and creak clicks. For each click, a noise floor was defined at the 40th percentile of energy, based on empirical analysis of the data. All points whose Teager energy was 100 times greater than the noise floor were tagged and grouped as belonging to a single click if they were less than 500 µs apart. If multiple clicks were present, clicks were ranked by maximum Teager energy and the strongest clicks were selected such that one click was chosen per 15 ms of data. Methods for determining the start and end points of symmetric on-axis click waveforms have been developed (Au, 1993), however, clicks obtained from random axis orientations may have distorted asymmetric waveforms which include reverberations caused by reflections within the head, from the external environment or both (Au et al., 1978) and therefore require a different analysis technique. To obtain the complete click including reverberations, a 10-point running mean of the Teager energy was calculated and start and end points were determined as the first and last point that were three times greater than the noise floor (Figure 2.2).

The spectral characteristics of clicks were quantified for the 1.33 ms of data following the start of each click by calculating a 256-point FFT with a Hann window. Noise spectra were calculated from the remaining data, excluding extraneous clicks, and were averaged within each recording session. Spectral-means-subtraction was performed on each click spectrum by subtracting the mean noise spectrum from the corresponding recording session. Spectral magnitudes were normalized between 0 and 1, and the mean and standard deviation of the normalized click spectra were calculated for each species. Additionally, concatenated spectrograms were created of all clicks analyzed for each species.

Click selection and statistical analysis

The original data lack the independence required for statistical analysis because click trains represent multiple clicks from one individual and an individual likely produces multiple click trains over a recording session. To reduce over-representation of an individual's clicks, a two stage process was established to limit the number of clicks and click trains analyzed from each recording session. Click trains were randomly selected from each recording session until either all trains were selected or the number of selected trains was twice the estimated group size. From each sampled click train, a single click was selected at random. Click trains were defined as clicks that were separated by less than 0.5 seconds; overlapping click trains, although likely to have been produced by different individuals, were grouped as a single train to reduce over-representation.

To examine spectral peak and notch structure and its variability in the frequency domain across clicks, the frequency value of consistent spectral peaks and notches was quantified for clicks of each species. Variability exists among clicks, such that the frequency value of the peaks and notches may vary, the peak or notch may not exist at all, and additional peaks and notches may exist that are not consistent across clicks. To establish and select consistent peaks and notches for statistical analysis while avoiding circularity, clicks were randomly divided into two equal groups, denoted the training and testing data. Training data clicks were used to establish expected frequency ranges for consistent peaks and notches across clicks of a given species. Testing data clicks were used for statistical comparison among species, such that the values of peaks and notches found within the established frequency ranges were quantified and analyzed. Details of the analysis of clicks from the training and testing data follow.

Using the training data clicks to establish the frequency ranges of consistent peaks and notches, a first-order regression-based peak and notch selection algorithm was implemented on the normalized click spectra. To avoid selecting minor peaks or notches, the spectra were smoothed using a 5-point window and a threshold was set such that the peak or notch was required to deviate by at least 2 dB. The number of peaks and notches selected per click spectra varied, ranging between zero and twenty and averaging eight. A histogram was generated from the frequency values of all selected peaks or notches combined across all training data clicks for each species. The histogram was calculated such that each bin was 750 Hz wide to correspond with the FFT frequency resolution. Peak and notch selections existed at all frequencies resulting in "background noise" in the histogram from which consistent peak and notch frequencies needed to be distinguished. To estimate the background noise in each histogram, peaks and notches from each click were randomly reassigned frequency values and a noise estimate histogram was generated. Actual counts of frequency values were compared to estimated background noise counts using a one-tailed z-test (alpha 0.5) (Zar, 1999) for each species. Peak and notch frequency values were established as consistent if they met three conditions: 1) actual counts were significantly greater than estimated noise counts; 2) the frequency value was greater than 15 kHz (to exclude overlapping whistles); and 3) at least one adjacent frequency value was also consistent. A set of Gaussians are fit to the peak and notch histograms of each species using Gaussian mixture models (Huang et al., 2001). Frequency means and ranges are established from the mean (μ) and standard deviation (±σ) of the dominant Gaussian for each consistent peak or notch.

Using testing data clicks to examine differences in frequency values of peaks and notches among species, peaks and notches were statistically analyzed if they fell within the frequency ranges established using the training data. Peaks and notches from testing data clicks were selected using the peak/notch selection algorithm described above. If any peaks or notches fell within the established frequency ranges, a minimum of one per range was chosen, keeping the peak or notch that was nearest to the mean established from the training data. To examine variability in peak and notch frequencies among and within species, nested ANOVAs (Zar, 1999) were performed in SPSS 11.5 (SPSS, Inc., Chicago, IL). For each consistent peak and notch, a nested ANOVA was calculated examining the main effect of species differences in frequency value and the interaction effect of recording session nested within species. Recording session was included to test for effects due to the use of different recording systems among surveys. The nested ANOVA can only determine that differences exist among multiple comparisons; therefore post-hoc tests were performed to determine which, if any, recording sessions were different using Tukey's method (Zar, 1999).

To determine whether the spectral properties of clicks could be useful for classifying data from passive acoustic autonomous seafloor recorders, in this case HARPs (Wiggins and Hildebrand, 2007), 1300 days of data were reviewed for the presence of unique spectral patterns. Long-term spectral averages (LTSAs, Wiggins and Hildebrand, 2007) were created using the Welch algorithm (Welch, 1967) by coherently averaging 4000 spectra created from 1000 point, 0% overlapped, Hann-windowed data. The resulting LTSAs had resolutions of 100 Hz and 5 seconds in the frequency and time domains, respectively. LTSAs were manually inspected for click bouts, and bouts containing unique spectral patterns were noted. Total counts of each type of click bout are presented.

RESULTS

The total numbers of recording sessions per species included in this analysis were: 4 from long-beaked common dolphins, 17 from short-beaked common dolphins, 6 from Risso's dolphins, 22 from Pacific white-sided dolphins and 7 from bottlenose dolphins (Table 2.3). School sizes ranged between 1 and 500 animals, with the two common dolphin species typically occurring in larger schools than the other three species (Table 2.3). The total number of clicks recorded per session ranged from 3 to almost 11,000 while total number of click trains ranged between 1 and 582 (Table 2.3). Example waveforms and spectra are presented for each of the five species described (Figure 2.3).

Concatenated spectrograms of the individual clicks and mean spectral plots of clicks for the five dolphin species investigated reveal consistent spectral characteristics for both Pacific white-sided and Risso's dolphins (Figure 2.4). Alternating high and low amplitude bands are evident at certain frequencies across the clicks of these two species. These frequency bands appear consistent for the majority of clicks across multiple recording sessions as well as for various hydrophone array configurations. No such pattern is evident for long-beaked common, short-beaked common or bottlenose dolphins (Figure 2.4).

The existence of consistent spectral peaks and notches in only two of the species is reinforced when comparing actual counts of selected peaks or notches to estimated noise counts for frequency values in the training data. Only Pacific white-sided dolphin and Risso's dolphin clicks exhibit frequency values at which the counts of peaks and notches are greater than expected by chance. The remaining three species' clicks did not have significantly greater counts of peaks or notches at any frequency values (Figure 2.5). Univariate Gaussian mixture models fit to the peak histograms and notch histograms (Figure 2.6) from Pacific white-sided dolphin and Risso's dolphin training data clicks provide estimates of means and standard deviations for each of the consistent peaks and notches (Table 2.4).

For the two species with spectral peaks and notches, calculations of the percentage of clicks from the testing data that have peaks or notches within the expected frequency ranges show that these consistent peaks and notches occur in the majority of recorded clicks, with percentages ranging between 44% and 89% (Table 2.4). The two species share similar spectral peaks at mean frequencies 22.2 and 37.3 kHz for Pacific white-sided dolphins and 22.4 and 38.8 kHz for Risso's dolphins. Risso's dolphins have two additional spectral peaks at mean frequencies 25.5 and 30.5 kHz and spectral notches at 19.6, 27.7, and 35.9 kHz, while Pacific white-sided dolphin clicks have spectral peaks at mean frequencies 26.6 and 33.7 kHz, and notches at 19.0, 24.5, and 29.7 kHz (Table 2.4).

Nested ANOVA analyses indicate that some click variables are distinct both between species and among subsets of recording sessions. Five of the seven frequency peaks and notches are significantly different between Pacific white-sided and Risso's dolphins (Table 2.5). Only the lowest frequency peak and notch are not significantly different. In addition to the distinct separation of five peaks and notches between the two species, four of those five peaks show significant differences among recording sessions within species. Tukey post-hoc tests of recording session differences indicate that 1) there are no significant differences among recording sessions of Risso's dolphins and 2) there are significant differences between two distinct subsets of recording sessions of Pacific white-sided dolphins (Table 2.6). Click peaks and notches are consistent across recording sessions within these Pacific white-sided dolphin subsets, but distinct between them. Additionally, these subsets do not differ among surveys with different recording gear: subset A includes sessions from all surveys, including FLIP, while subset B only includes sessions from the FLIP survey. Only two sessions, both recorded from the FLIP survey, are not significantly different from either subset.

To obtain a clearer picture of what these two subsets of Pacific white-sided dolphin recording sessions represent, concatenated spectrograms and mean click spectra are generated for each subset (Figure 2.7). The two subsets appear to represent two distinct click types in which the spectral peaks are more closely spaced in subset B. In particular, the second peak is strikingly different with mean values of 26.1 ± 0.7 kHz and 27.4 ± 0.5 kHz for subset A and subset B, respectively. Additionally, inspection of the spectra from the two recording sessions that were not significantly different from either subset reveals the presence of both click types rather than clicks with peaks evenly distributed between these frequencies.

Finally, an analysis of 1300 days of long-term autonomous recorder data reveals the presence of hundreds of click bouts containing the three unique spectral peak and notch patterns found for Risso's and Pacific white-sided dolphins (Figure 2.8), as well as click bouts that do not contain consistent spectral peaks and notches and are therefore unidentifiable. The total number of click bouts containing clicks with patterns similar to these four click types are: 1769 Risso's dolphin type click bouts, 473 Pacific white-sided dolphin type A click bouts, 337 Pacific white-sided dolphin type B click bouts, and 9210 unidentifiable dolphin click bouts. Click bouts containing mixed Risso's and Pacific white-sided clicks or mixed Pacific white-sided type A and type B clicks occurred in only 14 and 10 bouts, respectively.

DISCUSSION

We provide evidence for three levels of classification of echolocation clicks from wild dolphins within the Southern California Bight. The first level represents the presence or absence of click spectral structure: a consistent and distinctive spectral peak and notch pattern is evident for clicks from Risso's and Pacific white-sided dolphins, while no such pattern occurs in the clicks of bottlenose and common dolphins. Therefore, clicks can be separated into two groups – those that contain consistent peaks and notches and those that do not. If this spectral structure is present, bottlenose and common dolphins can be ruled out, and the clicks can be further analyzed at the second level for species-specific differences. However, if this spectral structure is absent, no further distinction can be made until a method to classify these types of clicks is developed.

At the second level of classification, Risso's dolphins and Pacific white-sided dolphins can be distinguished to species by the frequency values of the spectral peaks and notches. In combination with the other peaks and notches, the presence of a peak or notch at 30 kHz is particularly useful for distinguishing between these two species, as 82% of Risso's dolphin clicks contain a peak while 75% of Pacific white-sided dolphin clicks contain a notch at this frequency. On the other hand, 72% and 89% of clicks from Risso's and Pacific white-sided dolphins, respectively, contain a peak at 22 kHz which is not significantly different between the two species. If recordings are limited to a 24 kHz Nyquist frequency, as is common to Digital Audio Tape (DAT) recorders and other systems, then only the distinction that one of these two species was present could be made, but not which one. A minimum Nyquist frequency of 40 kHz is needed to classify these clicks at the species level.

Finally, at the third level of classification, Pacific white-sided dolphin clicks can be separated into two click types, type A and type B. In combination with the other peaks and notches, a frequency peak near either 26.1 or 27.4 kHz can distinguish these clicks as type B or A, respectively. The significance of these two click types remains unknown, but in 90% of the recording sessions in this study, one click type is prevalent per school of dolphins. Numerous inter-school differences could account for the differential use of the two click types including group size, composition, behavior or prey type. Another hypothesis is that the two click types are population-specific, as supported by the presence of two genetically and morphologically distinct populations of Pacific white-sided dolphins whose distributions overlap in the southern California region (Walker et al., 1986; Lux et al., 1997). These populations are morphologically distinguishable by cranial measurements, in particular the condylobasal length (Walker et al., 1986), a characteristic which could influence the sound production pathway. These populations are not visually distinguishable (Walker et al., 1986) making visual field identification impossible. The ability to distinguish them acoustically could offer insight into differences in the biology of each population. Recordings from other areas in the eastern North Pacific and field studies incorporating acoustic recording with biopsy sampling could provide additional information for this question.

While several biases in data collection or analysis could account for the differentiation found among these clicks, the authors consider species- and subspecies-specificity to be the most viable explanation. *Potential bias 1*: The use of different recording systems among the surveys included in this analysis could result in differences between click recordings. However, the consistency of the spectral characteristics within a species across surveys compared to the differences between species recorded within the same surveys strengthens the argument that these differences are related to the animals rather the recording instrumentation. *Potential bias 2*: The recording of clicks from animals with unknown acoustic orientations could result in aspect-dependant spectral features due to the narrow echolocation beamwidth of dolphins (e.g. Madsen et al. (2004) describe increasing spectral notch structure with increasing degree off-axis within the clicks of Risso's dolphins). The authors assume that clicks recorded in the wild come from random acoustic orientations since dolphins are highly mobile and typically acoustically scan their environment. Therefore, while aspect-dependent variability may exist, it does not significantly affect the frequency value of spectral peaks and notches, as the variation within species is less than that between species. It is possible that the 15-20% of clicks that do not contain some of the peaks or notches may be due to aspect-dependency. For this reason, it is important that a species- or sub-species classification be based on multiple clicks. *Potential bias 3*: The use of a relatively long 1.33 ms analysis window to calculate spectra could result in the inclusion of surface reflections whose effect on the spectra remains unknown and could account for the variability between the two click types recorded from Pacific white-sided dolphins. To investigate this potential bias, a subset of Pacific white-sided dolphin clicks from the FLIP survey was examined for the presence of reflections. Of 100 randomly chosen clicks which included both click types, only 9 clicks exhibited an obvious surface reflection, while 62 clicks clearly did not have a surface reflection within the analysis window. All of these clicks contained spectral peak and notch patterns whose frequency values were not affected by the presence or absence of a reflection. Additionally, it is unlikely that surface reflections from thousands of clicks would exhibit the consistent timing necessary to result in the consistent spectral pattern that we demonstrate, given the expected variability in dolphin depths and distances. *Potential bias 4*: The lack of recordings from other species that occur within the Southern California Bight means clicks from autonomous recordings cannot definitively be classified to species. While those species which have been recorded and have different spectral patterns can be excluded, it is possible that an unrecorded species could have the exact same spectral pattern. While this will remain unknown until all species have been recorded during concurrent acoustic and visual surveys within this area, the probability of correctly classifying the clicks to species remains high as unrecorded species have low occurrence within this region.

An intriguing question remains as to why some species of dolphins' clicks exhibit these species-specific spectral characteristics while others do not. Researchers in the bioacoustics field have speculated many causes for interspecific call differences including phylogenetic constraints, size constraints, morphological differences, prey preferences, niche partitioning, and environmental variability including noise conditions (Dudok van Heel, 1981; Kamminga et al., 1986; Wang et al., 1995; Madsen et al., 2004; Oswald, 2006). We hypothesize that the morphology of the sound production pathways, including the monkey lip dorsal bursae (MLDB) complex, the melon, airspaces and skull, is likely to be important. There are several morphological similarities in the sound production pathways between Pacific white-sided and Risso's dolphins that are different from bottlenose and common dolphins. Pacific white-sided and Risso's dolphins have only slightly asymmetrical skulls and MLDB complexes, while bottlenose and common dolphins show strong asymmetry (Cranford et al., 1996). Perhaps the minor asymmetry results in sound production organs producing clicks of similar central frequencies and amplitudes which result in the interference pattern observed, similar to beat structure for tonal sounds made up of two similar frequencies. Additionally, Pacific white-sided and Risso's dolphins lack an extended rostrum or beak, and both species exhibit protrusions into the melon: a vertical cleft is present on the anterior surface of Risso's dolphin melon (White and Norris, 1978); and a vertical connective tissue column is present in the central melon of Pacific white-sided dolphins (Cranford et al., 1996). These differences could also affect the sound production pathway potentially resulting in the click patterns described in this study.

Autonomous acoustic recording packages have been deployed throughout this region and long-term spectral averages (Wiggins and Hildebrand, 2007) of the data reveal echolocation click bouts exhibiting the same peak and notch structure as described above (Figure 2.8). The abundance of occurrences of click bouts from autonomous recordings which contain the spectral patterns described in this study demonstrate that these spectral patterns are distinct, repeatable and useful for classifying Risso's and Pacific white-sided dolphin clicks during passive acoustic monitoring surveys. Ideally, an automated classification scheme could be developed to objectively classify the large amounts of acoustic data collected by these sea-floor instruments. Oswald et al. (2007) have shown that automated methods can be used to classify dolphin whistles and a classifier which used all call types produced by dolphins in the 5-24 kHz range suggests that clicks can be used to automatically classify dolphin recordings (Roch et al., 2007). Additionally, computer learning techniques such as those used by Roch et al. (2007) are often able to classify patterns that humans cannot easily distinguish such as those found in bottlenose and common dolphin clicks. Automated classifiers that incorporate higher bandwidth click data (up to 100 kHz) are currently being developed by the authors. The ability to identify dolphin clicks to species will allow researchers to investigate long-term trends in their abundance and distribution patterns using passive acoustic monitoring.

CONCULSIONS

This study is the first to describe a technique for classifying dolphin recordings to species using unique spectral features of echolocation clicks. Clicks can be distinguished at three levels: 1) at the supra-species level by the presence (Pacific white-sided and Risso's dolphins) or absence (bottlenose and common dolphins) of spectral peaks and notches; 2) at the species level by the frequency values of peaks and notches in Pacific white-sided and Risso's dolphin clicks; and 3) at the subspecies level into two distinct click types of Pacific white-sided dolphins. By extending passive acoustic monitoring equipment to higher frequencies (up to 100 kHz), some delphinid clicks can now be classified to species which may enable researchers using passive acoustics to study their temporal and spatial distribution and abundance patterns. As the technology behind passive acoustic monitoring continues to advance, even higher frequency sampling could provide recordings from less abundant and elusive species to determine if similar spectral patterns exist. Automatic classification algorithms could be developed to objectively distinguish delphinid species by their clicks, which, along with higher sample rate recordings, may allow all delphinid species to be classified by their clicks. Furthermore, the inclusion of all call types produced by delphinids could potentially strengthen the ability to classify periods of calling to species.

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Chapter 2, in full, is a reprint of the material as it appears in the Journal of the Acoustical Society of America, 2008: Soldevilla, M.S., Henderson, E.E., Campbell, G.S., Wiggins, S.M., Hildebrand, J.A. and Roch, M.A. Classification of Risso's and Pacific white-sided dolphins using spectral properties of echolocation clicks. Journal of the Acoustical Society of America 124: 609-624. The dissertation author was the primary investigator and author of this paper.

FIGURES

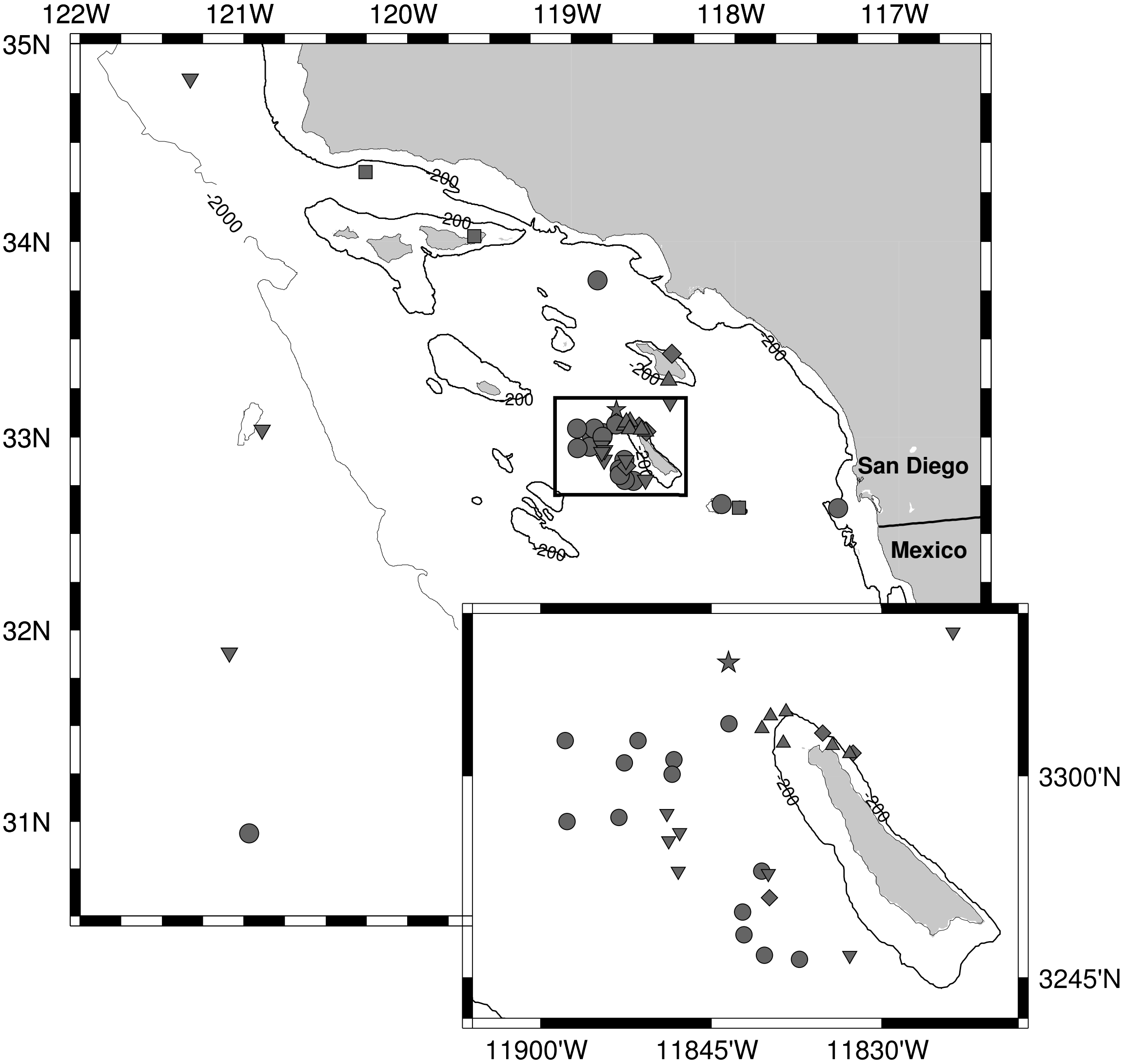


Figure 2.1. Map of study area and delphinid recording locations offshore of southern California, USA. Coastline, -200 m, and -2000 m bathymetric contours are represented. Inset shows cluster of recordings from San Clemente Island area. This cluster represents increased effort, not increased presence. ∃ FLIP location represents multiple sightings from Table 2.5. ● *Delphinus delphis,* ■ *Delphinus capensis,* ♦ *Grampus griseus,* ▼ *Lagenorhynchus obliquidens,* ▲ *Tursiops truncatus*

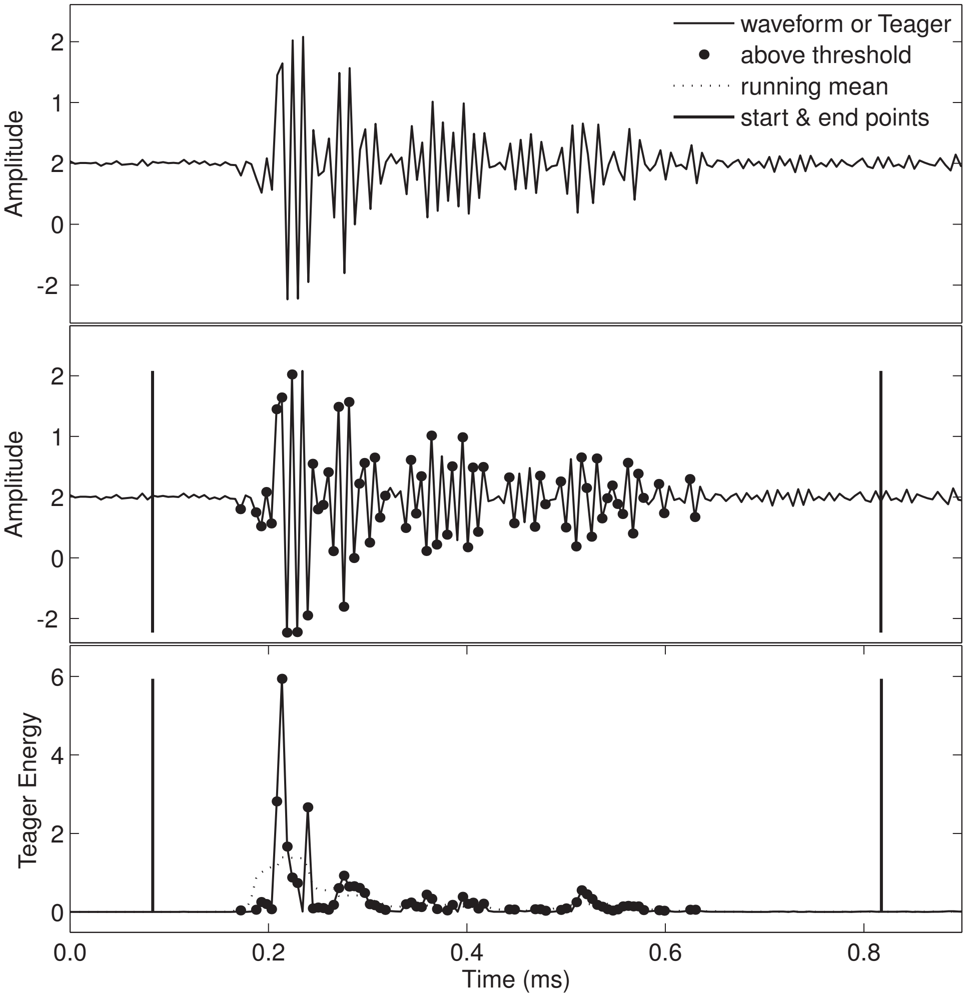


Figure 2.2. Example waveform and corresponding Teager energy of a Pacific white-sided dolphin click. Note the reverberations present in the waveform. a) the click waveform b) the click waveform with denotations of click endpoints and data points above Teager energy noise floor threshold, c) the Teager energy of the waveform, the running mean of the Teager energy, denotations of click endpoints and data points above the noise floor threshold. Solid vertical bars represent the time range of the complete click peak.

Figure 2.3. Example spectra and waveforms for a) *Delphinus capensis*, b) *Delphinus delphis*, c) *Grampus griseus*, d) *Lagenorhynchus obliquidens*, and e) *Tursiops truncatus*.

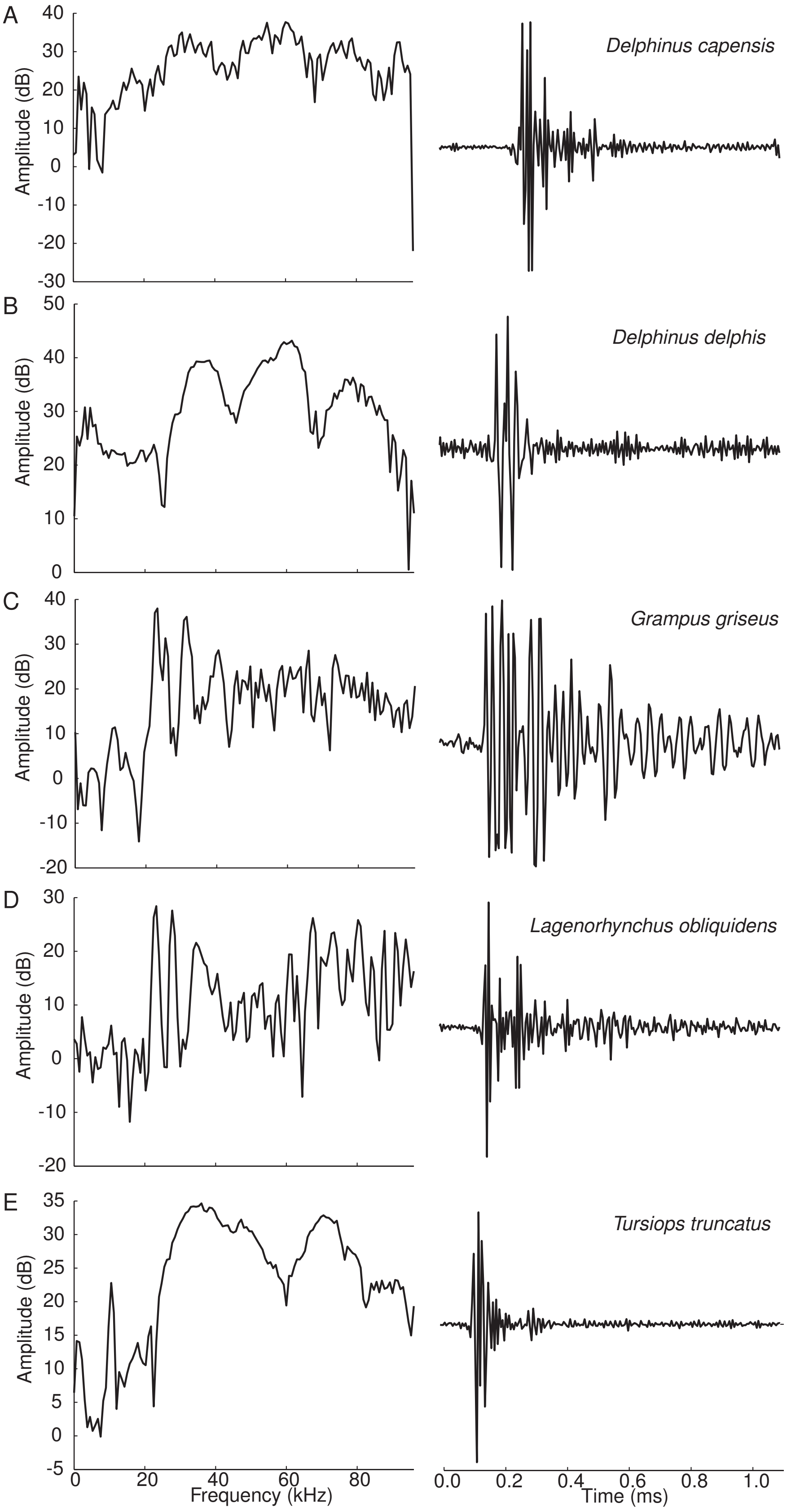

A
B
C
D
E
Amplitude (dB)
40
30
20
10
0
-10
-20
-30
50
-5
5
15
25
35
Delphinus capensis
Delphinus delphis
Grampus griseus
Lagenorhynchus obliquidens
Tursiops truncatus
Frequency (kHz)
0
20
40
60
80
Time (ms)
0.0
0.2
0.4
0.6
0.8
1.0

Figure2.4. Concatenated spectrograms and mean normalized spectral plots of complete clicks for each species using Hann-windowed data. a) *Delphinus delphis*, b) *Delphinus capensis*, c) *Grampus griseus*, d) *Lagenorhynchus obliquidens*, and e) *Tursiops truncatus*. For the concatenated spectrograms, frequency is plotted on the y-axis. Click number, rather than continuous time, is plotted on the x-axis. The magnitude of the frequency content is represented by the color such that lighter blue represents greater magnitude. Alternating high and low amplitude spectral bands are apparent between 20 kHz and 40 kHz for *G. griseus* and *L. obliquidens*. Black vertical lines in spectrograms represent breaks between recording sessions. For the mean normalized spectral plots, the solid line represents the mean and the dotted lines represent one standard deviation.

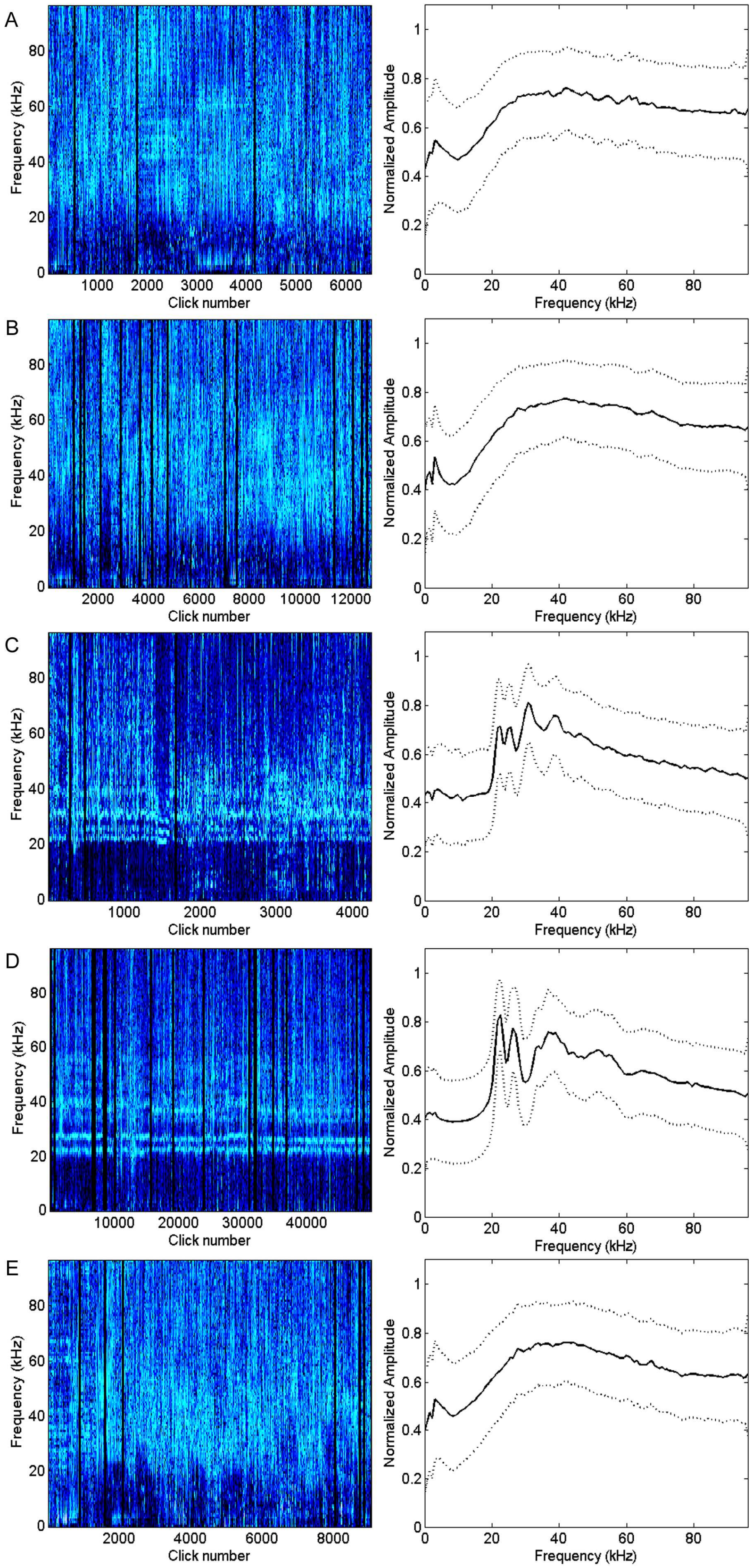
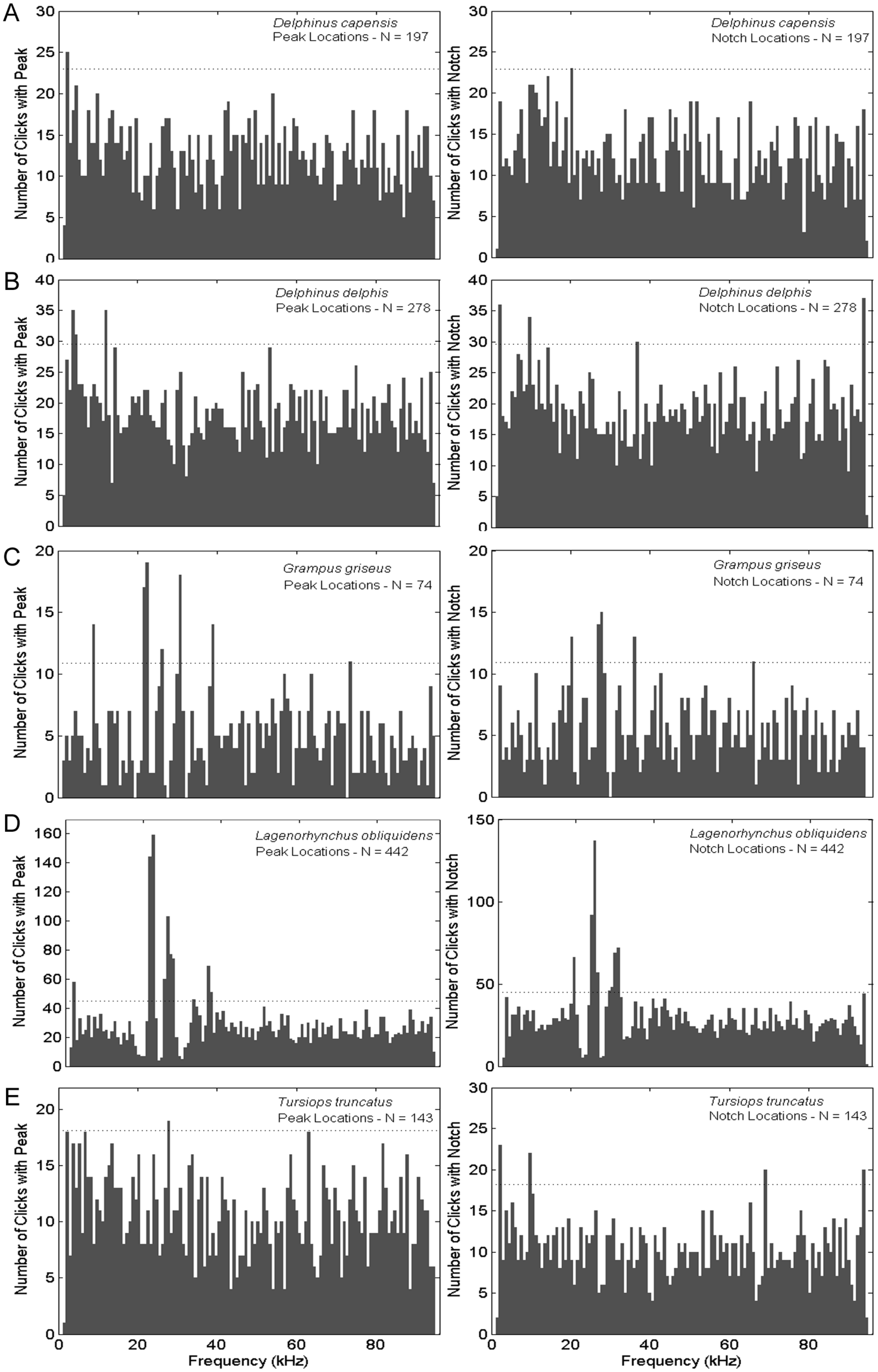

A
B
C
D
E
Frequency (kHz)
Click number
Normalized Amplitude
Frequency (kHz)
0
20
40
60
80
1000
2000
3000
4000
5000
6000
8000
10000
12000
20000
30000
40000
0.2
0.4
0.6
0.8
1

Figure2.5. Histograms of frequency values of spectral peaks (left) and notches (right) for a) *Delphinus delphis*, b) *Delphinus capensis*, c) *Grampus griseus*, d) *Lagenorhynchus obliquidens and e) Tursiops truncatus.* Each bar represents one 750 Hz FFT frequency bin. Dotted lines represent the upper boundary of estimated histogram background noise as determined from peak and notch randomization procedure. Groups of bars that rise above this line represent consistent peaks or notches that are analyzed further.


A
Delphinus capensis
Peak Locations - N = 197
Delphinus capensis
Notch Locations - N = 197
B
Delphinus delphis
Peak Locations - N = 278
Delphinus delphis
Notch Locations - N = 278
C
Grampus griseus
Peak Locations - N = 74
Grampus griseus
Notch Locations - N = 74
D
Lagenorhynchus obliquidens
Peak Locations - N = 442
Lagenorhynchus obliquidens
Notch Locations - N = 442
E
Tursiops truncatus
Peak Locations - N = 143
Tursiops truncatus
Notch Locations - N = 143
Number of Clicks with Peak
Number of Clicks with Notch
Frequency (kHz)
0
20
40
60
80

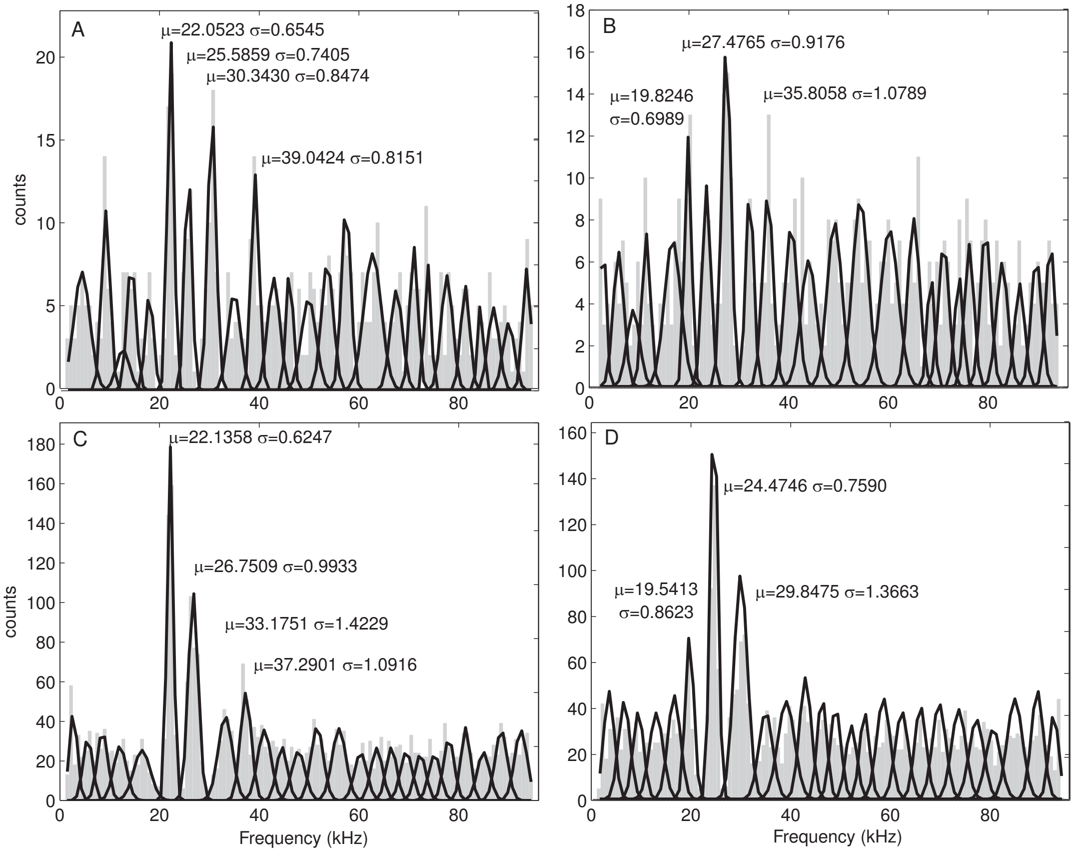


Figure2.6. Univariate Gaussian mixture model fits to spectral peak and notch histograms from the training data set for *Grampus griseus* a) peaks and c) notches and *Lagenorhynchus obliquidens* b) peaks and d) notches. Each bar represents one 750 Hz FFT frequency bin. Mean and standard deviation estimates of the Gaussian distributions of consistent peaks and notches are noted.

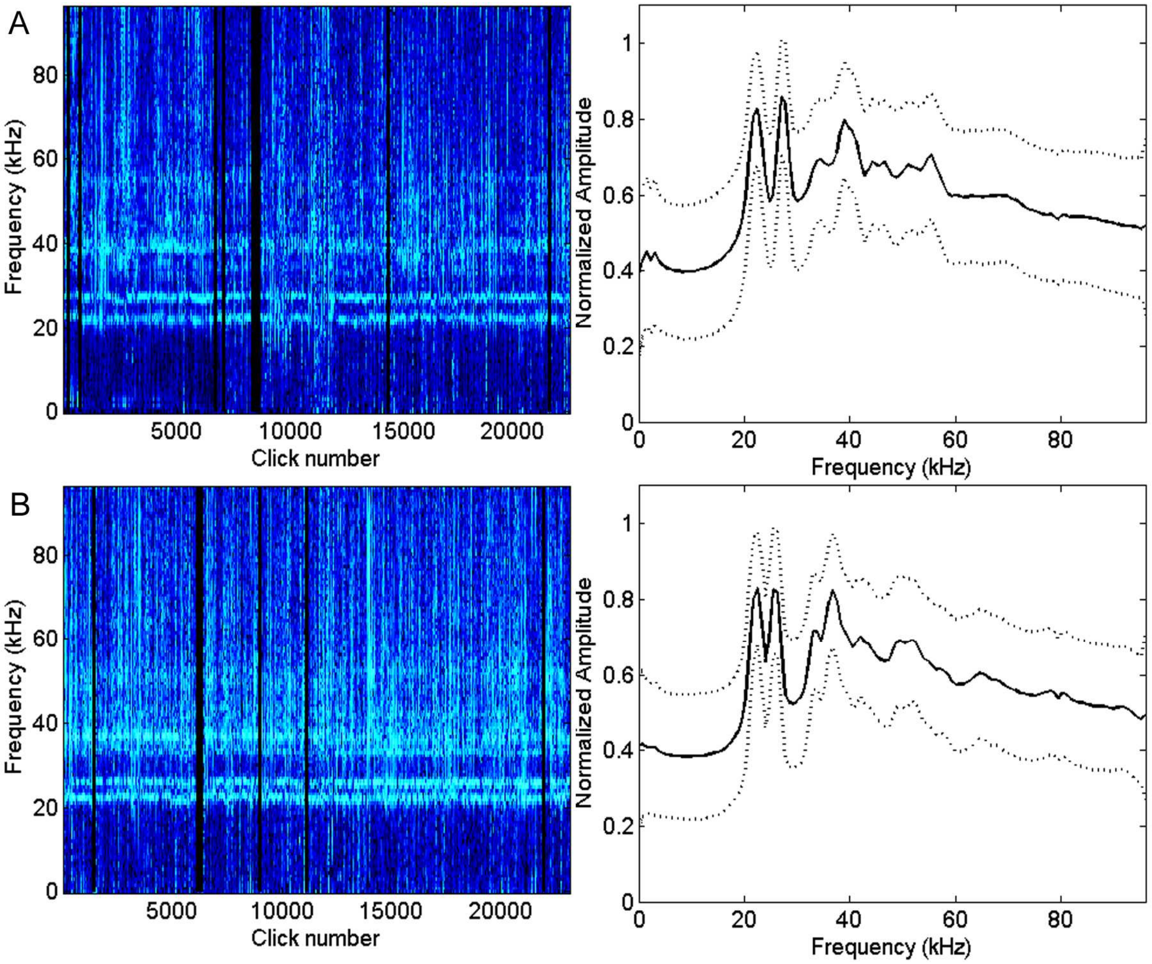


Figure2.7. Concatenated spectrograms and mean spectral plots for a) subset A and b) subset B of *Lagenorhynchus obliquidens* clicks using Hann-windowed data. Black vertical lines in spectrograms represent breaks between recording sessions. The consistency of spectral peaks and notches across recording sessions of each subset are apparent, as are the distinctions between clicks from the two subsets, revealing that *Lagenorhynchus obliquidens* produce two distinct click types.

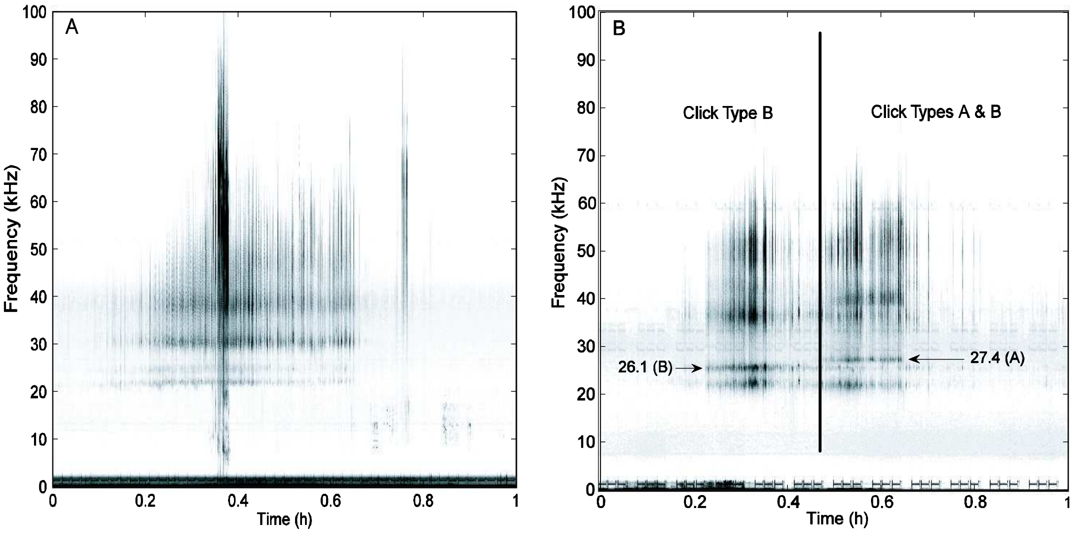


Figure2.8. Long-term spectral average of data from seafloor HARP instruments show echolocation bouts which exhibit similar spectral peak/notch structure to that found for a) *Grampus griseus* and b) *Lagenorhynchus obliquidens,* including both the 26.1 kHz (type B) and 27.4 kHz (type A) clicks. The first half hour has a group producing clicks of type B. In the second half hour, a group begins producing type A clicks while the type B clicks fade out. The vertical line represents the beginning of type A clicks. Each plot shows 1 hour of data.

TABLES

Table 2.1. Published click characteristics of common, Risso's, Pacific white-sided and bottlenose dolphins.

	Delphinus spp.	*G. griseus*		*L. obliquidens*	*T. truncatus*	
Recording situation	captive [a, b]	free-ranging [c]	captive [d, e]	captive [a, f, g]	free-ranging [h]	captive [d]
Duration (µs)	50 - 250	30 - 75	40 - 100	25 - 100	10 - 20	50 - 80
ICI (ms)	-	-	-	-	0 - 400+	-
Source Level (dB re 1µPa @ 1m)	160 - 170	202 - 222	170 - 215	170	-	228
Peak Frequencies (kHz)	23 - 67	40 - 110	30 - 105	50 - 80 100 - 120	40 - 140	110 - 130
-3dB bandwidth (kHz)	-	15 - 85	30 - 84	9.5 - 36	-	-
-10dB bandwidth (kHz)	-	20 - 125	100	-	-	-
Centroid Frequencies (kHz)	-	60 - 90	50 - 80	-	-	-
RMS bandwidth (kHz)	-	20 - 30	25	-	-	-

a. Fish and Turl (1975); b. Evans (1973); c. Madsen et al. (2004); d. Au (1993); e. Philips et al. (2003); f. Fahner et al. (2003); g. Nakamura and Akamatsu (2003); h. Akamatsu et al. (1998)

Table 2.2. Survey and instrumentation information. Frequency response and gain of the acoustic instruments are described in detail in the text. Surveys conducted from stationary or drifting platforms are indicated by a blank field under tow distance. Abbreviations: CC: CalCOFI oceanographic survey; SC: Southern California instrumentation survey; SCI: San Clemente Island survey; FLIP: FLIP moored observations.

Cruise Name	Dates	Platform	Tow Distance (m)	Hydrophone Depth (m)	Hydrophone Type	Circuit Board	A/D converter
CC0411	Nov 2004	RV Roger Revelle	--	30	ITC 1042	R100-A	MOTU 896HD
CC0604	Apr 2006	RV New Horizon	270	15-20	SRD HS150	R100-C	MOTU 896HD
SC03	May 2006	RV Gordon Sproul	270	15-20	SRD HS150	R100-C	MOTU 896HD
SCI0608	Aug 2006	RHIB	--	10-30	SRD HS150	R300	Fostex FR2
					ITC 1042	R300	Fostex FR2
FLIP0610	Oct 2006	FLIP	--	30	SRD HS150	R300	MOTU 896HD
SCI0704	April 2007	RHIB	--	10-30	SRD HS150	R300	Fostex FR2

Table 2.3. Summary of data included in click analysis. Survey platform, numbers of clicks, click trains and school sizes are presented for each recording of each species. Each recording session represents a new school of dolphins. Abbreviations: Dc: *Delphinus capensis*; Dd: *Delphinus delphis*; Gg: *Grampus griseus*; Lo: *Lagenorhynchus obliquidens*; Tt: *Tursiops truncatus.* CC: CalCOFI oceanographic survey; SC: Southern California instrumentation survey; SCI: San Clemente Island survey; FLIP: FLIP moored observations.

Species	Recording	Survey	Clicks	Click Trains	School Size
Dc	1	CC0411	1256	155	500
	2	CC0604	531	22	45
	3	SC03	2377	198	200
	4	FLIP0610	2338	145	45
Dd	1	CC0604	8	3	60
	2	SC03	192	52	18
	3	SC03	164	30	250
	4	SCI0608	1030	12	230
	5	SCI0608	245	12	175
	6	SCI0608	166	30	225
	7	SCI0608	636	113	320
	8	SCI0608	9	1	180
	9	SCI0608	804	75	430
	10	SCI0608	763	38	30
	11	SCI0608	475	25	85
	12	SCI0608	624	58	7
	13	SCI0608	2269	70	190
	14	SCI0608	455	13	370
	15	SCI0608	3884	48	20
	16	SCI0608	730	26	35
	17	SCI0608	361	25	320
Gg	1	SCI0608	6	1	1
	2	SCI0608	286	24	12
	3	SCI0608	190	45	12
	4	SCI0608	1194	105	40
	5	SCI0608	3	1	18
	6	FLIP0610	2564	446	10
Lo	1	CC0604	224	3	7
	2	CC0604	508	66	4
	3	CC0604	4	1	5
	4	SC03	24	2	10
	5	SCI0608	5961	262	12
	6	SCI0704	333	92	13
	7	SCI0704	1317	145	8
	8	SCI0704	95	26	13
	9	SCI0704	127	18	22
	10	SCI0704	197	17	25
	11	FLIP0610	1409	208	25
	12	FLIP0610	5503	543	50
	13	FLIP0610	3463	358	15
	14	FLIP0610	4761	431	20
	15	FLIP0610	7085	582	20
	16	FLIP0610	916	111	17
	17	FLIP0610	171	56	50
	18	FLIP0610	2688	491	25
	19	FLIP0610	2099	364	40
	20	FLIP0610	10843	544	75
	21	FLIP0610	1075	110	8
	22	FLIP0610	1226	235	50
Tt	1	CC0604	897	32	30
	2	SC03	707	66	30
	3	SCI0608	501	24	18
	4	SCI0608	5959	386	60
	5	SCI0608	687	59	6
	6	SCI0704	120	16	30
	7	SCI0704	205	18	50

Table 2.4. Means and standard deviations of local peaks and notches for *Grampus griseus* (Gg) and *Lagenorhynchus obliquidens* (Lo). Means from training data were estimated from Gaussian Mixture Models. Means from testing data represent frequency variability of the value of the peak or notch used for ANOVA analyses. The percentage of total clicks containing a peak in this frequency range is also presented.

	Peak Number				Notch Number		
Training data	1	2	3	4	1	2	3
Gg	22.1 (0.7)	25.6 (0.7)	30.3 (0.8)	39.0 (0.8)	19.8 (0.7)	27.5 (0.9)	35.8 (1.1)
Lo	22.1 (0.6)	26.7 (1.0)	33.1 (1.4)	37.3 (1.1)	19.5 (0.9)	24.5 (0.8)	29.8 (1.4)
Test data							
Gg	22.4 (0.8)	25.5 (1.0)	30.5 (1.1)	38.8 (1.1)	19.6 (1.3)	27.7 (1.1)	35.9 (1.2)
% N	72	45	82	48	46	64	54
Lo	22.2 (0.6)	26.6 (0.9)	33.7 (1.4)	37.3 (1.4)	19.0 (1.1)	24.5 (0.9)	29.7 (1.4)
% N	89	76	45	62	51	75	66

Table 2.5. Results of nested ANOVAs testing for variation in peaks and notches between species (Pacific white-sided and Risso's dolphins) and among recordings nested within species. Significant differences are indicated by asterisks. ANOVA tests among multiple comparisons, such as among recording sessions, only indicate that significant differences, not which sessions were different. See text on post-hoc analysis for further detail of the differences between recording sessions.

	Species			Recording(Species)		
	F	p		F	p	
Peak 1	0.12	0.733		1.84	0.011	
Peak 2	11.44	0.002	*	13.58	0.000	*
Peak 3	92.63	0.000	*	1.42	0.106	
Peak 4	12.21	0.001	*	2.09	0.003	*
Notch 1	2.46	0.121		1.27	0.189	
Notch 2	139.19	0.000	*	3.45	0.000	*
Notch 3	187.99	0.000	*	3.35	0.000	*

Table 2.6. Subsets of Pacific white-sided dolphin recording sessions as distinguished by Tukey post-hoc analyses. While different surveys used different recording gear, subset A includes recordings from all surveys, including FLIP, while subset B only includes recording sessions from FLIP. This suggests that differences between recording sessions are not a function of the differing gear used but rather represent two distinct click types produced consistently within a dolphin school as described in the text. Sessions 13 and 21, also recorded from FLIP, were not significantly different from either subset and visual inspection suggests that they contain both click types.

Subset A		Subset B	
Recording Session	Survey	Recording Session	Survey
1	CC0604	11	FLIP
2	CC0604	14	FLIP
4	SC03	17	FLIP
5	SCI0608	18	FLIP
6	SCI0704	19	FLIP
7	SCI0704	20	FLIP
8	SCI0704	22	FLIP
9	SCI0704		
10	SCI0704		
12	FLIP		
15	FLIP		
16	FLIP		

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CHAPTER 3

SPATIAL AND TEMPORAL PATTERNS OF RISSO'S DOLPHIN (*GRAMPUS GRISEUS*) ECHOLOCATION CLICK ACTIVITY IN THE SOUTHERN CALIFORNIA BIGHT

ABSTRACT

Temporal and geographical trends in clicking activity can lead to insights into the foraging and migratory behavior of pelagic dolphins. Using autonomous seafloor recording packages, the geographical, diel and seasonal patterns of Risso's dolphin (*Grampus griseus*) echolocation click activity are described for six locations in the Southern California Bight. Risso's dolphin echolocation click bouts are identified based on their unique characteristics in long-term spectral averages. Risso's dolphin clicks were detected on 739 of 1959 days of recording and were heard at all six sites, with the majority of detections occurring at the four nearshore sites. A significant diel pattern is evident in which there are both more hours with click bouts and higher click rates at night than during the day. At all nearshore sites, Risso's dolphins were heard year-round. Seasonal and interannual variability in occurrence was high across sites with peak occurrence in fall of most years at most sites. These results support suggestions that Risso's dolphins forage at night and indicate that Santa Catalina Island represents an important habitat throughout the year.

INTRODUCTION

Analysis of temporal patterns of dolphin activity and occurrence can provide insight into important behaviors such as foraging, mating and movement patterns. Seasonal patterns of pelagic dolphin movements are challenging to study using traditional techniques such as visual line-transects studies, as seasonal weather conditions and cost constraints limit the ability to obtain large sample sizes over long periods of time. Studies describing diel foraging activity have been limited to daylight hours (Wursig and

Wursig, 1979; Norris and Dohl, 1980; Amano et al., 1998). This has resulted in the inference of nighttime foraging activity from evening foraging activity and the fullness of dolphin stomachs caught in the morning compared to afternoon. Active acoustic studies have provided needed insight into dolphin foraging and dive patterns in relation to diel vertical changes in the depth of the sound-scattering layer (Benoit-Bird and Au, 2003; Benoit-Bird et al., 2004), however, passive acoustic studies are more easily applied for long-term monitoring and avoid unknown effects of active acoustics on odontocetes (Cox et al., 2004). Passive acoustic monitoring techniques are increasingly being used in ecological studies to investigate the occurrence, distribution and behavior of vocal animals (elephants (Payne et al., 2003), bats (Yates and Muzika, 2006; Gorresen et al., 2008), birds (Farnsworth and Russell, 2007), whales (Moore et al., 1998; Watkins et al., 2000; Oleson et al., 2007), dugongs (Ichikawa et al., 2006), dolphins (Jacobs et al., 1993; Goold, 2000; Philpott et al., 2007) and porpoises (Amano et al., 1998; Carlstrom, 2005)). Passive acoustic monitoring is an alternative, cost-effective method of obtaining high-resolution, long-duration time-series which can be used to examine seasonal and diel patterns.

The role of Risso's dolphins in the Southern California Bight (SCB) ecosystem is not well understood. Descriptions of temporal patterns in the movements and distribution of Risso's dolphins of southern California are complex and sometime conflicting. Risso's dolphins are a tropical to temperate water species that range from the Gulf of Alaska to the equator in the Eastern North Pacific (Leatherwood et al., 1980). Research and anecdotal evidence over the last 150 years indicate that Risso's dolphin occurrence is highly variable off California with low sighting rates in some decades followed by high sightings in others, particularly at the northern extents of their range (Norris and Prescott, 1961; Leatherwood et al., 1980; Dohl et al., 1981; Dohl et al., 1983; Shane, 1995; Kruse et al., 1999). Leatherwood et al. (1980) describe these increases as correlated to extended periods of warm water, on seasonal to decadal time scales,; however Barlow and Forney (2007) find that abundance did not vary consistently among warm and cold years. Equally complex are descriptions of seasonal movements. Green et al (1992), and Forney and Barlow (1998) found evidence of changes in abundance consistent with movements between Oregon and Washington in spring and summer and California in fall and winter. In contrast, Dohl et al. (1983) found that seasonal patterns changed from year to year off central and northern California, and Dohl et al. (1981) suggested that Risso's dolphins in the SCB were year-round residents with inshore /offshore and north/south movements related to warm and cool waters, respectively. The conflicting reports may be due to the differing areas covered, for example the study by Dohl et al. (1983) covers Point Conception to the Oregon border, the study by Forney and Barlow (1998) covers the entire California coast and the study by Dohl et al. (1981) covers only the SCB. A consistent acoustic time series at numerous locations within the SCB could help to determine when and if temporal and spatial changes are occurring in this area.

On a shorter temporal scale, the diel behavioral activity levels of Risso's dolphins also remain unknown as animals cannot be seen at night. Kruse (1989) indicates that off Monterrey, feeding/foraging and traveling each represent 30% of daytime observations while the remainder of the daytime is spent milling, resting, socializing or zig-zagging. She observed no evidence of diurnal patterns. Based on observations of daytime activity patterns, Shane (1995) suggests that Risso's dolphins mainly feed at night, yet nighttime observations were not made. Risso's dolphins main prey are cephalopods (Orr, 1966; Clarke and Pascoe, 1985; Clarke, 1996), of which many species in the SCB are diel vertical migrators (Roper and Young, 1975; Gilly, 2006). While Risso's dolphins may be capable of diving to the daytime depth of squid, as suggested by deep diving vascular system and ophthalmalogical adaptations (Clarke 1986, Dawson et al 1987, 1992), shallower dives result in lower energy expenditure (Williams et al., 1999) so that foraging on prey when they are in shallower waters at night is most likely energetically advantageous. Hawaiian spinner dolphins, which also feed on diel vertical migrating prey, exhibit stereotypical diel patterns of behavior in which they rest in protected bays in the morning, socialize and travel in the afternoon and forage in offshore waters during nighttime (Norris et al., 1994). These differing levels of behavioral activity are reflected in acoustical activity, such that highest rates of all call types, including echolocation, occur during evening & nighttime foraging, moderate levels occur during traveling and low levels occur during rest. Odontocetes use echolocation clicks to investigate their environment for objects, prey, predators, conspecifics and navigational cues (Au, 1993; Akamatsu et al., 2005). Concurrent behavioral and acoustical studies of numerous odontocete species indicate higher click rates and occurrence during foraging behaviors, moderate rates during traveling and socializing behaviors and low click rates and occurrence during resting behaviors (Norris et al., 1994; Barrett-Lennard et al., 1996; Van Parijs and Corkeron, 2001; Nowacek, 2005). Long-term recordings can be used to examine diel variability in acoustic activity and indicate whether Risso's dolphins exhibit diel patterns of activity and rest.

This study uses long-term passive acoustic recordings to examine temporal trends in Risso's dolphin echolocation behavior and movement patterns. To determine if Risso's dolphins exhibit variability in diel activity levels and whether they exhibit consistent seasonal movements in the SCB, we examine 2.5 years of data from autonomous seafloor recording packages at six sites throughout the SCB for the presence of Risso's dolphin echolocation click bouts. In the SCB, Risso's dolphin echolocation clicks can be identified by the presence of a unique spectral peak and notch pattern, providing the opportunity to acoustically monitor the echolocation activity of this species (Soldevilla et al, 2008). Click bout occurrence and click rates are compared between light and dark photoperiods. Diel and seasonal trends in echolocation behavior are described and the implications for foraging and movements are discussed.

METHODS

Instrumentation and Data Collection

High-frequency Acoustic Recording Packages (HARPs) were deployed at six locations throughout the SCB between August 2005 and December 2007 at depths ranging between 300-1330m (Figures 3.1 & 2). A brief description of these autonomous seafloor-mounted recorders is provided here for clarity; see Wiggins and Hildebrand (2007) for a detailed description of HARP design and capabilities. The HARP data-logging system includes a 16-bit A/D converter, up to 1.9 TB of storage capacity, a hydrophone suspended 10m above the seafloor, a release system, ballast weights, and flotation. The dataloggers are capable of sampling up to 200 kHz and can be set to record continuously or on a duty cycle to accommodate variable deployment durations. This study includes data from 30 HARP deployments each lasting from 1-4 months. Temporal coverage at each of the six sites is variable due to cruise timing constraints and occasional instrument failures, as illustrated in Figure 3.3. Data from all deployments included in this study were sampled at 200 kHz, resulting in a recording bandwidth of 1-100 kHz. A variety of duty cycles were used across deployments ranging from continuous sampling to sampling 5 minutes followed by a break as great as 15 minutes (Figure 3.3).

Acoustical Analysis

Acoustic data were analyzed with a custom Matlab program, *Triton*. Raw acoustic HARP data were converted to XWAV format, a format similar to WAV format that incorporates instrument meta-data in an expanded header file, including recording start and stop times. This timing information is crucial when analyzing duty-cycled data. Each HARP deployment resulted in 1.6 - 1.9 TB of data which is impractical to analyze manually in original form. Therefore, these data were compressed for visual overview by creating long-term spectral averages (LTSAs, Wiggins and Hildebrand, 2007) from the XWAV files. LTSAs are effectively long-term spectrograms created using the Welch algorithm (Welch, 1967) by coherently averaging 4000 spectra created from 1000-point, 0%-overlapped, Hann-windowed data and aligning the resulting averaged spectra over time. The resulting LTSAs had resolutions of 100 Hz and 5 seconds in the frequency and time domains, respectively.

The method of spectral-averaging has proven effective for visually examining large acoustic data sets (e.g. Burtenshaw et al., 2004). At the described resolution, delphinid whistling and echolocation clicking bouts, rain bouts, ship passings, and other acoustic phenomenon can easily be distinguished from background noise. Soldevilla et al. (2008) describe distinct spectral patterns found in individual echolocation clicks of Risso's dolphins recorded during concurrent visual and acoustic ship-based surveys. Risso's dolphin clicks exhibit spectral peaks at 22, 25, 31 and 39 kHz with spectral notches at 20, 28 and 36 kHz. These spectral patterns are found in our autonomously recorded HARP data and are particularly striking as visualized in LTSAs (Figure 3.4). Start and end times of click bouts exhibiting the described spectral patterns were logged. Click bouts from mixed-species groups that included Risso's dolphin clicks were often distinguishable and were noted as such.

Hourly occurrence from presence and absence data only indicates that animals were heard during a given hour. Rates of calling can be used to distinguish between periods of high and low acoustic activity when the presence of animals is detected acoustically. An automatic detection algorithm was developed to simultaneously detect broadband clicks and whistles in the spectral domain, although only the click results are presented here. To obtain the best results for both whistles and clicks, spectra were calculated using a 1024-point Fast Fourier Transform (FFT) with 50% overlap and a Hann window. Spectral-means-subtraction was performed on each spectrum by subtracting the mean spectral vector of the surrounding 3 seconds of data. Individual spectra were selected as click candidates if a minimum percentage of frequency bins exceeded a minimum threshold within the bandwidth of interest. Values for minimum percentage, threshold and bandwidth were set as 12.5%, 13 dB and 15-95 kHz, respectively. For each click candidate, start and end times of 15 ms of data surrounding the click were extracted and overlapping segments were merged.

The click detector is not capable of classifying clicks to species so detected clicks needed to be assigned to species by linking them to the manual LTSA classifications. Detected clicks which occurred within start and end times of manually-classified LTSA click bouts were assigned to the appropriate delphinid click type. As individual clicks could not be identified to species using automated methods, data from mixed groups were not included in the diel click rate portion of the analysis. Mixed species groups accounted for 35% of the hourly Risso's dolphin click bout occurrences. No diel trend in occurrence was apparent for the mixed species groups removed from the analysis.

Temporal Analysis

Both presence/absence and click rate data were examined with reference to photoperiod. For each day with clicks at each site, photoperiods were categorized into day and night based on data obtained from the U.S. Naval Observatory website (http://aa.usno.navy.mil). Day and night were defined as the periods between nautical twilight, when the sun altitude was at -12^{o}. Each click bout was assigned a photoperiod. Click bouts that spanned multiple photoperiods were segmented and each segment was assigned the appropriate photoperiod.

To examine diel variation in the presence or absence of click bouts, ones and zeros were assigned to hour interval bins indicating the presence or absence, respectively, of click bouts. As photoperiod durations vary seasonally, the total number of hour bins per day that a click type was present within a photoperiod was normalized by the total number of hour bins per day within that photoperiod. Bins that crossed boundaries between photoperiods were assigned to the photoperiod that contained the greater portion of the hour. An analysis of variance was used to statistically test for differences in percent hours with clicks between photoperiods (Zar, 1999).

To examine diel variation in the click rates of Risso's dolphins, numbers of clicks per photoperiod needed to be normalized by the total recording time during that photoperiod. To account for duty-cycled data and occasional scheduling errors, total recording time was calculated from actual recording start times and durations. Click rates were calculated in clicks/min for each photoperiod and day as the total number of clicks divided by total recording time. Variability between days was accounted for by calculating a mean-adjusted calling rate in which the daily click rate was subtracted from the click rate for each photoperiod for each day. Diel variation in click rates was statistically tested by comparing mean-adjusted click rates among photoperiods using analysis of variance (Zar, 1999).

Data from the two northern nearshore sites (Point Conception and Santa Barbara Channel) and from the two southern nearshore sites (Santa Catalina Island and San Clemente Island) were included in the seasonal portion of the analysis while data from the two southern offshore sites were not included as they did not sample all seasons. Seasonal coverage across years and sites was variable (Table 3.1) and site-specific and interannual variations in occurrence are unknown. Therefore year and site were included in statistical tests for Risso's dolphin seasonality. The total number of days with detections per weekly period was used as a test metric. Seasons were defined by quarters of the year. The hypotheses of equal means across seasons, years and sites were tested using the GLM ANOVA function in SPSS 11.5 (www.spss.com) with three-way full factorial design and type IV sum of squares to account for the unbalanced design. An ANOVA can only test if all means are equal or not; Tamhane's T2 post-hoc test was used to determine which seasons, sites or years were different (Zar, 1999; Garson, 2008).

RESULTS

About 2000 instrument days of data were recorded and analyzed from the six instruments in the SCB, with the majority of effort at the Santa Catalina Island, Santa Barbara Channel, Point Conception and San Clemente Island sites (Table 3.2). These four sites recorded during each season during at least one year, while the remaining two sites, Tanner & Cortez Banks and San Clemente Basin, did not have complete seasonal coverage (Figure 3.3). Therefore, these two sites were not included in the remaining seasonal analyses.

Risso's dolphin clicks were heard at all six locations on a total of 739 instrument days (38% of all recording days). They were heard most often at the nearshore sites, in particular at Santa Catalina Island where click bouts were recorded on 75% of the recording days. At the remaining nearshore sites at Point Conception, Santa Barbara Channel and San Clemente Island, Risso's dolphin clicks were detected on 19-36% of recording days. Risso's dolphin clicks were rarely detected at the two farther offshore sites Tanner & Cortez Banks and San Clemente Basin sites (<1% of recording days) (Table 3.2).

A distinct diel pattern was evident in the presence of Risso's dolphin echolocation click bouts across hours of the day. At the four sites with multiple detections, there was a sharp increase in click detections during the early part of the night, with a slight decrease in the middle of the night followed by another increase before sunrise (Figures 3.5 & 3.6). This was followed by a sharp decrease after sunrise, though an additional peak was evident in the late morning. Click bouts were detected least often in the afternoon (Figures 3.5 & 3.6). Comparisons of the effect of photoperiod on click bout occurrence and click rate reveal that click bouts occurred significantly more often and that click rates are significantly higher at night than during the day (ANOVA, $F = 235$, $p < 0.01$, and $F = 93$, $p < 0.001$, respectively) (Figure 3.7).

Risso's dolphins were heard throughout the year at the four sites that contained multiple detections (Figure 3.8). The number of hours per day that Risso's dolphin click bouts were present is highly variable throughout the year, ranging from zero to eighteen. Variability in occurrence is high between seasons, sites and years (Figure 3.9). ANOVA results indicate that season, site, season*site, season*year and season*site*year were significant sources of variation in mean occurrence of Risso's dolphins (Table 3.3). Tamhane's T2 test demonstrates that mean occurrence was significantly higher in fall than in winter, and that Risso's occurred significantly more often at Santa Catalina Island and significantly less often in the Santa Barbara Channel than at the other three sites, respectively. At Santa Catalina, years 2006 and 2007 showed increases in occurrence during summer and fall, but decreased during fall in 2005. At San Clemente Island, data were only available for 2007, in which there were peaks in occurrence in spring and fall. At Point Conception and in the Santa Barbara Channel, winter and fall had higher occurrence during 2007 while summer was higher than fall during 2005.

DISCUSSION

The use of high-temporal resolution, passive acoustic recordings has provided detailed hourly information on diel patterns in occurrence of Risso's dolphin echolocation bouts. Hourly variability in Risso's dolphin click bout occurrence indicates high levels through the night, moderate levels during the morning and low levels during the afternoon. When these data are compared as a function of photoperiod, a diel pattern is evident in which there are both more hours with click bouts and higher click rates at night than during the day. Prior studies indicate higher click rates and occurrence during foraging behaviors, moderate rates during traveling and socializing behaviors and low click rates and occurrence during resting behaviors (Norris et al., 1994; Barrett-Lennard et al., 1996; Van Parijs and Corkeron, 2001; Nowacek, 2005). We suggest that the highest rates of echolocation found at night represent foraging due to related diel patterns in prey vertical migration (Gilly, 2006), consistent with Shane's (1995) hypothesis that Risso's dolphins forage at night. This activity pattern is similar to that found for Hawaiian spinner dolphins which actively forage at night on diel vertically migrating prey (Norris et al., 1994). However, it appears that afternoon is an important period of rest for Risso's dolphins, given the low levels of vocal activity at this time. Spinner dolphins exhibit low vocal activity while resting during the morning (Norris et al., 1994). Perhaps the moderate levels of morning activity represent social and traveling behavior similar to that found in the afternoon for spinner dolphins.

Diel periods of vocal activity have been described for several other odontocete species. A T-Pod study off Scotland indicates that harbor porpoise showed greater echolocation activity at dawn and night (Carlstrom, 2005), while off Ireland, bottlenose dolphins exhibited no distinct diel pattern (Philpott et al., 2007). Goold (2000) found that common dolphins (*Delphinus delphis*) off New Zealand produced significantly more vocalizations during dusk and night which may be related to greater foraging activity as common dolphins forage on diel-vertically migrating prey.

A comparison of the hourly occurrence of Risso's dolphin click bouts and squid dive patterns reveals interesting similarities. In addition to increased activity during the night compared to day, a decrease in hourly detections is apparent in the middle of the night compared to the early and later parts of the night. This pattern is observed across all sites over periods as long as 2.5 years (Figure 3.5). Recent tagging work on jumbo squid (*Dosidicus gigas)*, a known prey item of California Risso's dolphins (Orr, 1966), indicates a similar temporal pattern to their dive behavior (Gilly, 2006). The tagged squid were shallow during the early part of the night, often returned to depth during the middle of the night, and subsequently returned to shallow waters before dawn. While detailed dive patterns of other cephalopod prey have not been described, many squid species found in the SCB are known to follow diel vertical migrations such that they are available to Risso's dolphins at the surface at night (Roper and Young, 1975). Spinner and dusky dolphins have both been shown to follow the vertical movements of their diel-vertically migrating prey while near surface waters (Benoit-Bird and Au, 2003; Benoit-Bird et al., 2004). Our results for Risso's dolphins suggest a similar pattern in which Risso's dolphins are actively feeding and echolocating when squid are within a preferred shallow depth range.

Geographically, Risso's dolphin detections were mostly confined to the four nearest-shore sites with rare detections occurring at the two offshore sites. This distribution is similar to that found by Forney and Barlow (1998) during visual surveys off California. Okutani and McGowan (1969) provide distributions for paralarvae of a variety of squid species found in the SCB. Market squid, *Loligo opalescens*, a known prey item of Risso's dolphins off Monterey (Kruse, 1989), are the only squid with neritic spawning grounds and these grounds closely match the distribution of Risso's dolphin detections. Stomach content analyses off California are rare (e.g. Orr, 1966) so preferred prey in this area is unknown. These distribution results suggest that *L. opalescens* is likely a preferred prey item. However, this study only includes six sites so it is possible Risso's dolphins inhabit other regions outside of *L. opalescens* spawning grounds. Additionally, sampling at the 2 offshore sites did not cover the entire year, so it is possible that they inhabit offshore regions during winter or spring.

This study provides additional data on inter- and intra-annual changes in Risso's dolphin distribution for the SCB. Dolphins were heard throughout the year at all inshore sites. Seasonal and interannual variability were high at all sites. Acoustic occurrence was generally higher during fall across sites, particularly during 2007, though at the northern sites the peak occurred during summer in some years. Dohl et al. (1981) report similar results from visual surveys of the entire SCB in which dolphins are present year-round with a peak in sightings occurring during September. Based on ship-board and aerial visual survey results, Green et al. (1992) and Forney and Barlow (1998) indicate that dolphins move from Oregon and Washington during spring and summer to California in fall and winter. Acoustic occurrence, in the present study, remained high during spring 2007 at San Clemente Island. Several possible explanations for this high occurrence include: the year 2007 was an anomalously cold year to the north of the SCB; only a portion of the population moves out of the region during spring and summer; or a resident population remains in the region year-round. Risso's dolphins were heard on 75% of days recorded at Santa Catalina Island. This is clearly an important habitat for these animals, but it remains unknown whether this represents a habitat of a resident population or if it is just a common feeding ground for animals moving over a larger area. Photo-identification studies such as those conducted by Shane (1994) and Kruse (1989) could help answer this question.

When considering highly mobile species such as dolphins, it is unclear whether a lack of acoustic detections represents true absence of the dolphins from the study site or presence of non-vocalizing animals. Dolphins are capable of moving into and out of a study site within a day, as shown by visual surveys of spinner dolphins off Hawaii that exhibit diel movements between inshore resting areas during the day to offshore feeding zones at night (Benoit-Bird and Au, 2003). The diel variation in occurrence of Risso's dolphin clicks could therefore represent movements out of the area during the day and movements into the area during the night. Conversely they could represent increased echolocation activity as a function of varying behavior state. Since Risso's dolphins exhibited greater vocal activity at night at all sites it seems likely that this variation represents a changing behavioral state, particularly when one considers the correspondence of increased click activity with squid diving behavior. The development of compact acoustic tags, similar to those used on larger whales, may provide more definitive answers.

Similarly, seasonal patterns of occurrence may represent movements into and out of the area or seasonal variation in calling. Echolocation clicks of dolphins are used for foraging and navigation. Unlike larger baleen whales that have large blubber stores to sustain them when migrating between feeding and breeding grounds, odontocetes have thin blubber layers and need to feed frequently (Smith and Gaskin, 1974; Lockyer, 1981) which suggests that dolphins are unlikely to exhibit long periods of fasting. Therefore, one would expect that seasonal variations in echolocation occurrence represent movements into and out of the area.

Additional factors which may affect the probability of detecting calling animals include distance from hydrophone, propagation conditions, masking and misclassifications of species. Although the HARPs at different sites are located at different depths with different oceanographic conditions, at the frequencies used for echolocation, attenuation severely limits detection range, and therefore the potential for significant variation owing to seasonal variations is reduced. Detection distances may be smaller for sites at greater depths; echolocation click detection ranges are approximately 4 km (E. Henderson, personal communication) such that the maximum of 1 km difference in depth for this study could result in as much as 10% loss in detection range at the deepest sites, too low to account for the spatial differences found in this study. Ships, sonars, other animals, rain, wind and waves may produce sounds that mask the echolocation click of our chosen species so it is important to consider seasonality in these sources. Preliminary analysis indicate that shipping noise is consistent throughout the year at all sites except Santa Catalina Island where there is an increase in occurrence during the summer (May-Sept), while wind and rain noise within the frequency band of clicks occurs minimally throughout the year. A more thorough investigation of seasonal variation related to these noise sources is the topic of another study.

Several biases are present in our method of counting clicks for diel click rate portion of this study that are worth consideration. If multiple species were calling during a click bout, and it was apparent in the LTSAs, these data were not included in the analysis, biasing the counts to be low. However, multiple species may have been present but not noticeable. This would cause the click counts to be biased high for the study species. We expect this bias will be minimal as we were conservative in our species classification. Additional considerations that would bias our results to be lower than actually occurred include: 1) many low quality clicks were present that did not exceed the thresholds; 2) during periods of intensive clicking, the surrounding data used for spectral-mean-subtraction would be relatively high resulting in good quality clicks being missed by the detector; 3) during periods with rapid click trains or click trains from multiple individuals in which the apparent interclick interval was greater than 15 ms, only 1 click was chosen per 15 ms. Overall, we expect these biases to consistent across all recordings so that comparisons between times and locations should not be affected.

CONCLUSIONS

Diel patterns exist for both occurrence of calls and calling rates. Risso’s dolphins call more often and at greater rates during the nighttime across sites in the SCB. These diel patterns provide insight into the behavioral ecology of these animals and add support to suggestions that Risso’s dolphins are nighttime foragers. This type of data is important when designing passive acoustic monitoring surveys. Oftentimes, duty cycles are necessary so it is imperative that survey designs should either sample each photoperiod equally or at least sample at the same time each day. Seasonal and interannual variations among sites in the SCB were high as has been found in during studies employing visual survey methods. The year-round occurrence of Risso's dolphins in the SCB and high occurrence rates at Santa Catalina suggest the possibility of a resident population in addition to a population that moves seasonally between California and Oregon/Washington waters. This should be investigated further with photo-identification techniques. While the time series described in this study is not long enough to examine interannual and interdecadal changes such as those described in previous studies (e.g. Shane, 1995; Kruse et al., 1999), it is on-going and has the potential to answer such questions in the future especially when coupled with detailed environmental observations.

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Chapter 3, in full, is currently being prepared for submission for publication of the material. Soldevilla, Melissa; Wiggins, Sean; Hildebrand, John. The dissertation author was the primary investigator and author of this material.

FIGURES

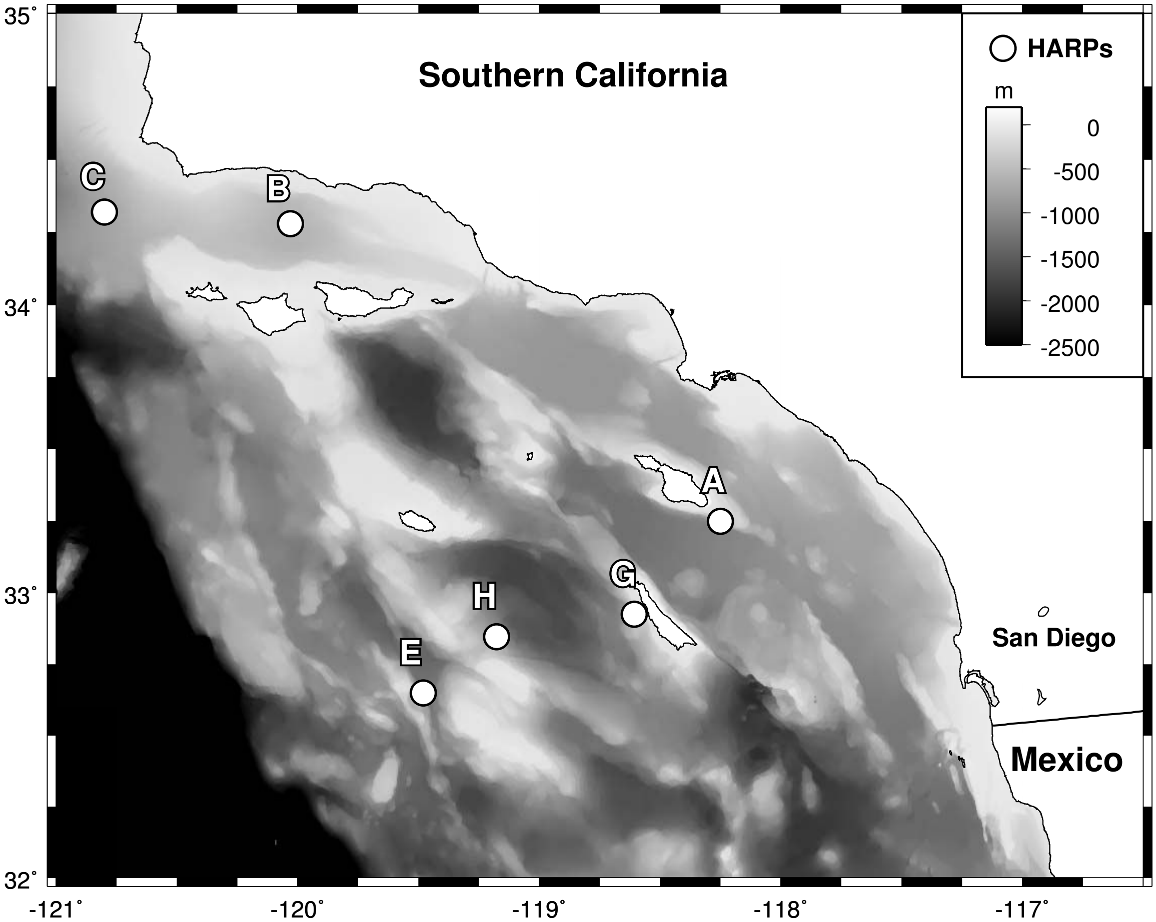

Figure 3.1. Map of study area including locations of HARP deployments. Depths are indicated by colorbar. Sites: A = Santa Catalina Island, B = Santa Barbara Channel, C = Point Conception, E = Tanner/Cortez Banks, G = San Clemente Island, and H = San Nicholas Basin.

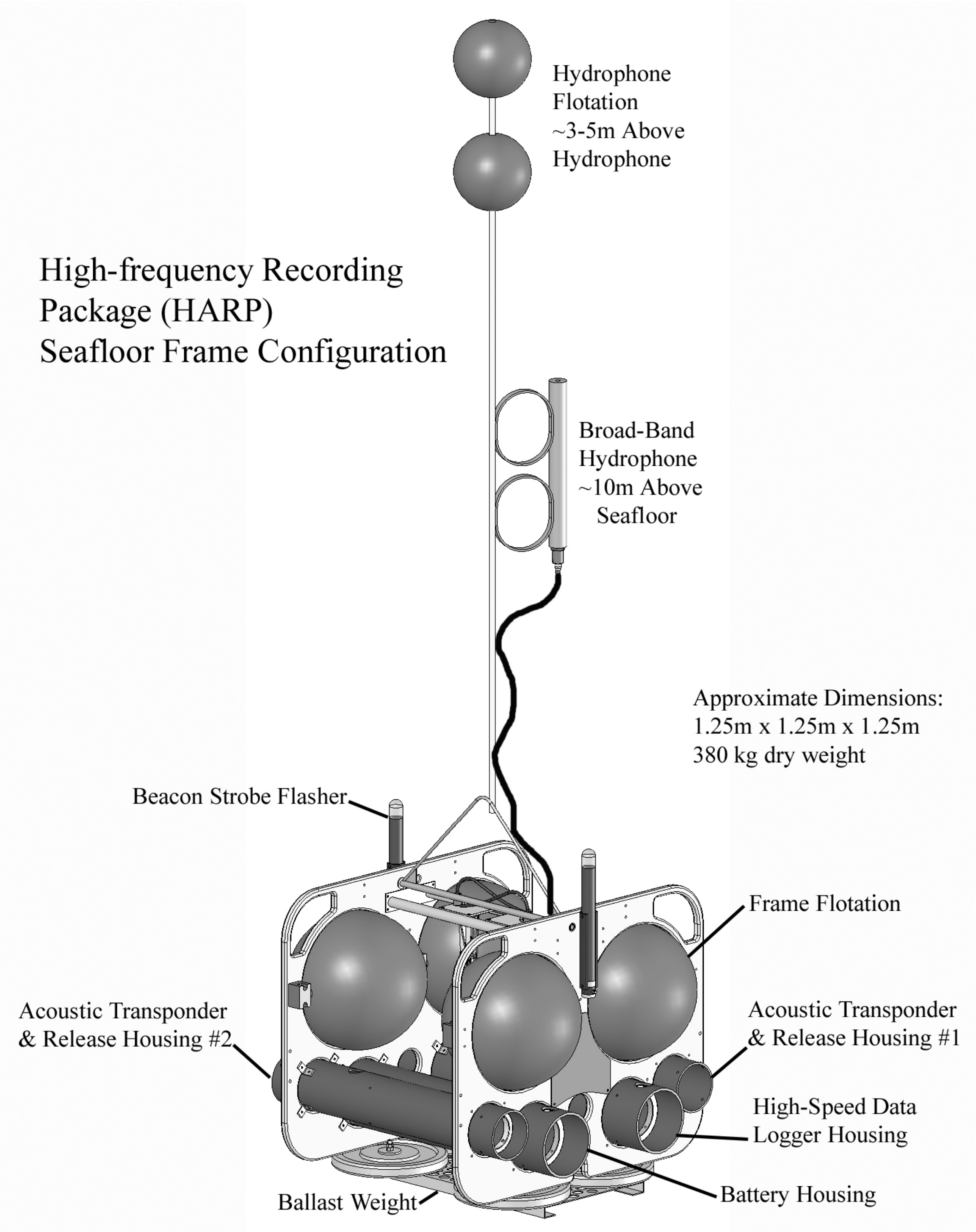

Figure 3.2. HARP schematic representation of sea-floor recording package.

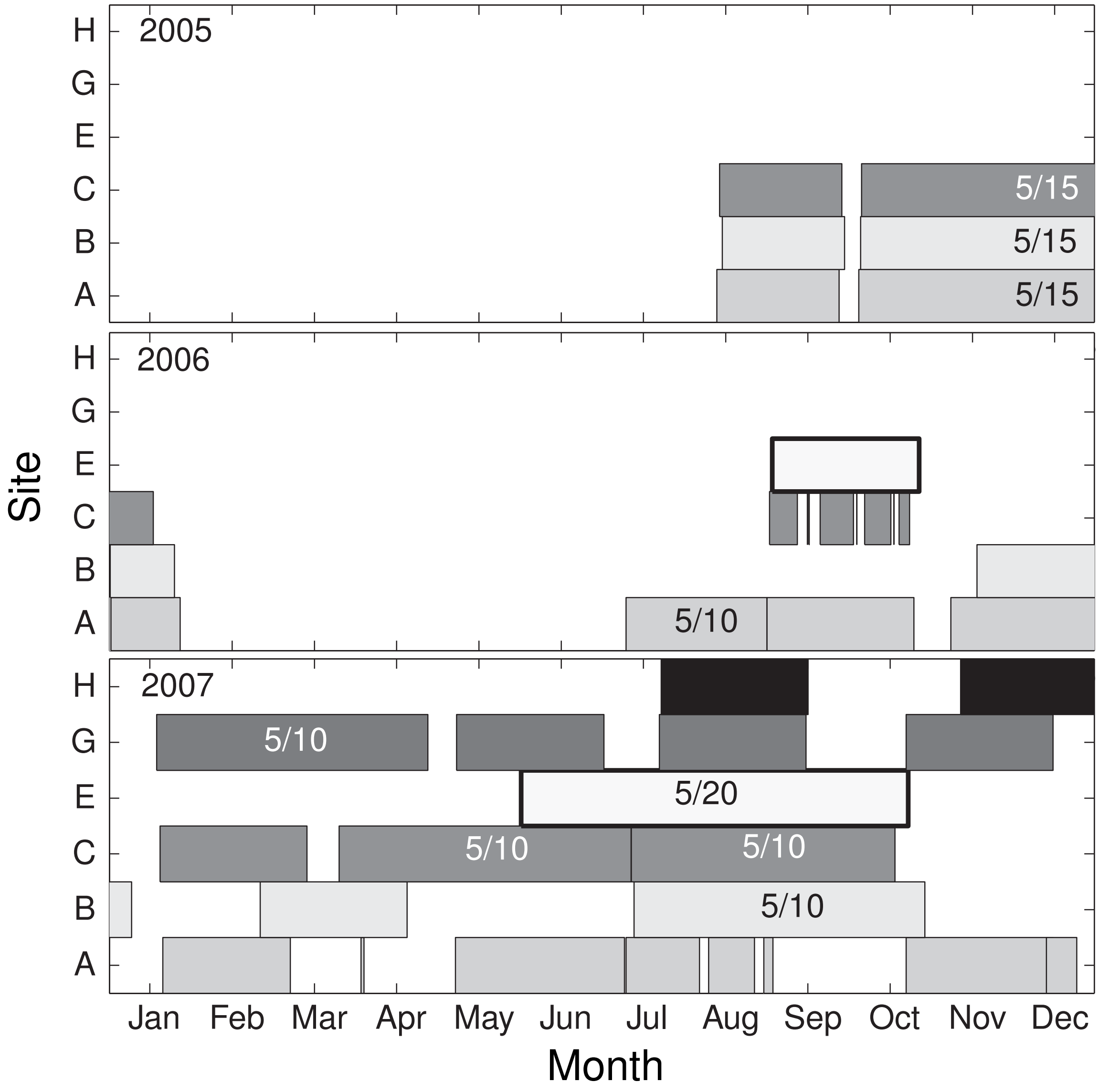

Figure 3.3. HARP data and duty cycle information at each of six sites in the SCB. A = Santa Catalina Island, B = Santa Barbara Channel, C = Point Conception, E = Tanner/Cortez Banks, G = San Clemente Island, and H = San Nicholas Basin. Shading represents dates when data is available at each site. Numbers within shaded regions represent the specified duty cycle as minutes on / minutes of total cycle. Shaded regions without numbers represent continuous data. Data spanning year boundaries follow the previous duty cycle.

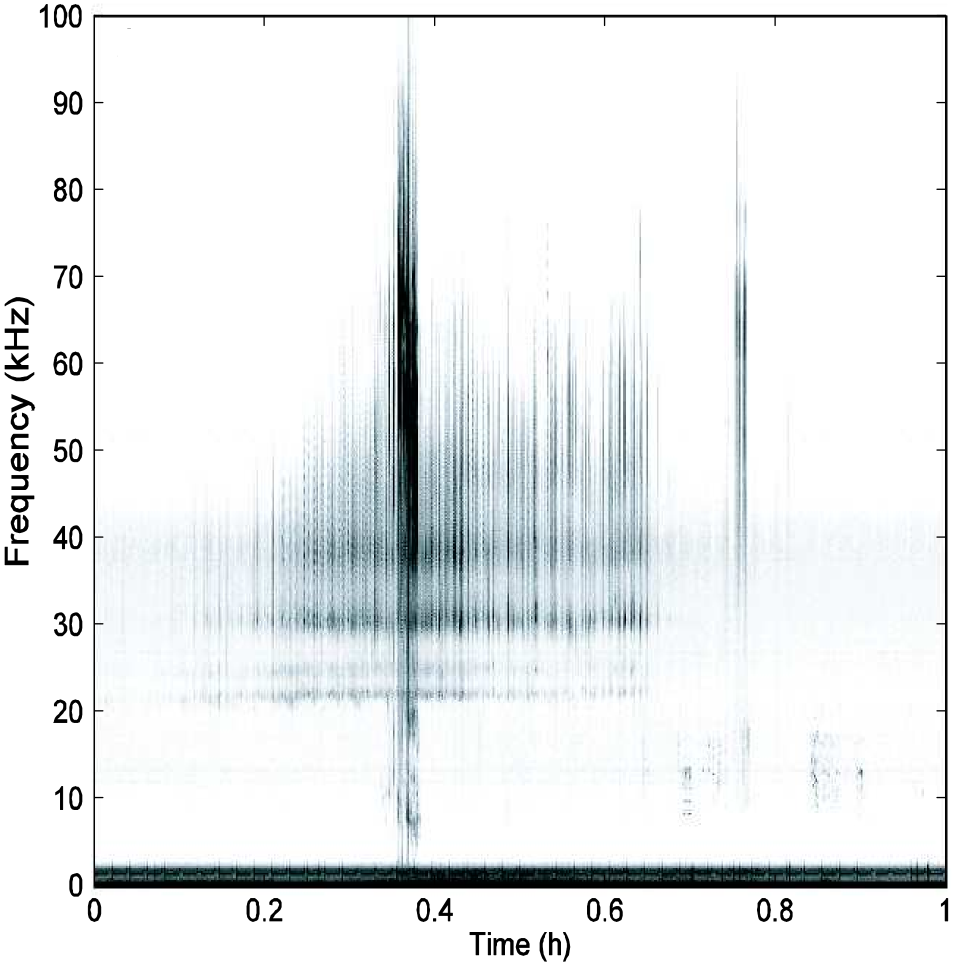

Figure 3.4. Example long-term spectral average illustrating echolocation click bout containing the unique spectral peak and notch structure described for Risso's dolphins by Soldevilla et al 2008. Spectral peaks occur in the clicks at 22, 25, 31 and 39 kHz.

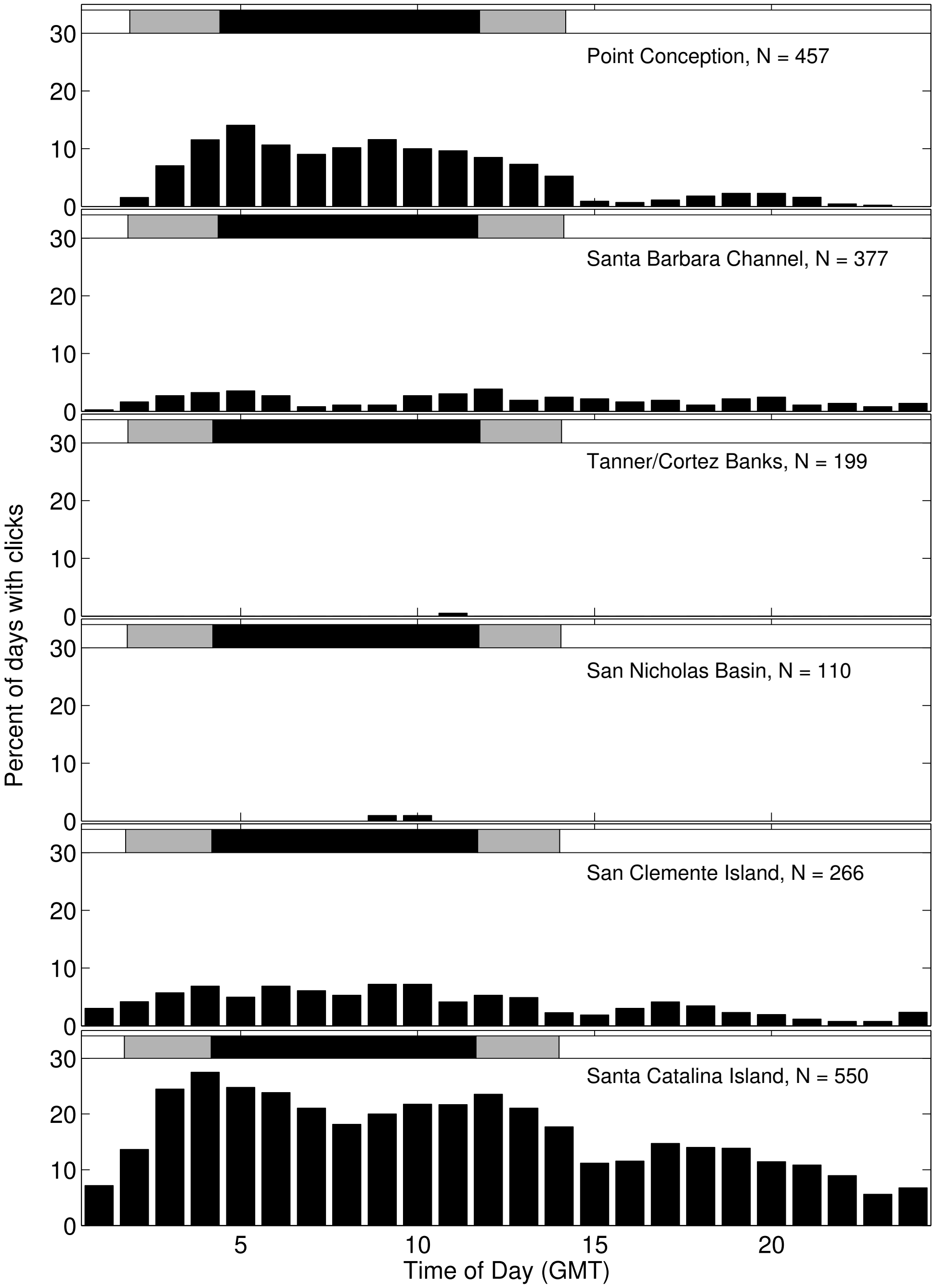

Figure 3.5. Diel patterns of Risso's echolocation click bouts at each of the six HARP locations. Vertical bars represent the percent of days that have clicks present in each hour time bin. N represents the number of recording days at each site. Horizontal bar indicates periods of light (white) or darkness (black). Gray areas represent periods that may be light or dark depending on time of year.

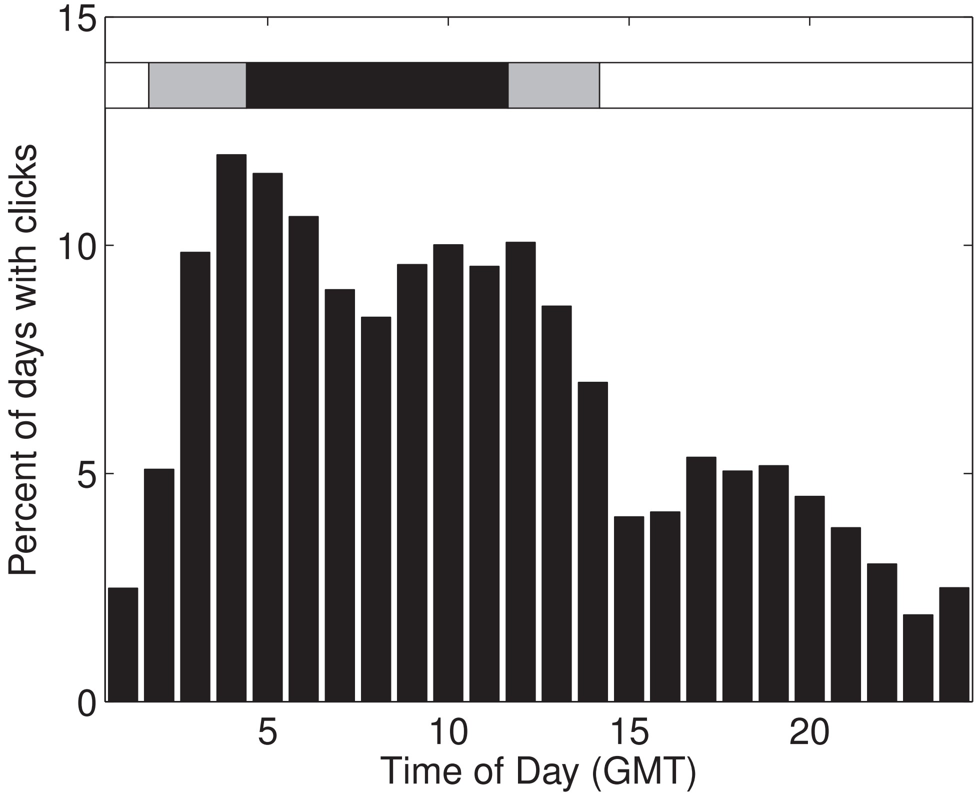

Figure 3.6. Diel patterns of Risso's echolocation click bouts combined across the six HARP locations. Vertical bars represent the percent of days that have clicks present in each hour time bin. Horizontal bar indicates periods of light (white) or darkness (black). Gray areas represent periods that may be light or dark depending on time of year.

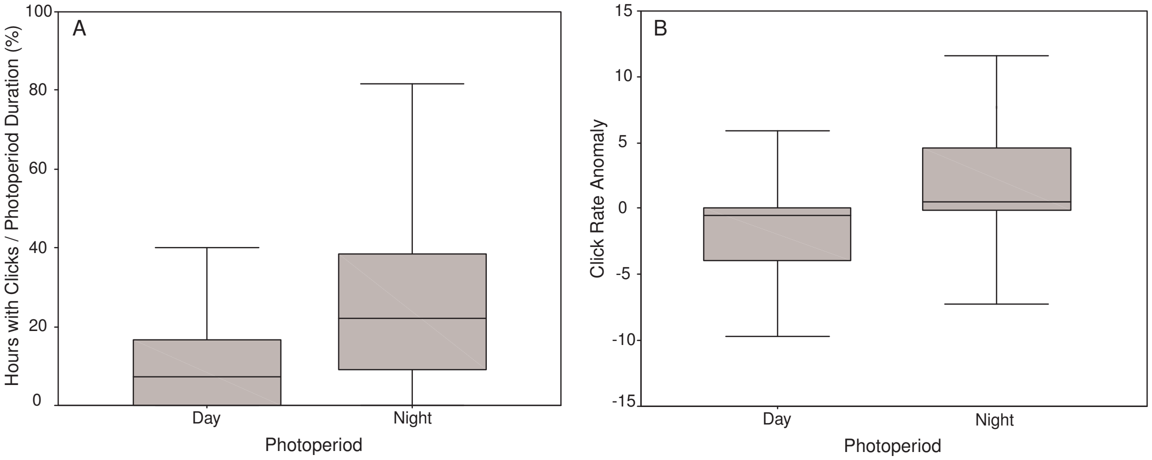

Figure 3.7. Variation in Risso's dolphin click bout occurrence (a) and daily click rate anomaly (b) between photoperiods. Central lines represent median value, boxes contain 25th to 75th percentiles and whiskers contain 5th to 95th percentiles of data. Click bout occurrence and daily click rate anomaly are both significantly higher during the night than during the day.

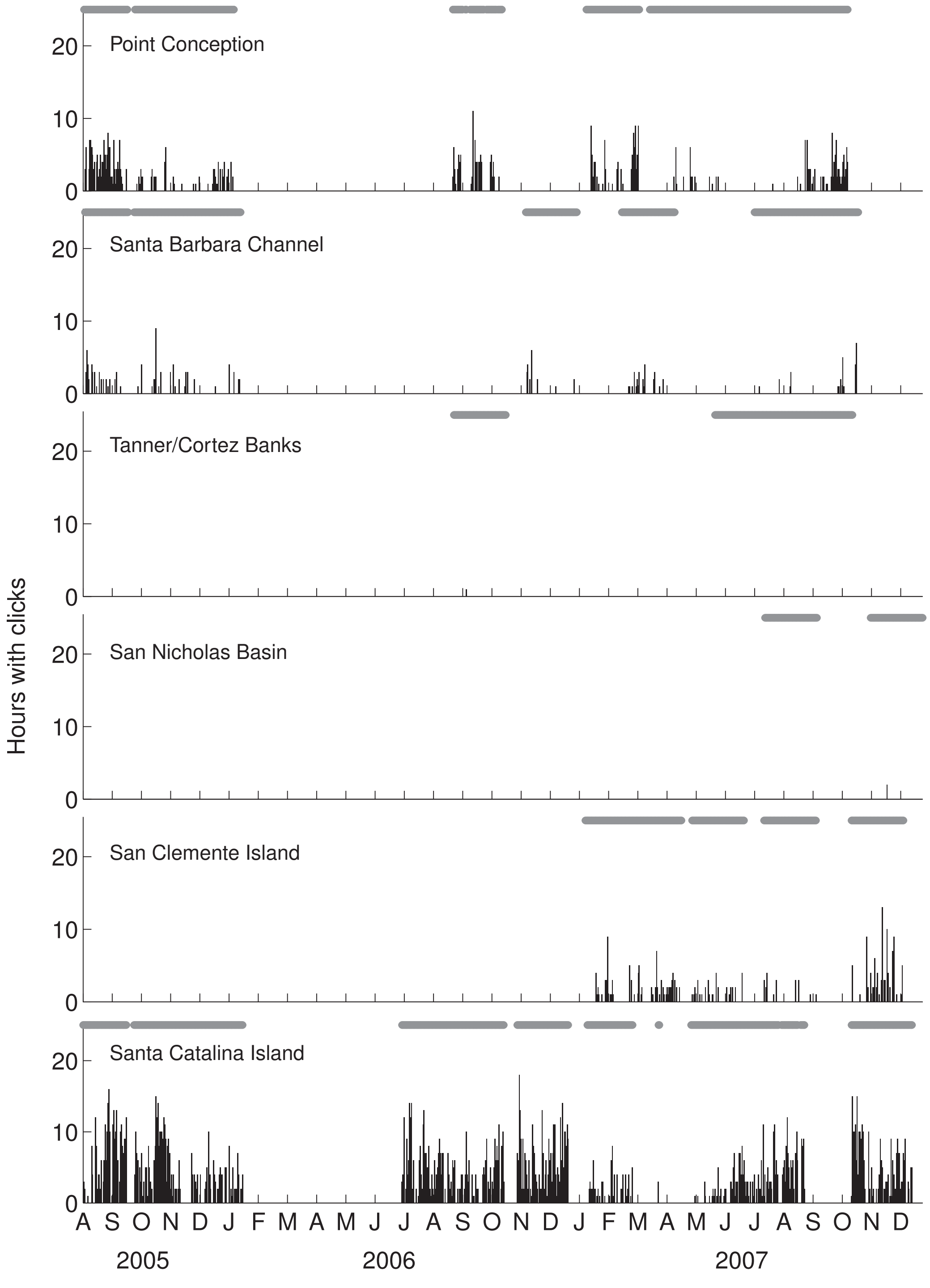

Figure 3.8. Time series representing presence of Risso's dolphin clicks at each of the six HARP sites. Plots represent the number of hour bins in which dolphin clicks were present each day. Gray bars at the top indicates times that data is available.

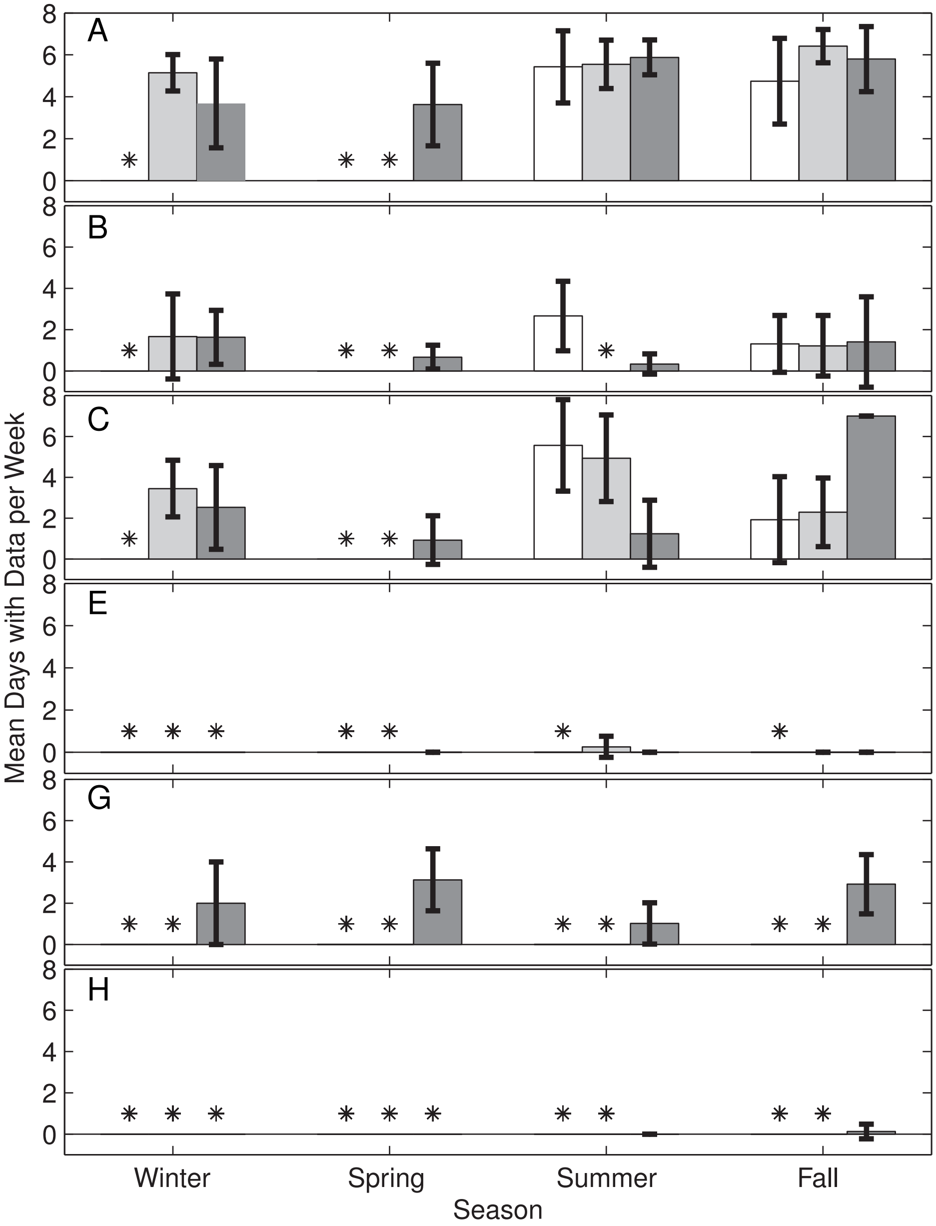

Figure 3.9. Seasonal and annual variation in mean days per week with Risso's dolphin click bouts across the six HARP sites. Bar colors indicate year: white = 2005, light gray = 2006, and dark gray = 2007. Error bars indicate standard deviation. Stars indicate no data available. Each plot is a separate site: A = Santa Catalina Island, B = Santa Barbara Channel, C = Point Conception, E = Tanner/Cortez Banks, G = San Clemente Island, and H = San Nicholas Basin

TABLES

Table 3.1. Seasonal coverage at each site across three years of study. Cells represent the number of week-long samples. Site abbreviations: A = Santa Catalina Island, B = Santa Barbara Channel, C = Point Conception, and G = San Clemente Island. The remaining two sites were not included in the seasonal part of this study because they were only deployed during part of the year in 2007 and did not sample across all seasons.

	Winter			Spring			Summer			Fall			Total
Site	2005	2006	2007	2005	2006	2007	2005	2006	2007	2005	2006	2007	
A	0	4	8	0	0	9	7	12	10	13	12	10	85
B	0	4	8	0	0	3	7	0	12	13	7	5	59
C	0	3	10	0	0	13	7	5	13	13	4	3	71
G	0	0	11	0	0	12	0	0	9	0	0	8	40
Total	0	11	37	0	0	37	21	17	44	39	23	26	255
		48			37			82			88		255

Table 3.2. Summary of recording days, days with Risso's click bouts present, and percent of days with Risso's click bouts present and mean instrument depth for each of the six HARP sites.

	Point Conception	Santa Barbara Channel	Tanner & Cortez Banks	San Nicholas Basin	San Clemente Island	Santa Catalina Island	Total
Recording Days	457	377	199	110	266	550	1959
Days with Risso's click bouts	166	70	1	1	90	411	739
Percent Days with Risso's click bouts	36	19	1	1	34	75	38
Instrument Depth	787	585	1013	1316	435	351	

Table 3.3. Results of 3-way ANOVA for seasonal, annual and site effects on Risso's dolphin occurrence

Source	Type IV Sum of Squares	df	Mean Square	F	Sig.	
Corrected Model	955.6	29	33.0	13.0	0.000	
Intercept	2083.1	1	2083.117	823.2	0.000	
SEASON	69.1	3	23.018	9.1	0.000	*
SITE	218.5	3	72.822	28.8	0.000	*
YEAR	1.0	2	0.5	0.2	0.822	
SEASON * SITE	126.5	9	14.1	5.6	0.000	*
SEASON * YEAR	106.2)	3	35.4	14.0	0.000	*
SITE * YEAR	20.5	4	5.1	2.0	0.092	
SEASON * SITE * YEAR	100.2	5	20.0	7.9	0.000	*
Error	569.32	225	2.5			
Total	3996.7	255				
Corrected Total	1525.0	254				

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CHAPTER 4

COMPARISON OF SPATIAL AND TEMPORAL PATTERNS OF ECHOLOCATION CLICK ACTIVITY FOR TWO CLICK TYPES PRODUCED BY PACIFIC WHITE-SIDED DOLPHINS (*LAGENORHYNCHUS OBLIQUIDENS*) IN THE SOUTHERN CALIFORNIA BIGHT

ABSTRACT

A comparison of temporal and geographical trends in different echolocation click types produced by Pacific white-sided dolphin (*Lagenorhynchus obliquidens*) can lead to insights into the significance of their usage by the dolphins. Using autonomous seafloor recording packages, the geographical, diel and seasonal patterns of Pacific white-sided dolphin (*Lagenorhynchus obliquidens*) echolocation click activity are described for six locations in the Southern California Bight. Click bouts of the two types of Pacific white-sided dolphin echolocation clicks are identified based on their unique spectral characteristics in long-term spectral averages. Pacific white-sided dolphin type A clicks were detected on 317 of 1959 instrument recording days and were heard at all six sites, with the majority of detections occurring at San Clemente Island and Point Conception. Pacific white-sided dolphin type B clicks were detected on 130 instrument days and were only heard at the two southern inshore sites. Significant diel patterns are evident for both click types: type A click bouts were detected during more hours and with higher click rates at night than during the day while type B click bouts exhibited the opposite behavior with greater activity during the day. At the southern sites, both click types exhibited a fall-winter peak in seasonal occurrence. At Point Conception, where only type A was detected, peak occurrence was during spring. Type A seasonality resembles described movement patterns northward along the west coast during spring and summer and southward into the SCB during fall and winter. Potential implications of the distinction between the two Pacific white-sided dolphin click types both spatially and temporally are discussed.

INTRODUCTION

Pacific white-sided dolphins are a cold-temperate pelagic species endemic to the North Pacific Ocean. They are found in the Sea of Japan, the southern Bering Sea, and along the west coast of North America as far south as the Gulf of California (Leatherwood et al., 1984). Offshore of California, they are one of the most abundant cetacean species (Barlow and Forney, 2007), often found in large schools and in association with other cetacean species.

Along the west coast of North America, abundance and distribution of Pacific white-sided dolphins is highly variable both seasonally (Green et al., 1992; Forney and Barlow, 1998) and annually (Shane, 1994; Benson et al., 2002; Barlow and Forney, 2007). This variability has led different researchers to suggest 1) north-south seasonal movements with animals moving north to Oregon and Washington in the summer and fall and south to California in the winter and spring (Forney and Barlow, 1998), 2) onshore-offshore movements with animals moving into nearshore waters during winter and spring and into offshore waters during summer and fall (Brown and Norris, 1956; Norris et al., 1961; Roest, 1970; Dohl et al., 1983; Black, 1994), 3) movements from southern California in winter and spring into central California in summer and fall (Black, 1994), 4) movements from southern California in winter and spring into Mexican waters during summer and fall (Leatherwood et al., 1984) and 5) that movements may be related to large-scale temperature changes (Leatherwood et al., 1982; Dohl et al., 1983; Leatherwood et al., 1984; Benson et al., 2002). These hypotheses are not necessarily mutually exclusive.

Some of this complexity could be explained by different populations of Pacific white-sided dolphins exhibiting different movement patterns. The distributions of two genetically and morphometrically distinct Pacific white-sided dolphin populations are known to overlap in the Southern California Bight, such that a northern California-Oregon-Washington population occurs northward of 33°N and a southern Baja California population occurs southward of 36°N (Walker et al., 1986; Lux et al., 1997). Carretta et al (2004) have suggested these populations may exist sympatrically or occupy the region at different times seasonally or annually. The use of the region by two populations with distinct seasonal movement patterns could explain the disparate movement patterns suggested in previous studies, however answering this question has remained a challenge as visual surveys are unable to distinguish between the two populations in the field.

Recent spectral analyses of the echolocation clicks of Pacific white-sided dolphins off southern California has revealed the existence of two distinct echolocation click types (Soldevilla et al., 2008). The authors suggest that one explanation for these two click types is that they may be population-specific and represent the two populations which overlap within the SCB. A temporal analysis of long-term acoustic data from northern and southern regions within the SCB could indicate the direction of animals moving into and out of the SCB seasonally. If directional movements into and out of the SCB are indicated and are different for animals producing the two different click types, this would provide support to the hypothesis that the two click types represent the two populations.

On a shorter temporal scale, diel patterns of echolocation can indicate activity levels and can offer insight into behavioral patterns including feeding, traveling, and resting. Concurrent behavioral and acoustical studies of numerous odontocete species indicate higher click rates and occurrence during foraging behaviors, moderate rates during traveling and socializing behaviors and low click rates and occurrence during resting behaviors (Norris et al., 1994; Barrett-Lennard et al., 1996; Van Parijs and Corkeron, 2001; Nowacek, 2005). A daytime behavioral study off Monterey indicates that diurnal behavior patterns vary seasonally with Pacific white-sided dolphins feeding more often in the morning and socializing more often in the in the afternoon during oceanic season (Aug.-Oct.), while feeding occurred equally often during morning and afternoon during the upwelling (Mar.-Jul.) and Davidson (Nov.-Feb.) seasons (Black 1994). Milling, resting and traveling behaviors did not exhibit a diurnal cycle. A study of captive Pacific white-sided dolphins indicates nighttime rest associated with low vocal activity and high vocal activity during dawn and dusk associated with greater behavioral activity (Goley, 1996). Studies of diel patterns in foraging behavior indicate activity throughout the day and night, though night-time foraging has not been observed directly due to light constraints of visual observations. Daytime foraging has been indicated by direct observation or prey sampling (Brown and Norris, 1956; Black, 1994; Heise, 1997; Morton, 2000), respiration patterns in radio-tagging studies (Leatherwood and Evans, 1979; Black, 1994), presence as bycatch in daytime purse-seine sets (Walker et al., 1986) and captive sleep studies (Goley, 1999). Pacific-white-sided dolphin nighttime foraging has been inferred from stomach volumes in stomach content analyses of animals collected at various times of the day (Stroud et al., 1981) and by their presence as bycatch in nighttime sets of the purse-seine net fishery (Walker et al., 1986). Nighttime observations of wild dolphins are clearly needed to develop a complete understanding of diel behavioral activity patterns. Long-term recordings can be used to examine diel variability in acoustic activity and indicate whether wild Pacific white-sided dolphins exhibit diel patterns of activity and rest.

Overlap in the location of two populations of the same species can result in competition. This unusual occurrence may be mediated by mechanisms such as the use of portions of the SCB at separate times or through niche separation such as differential prey preferences. Taking into consideration that the two click types may represent the two populations found within the SCB, spatial or seasonal differences in click usage could be indicative of differences in spatial or seasonal use of the SCB by the two populations. In addition, the existence of distinct diel patterns between the click types could be an indication that the two populations are using the area differentially on a shorter diel time scale, possibly as a result of differences in prey preferences. An examination of the similarities and differences in the spatial and temporal occurrence of the two Pacific white-sided dolphin click types may answer: 1) what is the timing of seasonal occurrence patterns within the SCB; 2) is direction into and out of the SCB indicated by spatial differences in seasonal activity; 3) does dolphin echolocation activity vary between day and night; 4) do click bouts of the two types co-occur and if so, how often; 5) does the usage of the two click types vary spatially throughout the SCB; 6) do the two click types differ in their usage patterns throughout the day; and 7) do seasonal/annual differences exist in usage of the two click types. Answers to these questions can lead to insights into the significance of the two click types as well as the ecology of Pacific white-sided dolphins in the SCB.

This study uses long-term passive acoustic recordings to examine spatial and temporal trends in Pacific white-sided dolphin echolocation behavior and movement patterns. To determine if Pacific white-sided dolphins exhibit variability in diel activity levels and whether they exhibit consistent seasonal movements in the SCB, we examine 2.5 years of data from autonomous seafloor recording packages at six sites throughout the SCB for the presence of Pacific white-sided dolphin echolocation click bouts. Click bout occurrence and click rates are compared between light and dark photoperiods and diel and seasonal trends in echolocation behavior are described and compared between the two click types. Spatial and temporal differences are found between the two click types and the implications for foraging, movements and the significance of click types are discussed.

METHODS

Instrumentation and Data Collection

High-frequency Acoustic Recording Packages (HARPs) were deployed at six locations throughout the SCB between August 2005 and December 2007 at depths ranging between 300-1330m (Figures 4.1 & 4.2). A brief description of these autonomous seafloor-mounted recorders is provided here for clarity; see Wiggins and Hildebrand (2007) for a detailed description of HARP design and capabilities. The HARP data-logging system includes a 16-bit A/D converter, up to 1.9 TB of storage capacity, a hydrophone suspended 10m above the seafloor, a release system, ballast weights, and flotation. The dataloggers are capable of sampling up to 200 kHz and can be set to record continuously or on a duty cycle to accommodate variable deployment durations. This study includes data from 30 HARP deployments each lasting from 1-4 months. Temporal coverage at each of the six sites is variable due to cruise timing constraints and occasional instrument failures, as illustrated in Figure 4.3. Data from all deployments included in this study were sampled at 200 kHz, resulting in a recording bandwidth of 1-100 kHz. A variety of duty cycles were used across deployments ranging from continuous sampling to sampling 5 minutes followed by a break as long as 15 minutes (Figure 4.3).

Acoustical Analysis

Acoustic data were analyzed with a custom Matlab program, *Triton*. Raw acoustic HARP data were converted to XWAV format, a format similar to WAV format that incorporates instrument metadata in an expanded header file, including recording start and stop times. This timing information is crucial when analyzing duty-cycled data. Each HARP deployment resulted in 1.6 - 1.9 TB of data which is impractical to analyze manually in original form. Therefore, these data were compressed for visual overview by creating long-term spectral averages (LTSAs, Wiggins and Hildebrand, 2007) from the XWAV files. LTSAs are effectively long-term spectrograms created using the Welch algorithm (Welch, 1967) by coherently averaging 4000 spectra created from 1000 point, 0% overlapped, Hann-windowed data and aligning the resulting averaged spectra over time. The resulting LTSAs had resolutions of 100 Hz and 5 seconds in the frequency and time domains, respectively.

The method of spectral-averaging has proven effective for examining large acoustic data sets (e.g. Burtenshaw et al., 2004). At the described resolution, delphinid whistling and echolocation clicking bouts, rain bouts, ship passings, and other acoustic phenomenon can easily be distinguished from background noise. Soldevilla et al. (2008)

describe two distinct click types based on unique spectral patterns found in individual echolocation clicks of Pacific white-sided dolphins recorded during concurrent visual and acoustic ship-based surveys. Click type A can be identified by spectral peaks at 22, 27.5 and 38 kHz with spectral notches at 19, 24.5 and 30 kHz. Click type B can be identified by spectral peaks at 22, 26 and 36 kHz with spectral notches at 19, 24 and 30 kHz. These spectral patterns are found in our autonomously recorded HARP data and are particularly striking as visualized in LTSAs (Figure 4.4). By visually examining thirty minute long LTSA segments, start and end times of click bouts exhibiting the described spectral patterns were located and logged. Click bouts from mixed-species groups that included either of the Pacific white-sided dolphin click types were often distinguishable and were noted as such.

Hourly occurrence from presence and absence data only indicates that animals were heard during a given hour. Rates of calling can be used to distinguish between periods of high and low acoustic activity when the presence of animals is detected acoustically. An automatic detection algorithm was developed to simultaneously detect broadband clicks and whistles in the spectral domain, although only the click results are presented here. To obtain the best results for both whistles and clicks, spectra were calculated using a 1024-point Fast Fourier Transform (FFT) with 50% overlap and a Hann window. Spectral-means-subtraction was performed on each spectrum by subtracting the mean spectral vector of the surrounding 3 seconds of data. Individual spectra were selected as click candidates if a minimum percentage of frequency bins exceeded a minimum threshold within the bandwidth of interest. Values for minimum percentage, threshold and bandwidth were set as 12.5%, 13 dB and 15-95 kHz, respectively. For each click candidate, start and end times of 15 ms of data surrounding the click were extracted and overlapping segments were merged.

The click detector is not capable of classifying clicks to species so detected clicks needed to be assigned to species by linking them to the manual LTSA classifications. Detected clicks which occurred within start and end times of manually-classified LTSA click bouts were assigned to the appropriate click type. As individual clicks could not be identified to species using automated methods, data from mixed groups were not included in the diel click rate portion of the analysis. Mixed species groups accounted for 18% and 11% of the hourly Pacific white-sided dolphin types A and B click bout occurrences, respectively. No diel trend in occurrence was apparent for the mixed species groups removed from the analysis.

Temporal Analysis

Both presence/absence and click rate data were examined with reference to photoperiod. For each day with clicks at each site, photoperiods were categorized into day and night based on data obtained from the U.S. Naval Observatory website (http://aa.usno.navy.mil). Day and night were defined as the periods between nautical twilight, when the sun altitude was at -12^{o}. Each click bout was assigned a photoperiod. Click bouts that spanned multiple photoperiods were segmented and each segment was assigned the appropriate photoperiod.

To examine diel variation in the presence or absence of click bouts, ones and zeros were assigned to hour interval bins indicating the presence or absence, respectively, of click bouts. As photoperiod durations vary seasonally, the total number of hour bins per day that a click type was present within a photoperiod was normalized by the total number of hour bins per day within that photoperiod. Bins that crossed boundaries between photoperiods were assigned to the photoperiod that contained the greater portion of the hour. An analysis of variance was used to statistically test for differences in percent hours with clicks between photoperiods (Zar, 1999).

To examine diel variation in the click rates of Pacific white-sided dolphins, numbers of clicks per photoperiod needed to be normalized by the total recording time during that photoperiod. To account for duty-cycled data and occasional scheduling errors, total recording time was calculated from actual recording start times and durations. Click rates were calculated in clicks/min for each photoperiod and day as the total number of clicks divided by total recording time. Variability between days was accounted for by calculating a mean-adjusted calling rate in which the daily click rate was subtracted from the click rate for each photoperiod for each day. Diel variation in click rates was statistically tested by comparing mean-adjusted click rates among photoperiods using analysis of variance (Zar, 1999).

Data from the two northern nearshore sites (Point Conception and Santa Barbara Channel) and from the two southern nearshore sites (Santa Catalina Island and San Clemente Island) were included in the seasonal portion of the analysis while data from the two southern offshore sites were not included as they did not sample all seasons. Seasonal coverage across years and sites was variable (Table 4.1) and site-specific and interannual variations in occurrence are unknown. Therefore year and site were included in statistical tests for Pacific white-sided dolphin seasonality. The total number of days with detections per weekly period was used as a test metric. Seasons were defined by quarters of the year. The hypotheses of equal means across seasons, years and sites were tested using the GLM ANOVA function in SPSS 11.5 (www.spss.com) with three-way full factorial design and type IV sum of squares to account for the unbalanced design. An ANOVA can only test if all means are equal or not; Tamhane's T2 post-hoc test was used to determine which seasons, sites or years were different (Zar, 1999; Garson, 2008).

RESULTS

About 2000 instrument days of data were recorded and analyzed from the six instruments in the SCB, with the majority of effort at the Santa Catalina Island, Santa Barbara Channel, Point Conception and San Clemente Island sites (Table 4.2). These four sites recorded during each season at least once during the 2.5 year period, while the remaining two sites, Tanner & Cortez Banks and San Clemente Basin, did not have complete seasonal coverage (Figure 4.3).

Pacific white-sided dolphin type A clicks were heard at all six locations on a total of 317 instrument days (16% of all recording days) (Table 4.2). They were heard most often at San Clemente Island and Point Conception where click bouts were recorded on 45% and 25% of the recording days, respectively. While type A clicks were heard on 21% of the recording days at San Nicholas Basin, this may be a biased estimate as this instrument only recorded during 1/3 of the year and seasonal variations may have been missed. At the remaining sites, type A clicks were detected between 2-8% of recording days. Pacific white-sided dolphin type B clicks were only heard at the two southern inshore sites for a total of 130 instrument days (7% of all recording days) (Table 4.2). At Santa Catalina and San Clemente Islands, they were heard between 14-21% of the recording days. They were never heard at the northern sites in over 800 instrument days of recordings, or at the southern offshore sites over 300 instrument days of recordings. The two Pacific white-sided dolphin click types clearly exhibit distinct geographical occurrences in which type A is heard throughout the region while type B is only heard in the south (Table 4.2).

Across the six sites, Pacific white-sided dolphin type A click bouts occur most frequently at night, with an increase around sunset, followed by a slight decrease during the middle of the night. Click bout occurrence increases again before dawn and then occurs at a lower level through out the day (Figure 4.5). When these data are segregated by site, the Point Conception and San Nicholas Basin sites appear to dominate the overall signal (Figure 4.6). Hourly type A click bout occurrence at Tanner & Cortez Banks exhibits the inverse pattern to San Nicholas Basin, while the hourly pattern at San Clemente Island is nearly uniform. A comparison of percent of hours with clicks present per photoperiod (day and night) reveals that type A is detected during significantly more hours of the night (mean 16%) than of the day (mean 10%) ($F = 24.4$, $p < 0.001$, $N = 316$) (Figure 4.7a). The mean adjusted click rate of type A clicks is also significantly higher during the night (mean 3.27) than during the day (mean -2.68) ($F = 35.7$, $p < 0.001$, $N = 272$) (Figure 4.7b).

Pacific white-sided type B clicks exhibit a more consistent hourly pattern across the two southern sites such that click bouts are less likely to occur during the night than during the day (Figures 4.5 & 4.6). This pattern is nearly the inverse of that seen for type A clicks. On the other hand, a comparison of percent of hours with type B clicks present per photoperiod reveals they are detected during significantly more hours of the day (mean 24%) than of the night (mean 15%) (F = 10.8, p = 0.001, N = 130) (Figure 4.7a). Similarly, the mean adjusted click rate of type B clicks is significantly higher during the day (mean 1.95) than during the night (mean -1.80) (F = 5.6, p < 0.018, N = 111) (Figure7b).

Pacific white-sided dolphin type A clicks were heard throughout the year across the six HARP sites although they appear to exhibit temporal clumping (Figure 4.8). The number of hours per day that type A click bouts were present is highly variable throughout the year, ranging from zero to fifteen. Pacific white-sided dolphin type B clicks were heard sporadically at the two southern inshore sites with what appears to be a fall-winter seasonal cycle (Figure 4.9). The number of hours per day that type B click bouts were present ranges from zero to twenty with days of high activity tightly clumped in time.

Occurrence of Pacific white-sided dolphin type A click bouts exhibited seasonal, annual and site-specific variability (Figure 4.10). Results of ANOVA analyses indicate that site, year and the interaction between season and site were significant sources of variability in mean occurrence (Table 4.3). Tamhane's T2 post-hoc analyses demonstrate that click bouts occurred significantly more often at San Clemente Island than all other sites and significantly more often at Point Conception than at the remaining two sites. Additionally click bouts were detected significantly more often in 2007 than 2005. A plot of the interaction effects of season and site indicate that clicks were heard most during the winter at Santa Catalina Island and in the Santa Barbara Channel, were most frequently heard during fall and winter at San Clemente Island and were most frequent during spring at Point Conception (Figure 4.11).

Similarly, occurrence of Pacific white-sided dolphin type B click bouts also exhibited seasonal, annual and site-specific variability (Figure 4.12). Results of ANOVA analyses indicate that season, site, site*year, site*season, year*season, and year*site*season were all significant sources of variability in mean occurrence (Table 4.4). Tamhane's T2 post-hoc analyses demonstrate that click bouts occurred significantly more often at San Clemente Island than all other sites and significantly more often at Santa Catalina Island than at the remaining two sites, as expected since there were zero type B click bouts recorded at the northern sites. Additionally click bouts were detected significantly more often during fall and winter than during spring and summer. A plot of the interaction between season and year indicated that the interaction was most affected by the low number of sightings occurring in 2005, while the remaining two years had similar seasonal effects (Figure 4.13). Similarly, a plot of the interaction between season and sites indicated that the lack of detections at Point Conception and the Santa Barbara Channel were the main cause of the seasonal site interaction while Santa Catalina and San Clemente islands had similar seasonal effects (Figure 4.14). Finally, the interaction between all terms was again affected by the low numbers of detections during 2005 in the south and the complete lack of detections at the two northern sites. A fall and winter peak in seasonal occurrence was evident at both southern sites across 2006 and 2007.

DISCUSSION

The use of long-term, high-temporal resolution, passive acoustic recordings has provided detailed hourly and seasonal information on Pacific white-sided dolphin echolocation patterns that have not been previously described. Distinct geographical and temporal patterns exist for the two click types produced by Pacific white-sided dolphins: 1) Type A clicks are heard throughout the region while type B clicks are only heard at the two southern inshore sites; 2) type A clicks exhibit peak in occurrence in spring off Point Conception, peaks during winter at Santa Barbara Channel and Santa Catalina Island and a fall-winter peak occurrence at San Clemente Island while type B clicks exhibit a fall-winter seasonal occurrence at both southern inshore sites; and 3) type A clicks exhibit generally increased activity at night, although some site specific variability exists, while type B clicks exhibit increased activity during the day.

Evidence of differential directional movement into the SCB by animals producing the two different click types would offer support to the hypothesis put forth by Soldevilla et al (2008) that these two click types represent the two populations of Pacific white-sided dolphins which overlap in the region. A comparison of the seasonal patterns of type A clicks support hypotheses of northward movements in spring and summer and southward movements during fall and winter (Green et al., 1992; Forney and Barlow, 1998) This would suggest that type A clicks represent the northern CA/OR/WA population of Pacific white-sided dolphins described by Walker et al (1986) and Lux et al (1997). The type B clicks were only heard in the southern inshore region which lends credence to the hypothesis that type B clicks represent the Baja California population. While no indication of movement from the south is available, the results indicate it is unlikely that they are moving in from the north or from offshore, as they were not heard in either the southern offshore or northern regions. It remains possible that they follow a narrow corridor from offshore in the unsampled area between these two regions.

Several other hypotheses for what interschool differences these two distinct click types could represent include: group size, group composition (including sex or age strata), behavior or prey type (Soldevilla et al., 2008). Given the spectral consistency and distinctiveness of the two click types as opposed to continuous variability, the occurrence of only two click types and the geographical differences in usage, we expect that group size, group composition stratified by sex or age, and behavioral differences would not result in both two distinct acoustic patterns and the observed spatial separation in usage. Further consideration of differential usage of click types while foraging on different prey types leads to conjectures of differences in prey such as two distinct size classes, (e.g. large and small prey), compositional differences in the prey, (e.g. reflective differences between squid and fish, or between fish with swim bladders and those without), or behavioral differences (e.g. schooling or non-schooling prey, school density, or diel behavior). Pacific white-sided dolphins forage opportunistically on epipelagic and mesopelagic schooling fish and cephalopods (Stroud et al., 1981) and their prey preferences typically reflect the most abundant prey in a region. Studies off southern California indicate that preferred prey include northern anchovy (*Engraulis mordax*), young Pacific hake (*Merluccius productus*), market squid (*Loligo opalescens*), jack mackerel (*Trachurus symmetricus*) and Pacific mackerel (*Scomber japonicus*) (Brown and Norris, 1956; Fitch and Brownell, 1968; Walker et al., 1986). Sardines (*Sardinops sadax*) were found in smaller quantities (Scheffer, 1950; Walker et al., 1986) but may be a more important prey item in recent years of greater sardine abundance. The clearest relationship between spatial distribution patterns of click types and these prey types is between click type B and Pacific mackerel. Pacific mackerel are found most frequently in inshore waters near the coast and islands from southern Baja California to and including the Southern California region (Mais, 1974). On the other hand, juvenile hake, anchovy and market squid distributions are distributed generally evenly throughout the six areas sampled in the SCB, (Okutani and McGowan, 1969; Mais, 1974; Agostini et al., 2006). This could suggest that click type B is used when dolphins are foraging on Pacific mackerel, while click type A is used when foraging on the remaining prey species. However, no obvious differences exist between Pacific mackerel and the remaining prey species that reveal a reason for a difference in click type. While Pacific white-sided dolphins typically feed on the smaller juvenile and young adult Pacific hake, jack mackerel and Pacific mackerel and similarly size adult anchovy, prey sizes can range from 10-60 cm and they vary across species (Fitch and Brownell, 1968; Heise, 1997). All four fish species school and contain similarly reflective swim bladders (Holliday, 1972; Mais, 1974; Diachok, 2001). While species-specific resonance patterns do occur between the fish species (Holliday, 1972), differences between fish and squid are likely to be greater due to acoustic differences between fish air-bladders and squid pens such as that described for acoustic reflectivity indicate a much lower (~15 dB target strength than for fish (Penrose and Kaye, 1979; Jefferts et al., 1987). Therefore, it may be more likely that a different click type would be used for squid rather than Pacific mackerel.

A more succinct explanation of the relationship between Pacific mackerel and click type B spatial distributions might be that the two populations of Pacific white-sided dolphins are foraging on different prey items such that the type-B-producing Baja California population preferentially forages on Pacific mackerel in the SCB. When two similar populations inhabit the same region, niche partitioning is one mechanism for reducing competition (MacLeod et al., 2003; Bearzi, 2005). Several other lines of evidence that support the hypothesis of niche separation through differential prey foraging include the infrequent occurrence of mixed schools producing the two click types (<3% of all click bouts for each click type in long-term HARP data (Soldevilla et al., 2008)) and the differences in diel click activity patterns such that type B clicks are more commonly heard during the day, and the type A clicks are more commonly heard at night. Higher echolocation activity is associated with foraging (Norris et al., 1994; Barrett-Lennard et al., 1996; Van Parijs and Corkeron, 2001; Nowacek, 2005). Diel activity patterns could indicate that type B foraging is occurring on daytime schooling fish such as Pacific mackerel, while type A foraging is mainly on diel migrating prey such as squid and myctophids, although daytime foraging on schooling fish is also evident at some sites. Prey analyses have not distinguished these two populations so actual differences in feeding remain unknown. However, similar niche separation through feeding on different prey types has been described for the temporally and spatially overlapping resident and transient populations of killer whales (*Orcinus orca*) off British Columbian waters (Barrett-Lennard et al., 1996).

Genetic analyses indicate limited interaction between the two Pacific white-sided populations and Lux et al (1997) suggest that the mechanisms for reproductive isolation could include 1) allopatry resulting from either a fixed geographic boundary or a shifting seasonal boundary, 2) partial sympatry in which some behavioral or morphological reproductive barrier prevents gene flow between them, or 3) they experience limited gene flow, possibly caused by a segregating mechanism that no longer exists. The results presented here which indicate the occurrence of both click types overlapping in space and time indicate that the first hypothesis of allopatry cannot be possible. Therefore, future analyses should focus on distinguishing between the remaining two hypotheses.

It is interesting to note that hourly variability in Pacific white-sided dolphin type A click bout occurrence off Point Conception is evident such that there is a decrease in hourly detections in the middle of the night compared to the early and later parts of the night. A similar pattern has been shown for Risso's dolphins (Soldevilla, 2008, Chapter 3). As suggested for Risso's dolphins, Pacific white-sided dolphin echolocation activity may indicate increased foraging reflecting the diel dive depth variations of squid, such as that seen in jumbo squid (*Dosidicus gigas)* (Gilly, 2006). The tagged squid were shallow during the early part of the night, often returned to depth during the middle of the night, and subsequently returned to shallow waters before dawn. While detailed dive patterns of other cephalopod prey have not been described, many squid species found in the SCB are known to follow diel vertical migrations and may follow a similar pattern (Roper and Young, 1975). Spinner and dusky dolphins have both been shown to follow the vertical movements of their diel-vertically migrating prey while near surface waters (Benoit-Bird and Au, 2003; Benoit-Bird et al., 2004). Our results for Pacific white-sided dolphins at Point Conception suggest that a similar situation may be occurring in which the dolphins are actively feeding and echolocating when squid are within a preferred shallow depth range.

When considering diel patterns of echolocation in highly mobile species such as dolphins, it is unclear whether a lack of acoustic detections represents absence of the dolphins from the study site or presence of non-vocalizing animals. Dolphins are capable of moving into and out of a study site within a day, as shown by visual surveys of spinner dolphins off Hawaii that exhibit diel movements between inshore resting areas during the day to offshore feeding zones at night (Norris et al., 1994; Benoit-Bird and Au, 2003). The diel variation in occurrence of Pacific white-sided dolphin clicks could therefore represent movements out of the area during periods of low activity and movements into the area during period of high activity. Conversely it could represent changes in echolocation activity as a function of varying behavior state. Increased echolocation has been associated with foraging and traveling (Norris et al., 1994; Barrett-Lennard et al., 1996; Van Parijs and Corkeron, 2001; Nowacek, 2005). The variability of type A click activity between sites may indicate that the dolphins change foraging location depending on prey availability at each site.

Similarly, seasonal patterns of occurrence may represent movements into and out of the area or seasonal variation in calling. Echolocation clicks of dolphins are used for foraging and navigation. Unlike larger baleen whales that have large blubber stores to sustain them when migrating between feeding and breeding grounds, odontocetes have thin blubber layers and need to feed frequently (Smith and Gaskin, 1974; Lockyer, 1981) which suggests that dolphins are unlikely to exhibit long periods of fasting. Therefore, one would expect that seasonal variations in echolocation occurrence represent movements into and out of the area.

Additional factors which may affect the probability of detecting calling animals include distance from hydrophone, propagation conditions, masking and misclassifications of species. Although the HARPs at different sites are located at different depths with different oceanographic conditions, at the frequencies used for echolocation, attenuation severely limits detection range, and therefore the potential for significant variation owing to seasonal variations in reduced. Detection distances may be smaller for sites at greater depths; echolocation click detection ranges are approximately 4 km (E. Henderson, personal communication) such that the maximum of 1 km difference in depth for this study could result in as much as 10% loss in detection range at the deepest sites. Ships, sonars, other animals, rain, wind and waves may produce sounds that mask the echolocation click of our chosen species so it is important to consider seasonality in these sources. Preliminary analysis indicate that shipping noise is consistent throughout the year at all sites except Santa Catalina Island where there is an increase in occurrence during the summer (May-Sept), while wind and rain noise within the frequency band of clicks occurs minimally throughout the year. A more thorough investigation of seasonal variation related to these noise sources in is the topic of another study.

Several biases are present in our method of counting clicks for the diel click rate portion of this study that are worth consideration. If multiple species were calling during a click bout, and it was apparent in the LTSAs, these data were not included in the analysis, biasing the counts to be low. However, multiple species may have been present but not noticeable. This would cause the click counts to be biased high for the study species. We expect this bias will be minimal as we were conservative in our species classification. Additional considerations that would bias our results to be lower than actually occurred include: 1) many low quality clicks were present that did not exceed the thresholds; 2) during periods of intensive clicking, the surrounding data used for spectral-mean-subtraction would be relatively high resulting in good quality clicks being missed by the detector; 3) during periods with rapid click trains or click trains from multiple individuals in which the apparent interclick interval was greater than 15 ms, only 1 click was chosen per 15 ms. Overall, we expect these biases to consistent across all recordings so that comparisons between times and locations should not be affected.

CONCLUSIONS

The movement of Pacific white-sided dolphin type A clicks in the SCB from north in spring to the south in fall and winter and the occurrence of type B clicks at only the southern inshore sites support the hypothesis that these two click types represent the CA/OR/WA and the Baja California populations of Pacific white-sided dolphins that are known to overlap ranges within the SCB. Additional evidence of daytime activity versus nighttime activity of the animals producing the two click types indicates that competition-reducing niche separation may occur through diel temporal separation possibly as a result of foraging on different prey. In particular this could indicate a preference for Pacific mackerel by the Baja California population as indicated by similar spatial distribution to the type B click bouts. Future studies should aim to confirm the acoustic separation of populations by both sampling the northern and southern ranges of these populations where mixing does not occur and through combined genetic and acoustic field sampling. Additionally, future stomach content analyses should indicate time and location of collection of Pacific white-sided dolphins and should preferably identify the population genetically to allow the niche-separation hypothesis to be tested.

Acoustic coverage at offshore sites in this study did not include a long enough duration to examine hypothesis about inshore-offshore seasonal movements of the populations, nor was a northern extent of migrations available to determine if animals occupying the SCB in winter/spring are moving to central California, Oregon/Washington or offshore during the summer and early fall. Extending the spatial coverage of long-term acoustic monitoring to include northern and offshore regions would be useful for answering this question. Similarly the extension of monitoring to the south could advance knowledge on the seasonal movements of the Baja California population. Finally, interannual and interdecadal variability in abundance and movement patterns have been described in previous studies of Pacific white-sided dolphins, however the short durations of the presented time-series preclude the in-depth examination of interannual and interdecadal changes. These time series are ongoing and have the potential to answer such questions in the future.

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Chapter 4, in full, is currently being prepared for submission for publication of the

material. Soldevilla, Melissa; Wiggins, Sean; Hildebrand, John. The dissertation author was the primary investigator and author of this material.

FIGURES

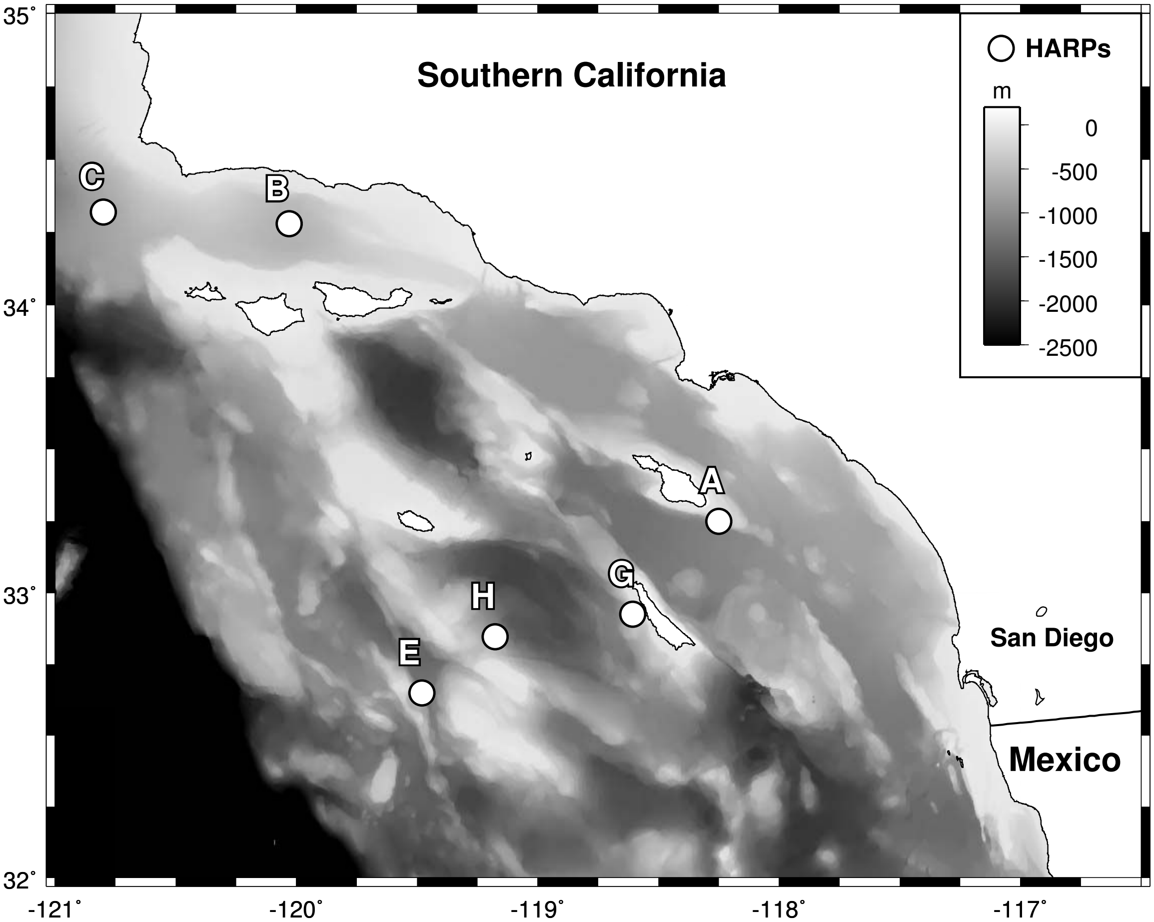

Figure 4.1. Map of study area including locations of HARP deployments. Depths are indicated by colorbar. Sites: A = Santa Catalina Island, B = Santa Barbara Channel, C = Point Conception, E = Tanner/Cortez Banks, G = San Clemente Island, and H = San Nicholas Basin.

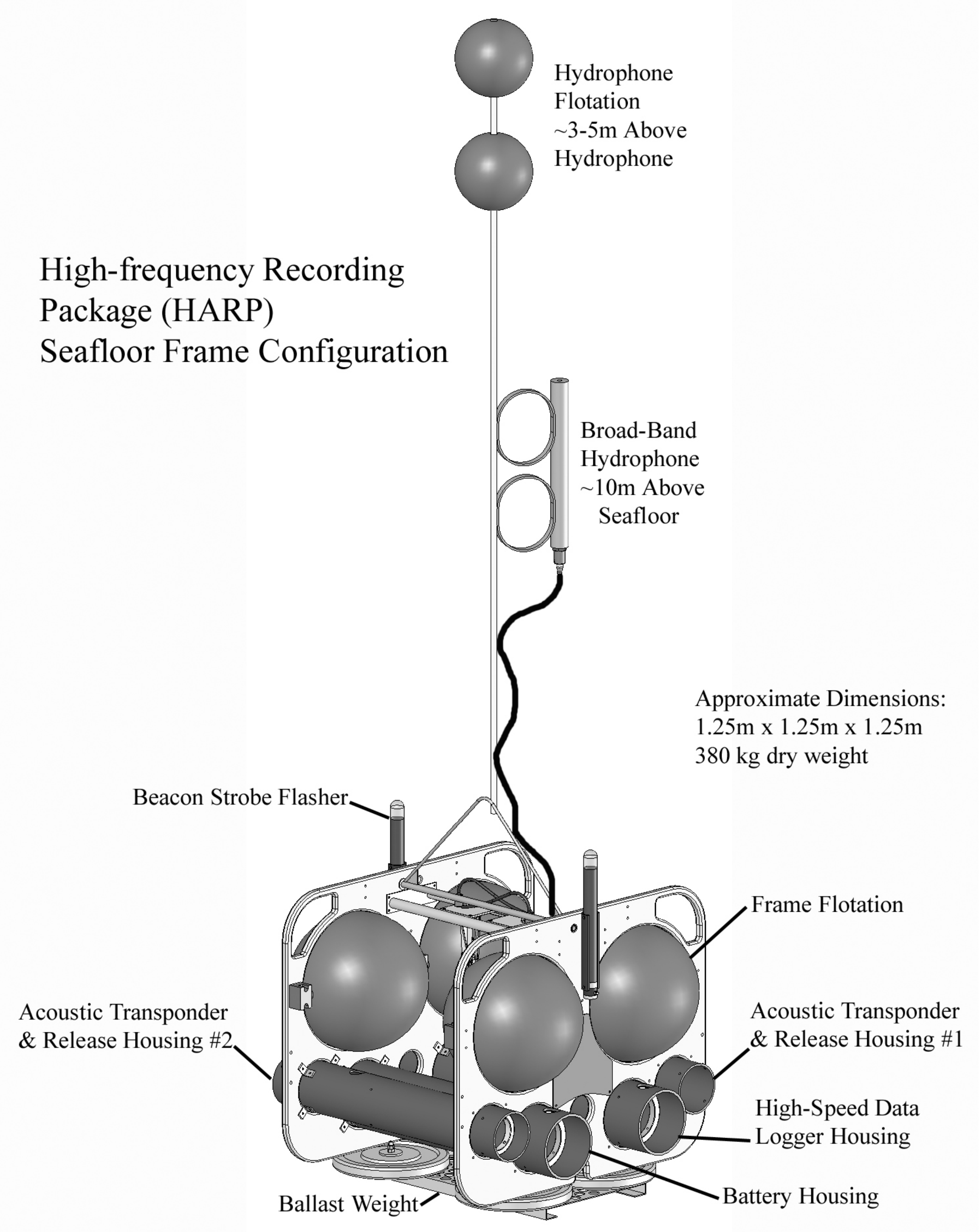

Figure 4.2. HARP schematic representation of sea-floor recording package.

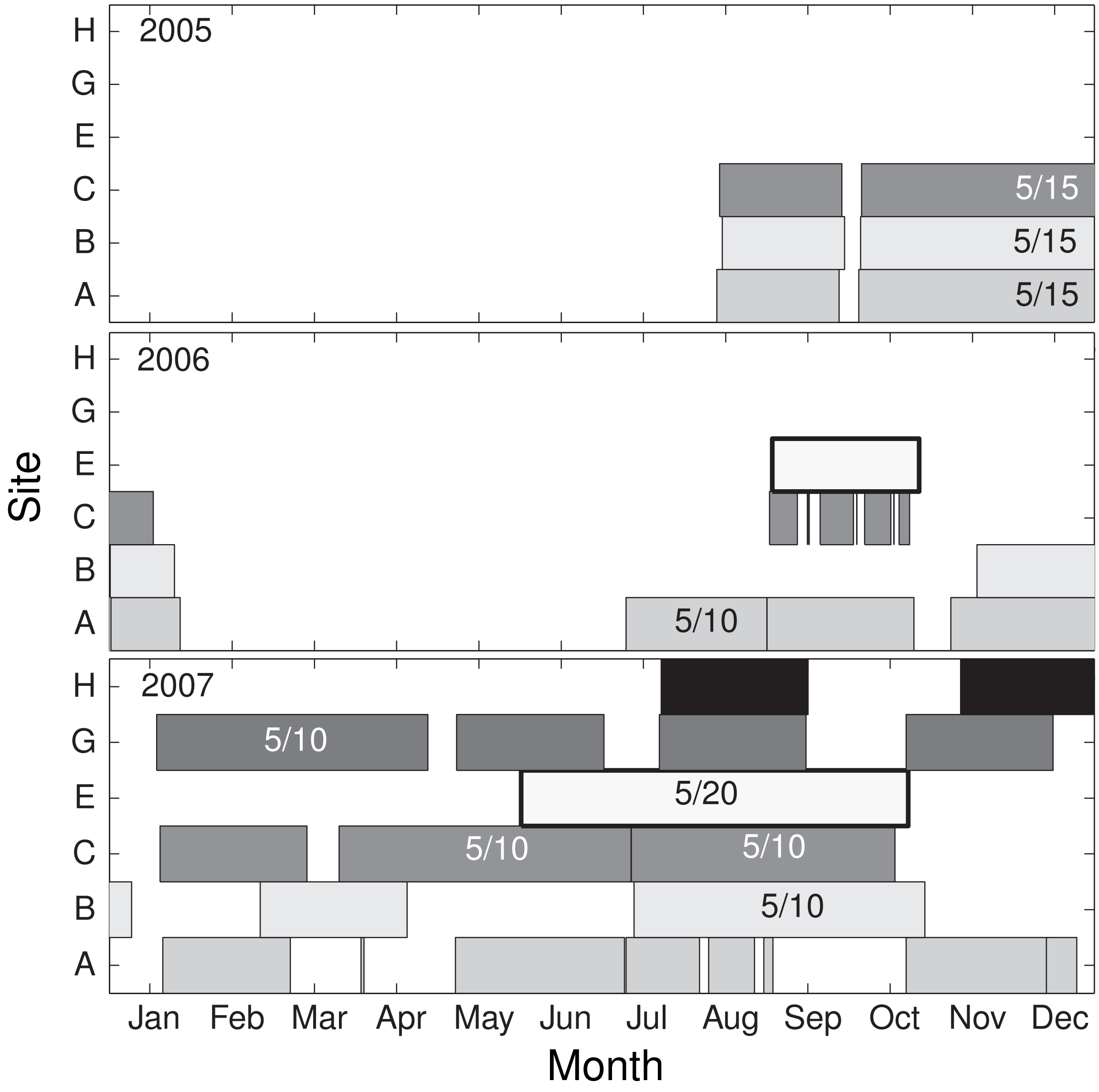

Figure 4.3. HARP data and duty cycle information at each of six sites in the SCB. A = Santa Catalina Island, B = Santa Barbara Channel, C = Point Conception, E = Tanner/Cortez Banks, G = San Clemente Island, and H = San Nicholas Basin. Shading represents dates when data is available at each site. Numbers within shaded regions represent the specified duty cycle as minutes on / minutes of total cycle. Shaded regions without numbers represent continuous data. Data spanning year boundaries follow the previous duty cycle.

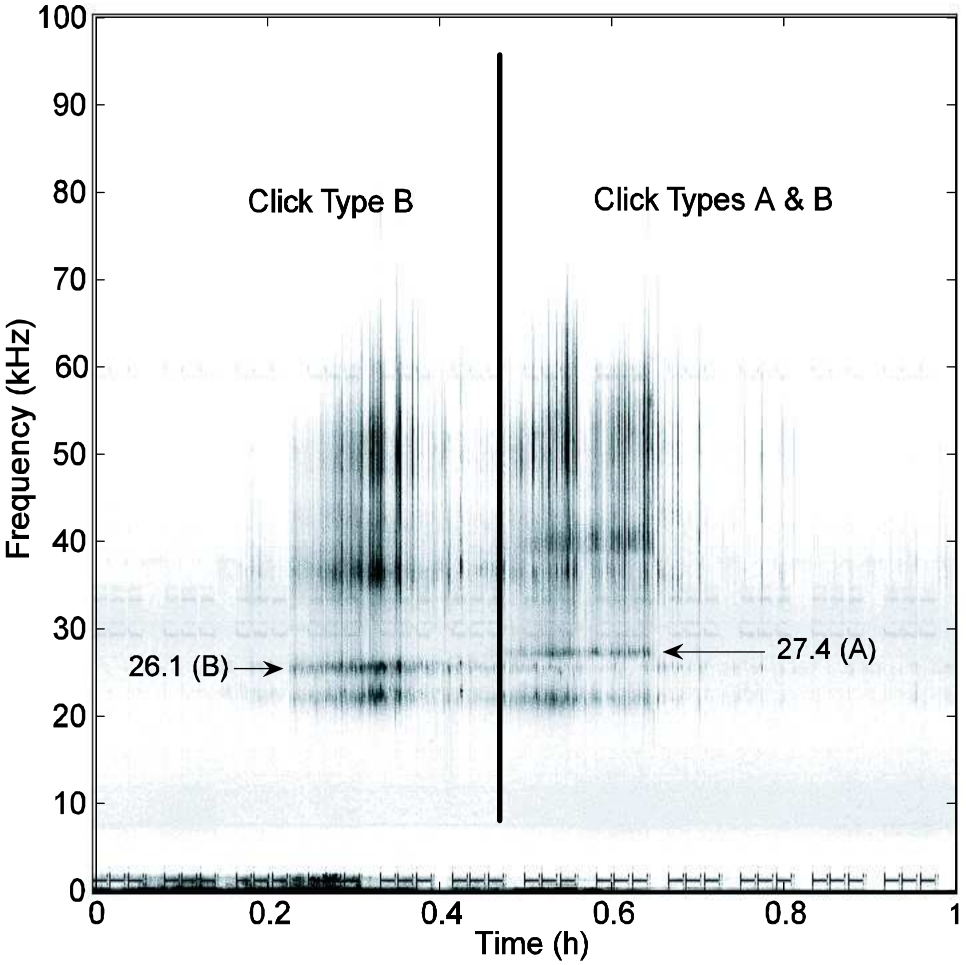

Figure 4.4. Example long-term spectral average illustrating echolocation click bouts containing the unique spectral peak and notch structure of the two Pacific white-sided dolphin click types described by Soldevilla et al 2008. Spectral peaks occur in the clicks around 22, 27.5 and 39 kHz in type A clicks and around 22, 26 and 37 kHz in type B clicks.

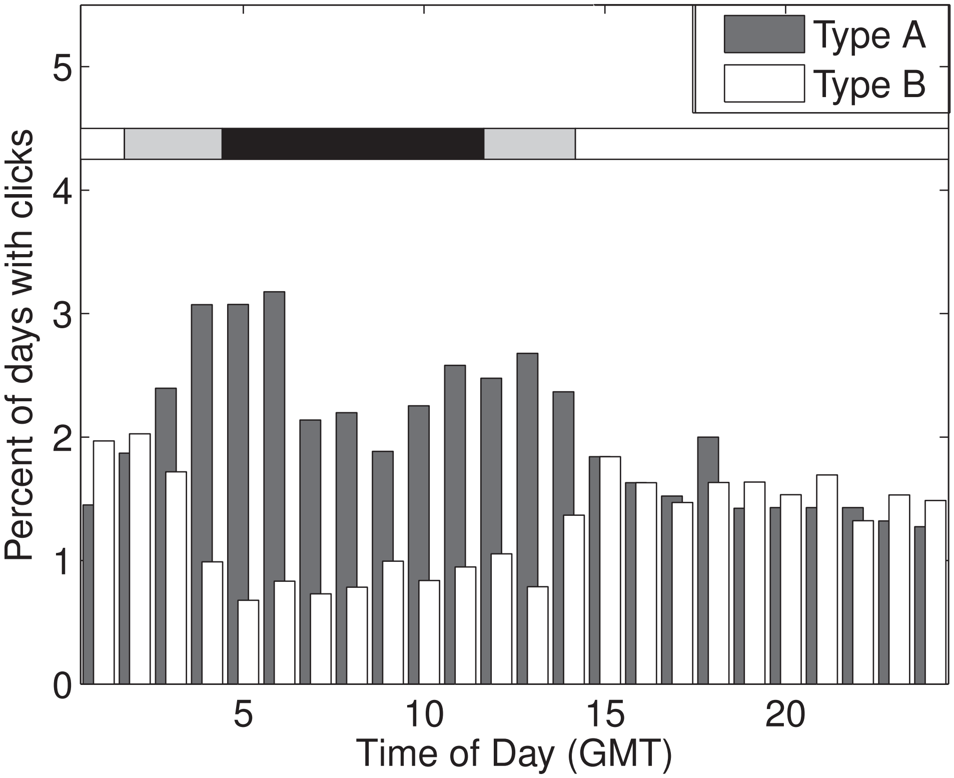

Figure 4.5. Diel patterns of Pacific white-sided dolphin echolocation click bouts combined across the six HARP locations. Vertical bars represent the percent of days that have clicks of each type (Type A: dark gray;Type B: white) present in each hour time bin. Horizontal bar indicates periods of light (white) or darkness (black). Light gray areas represent periods that may be light or dark depending on time of year.

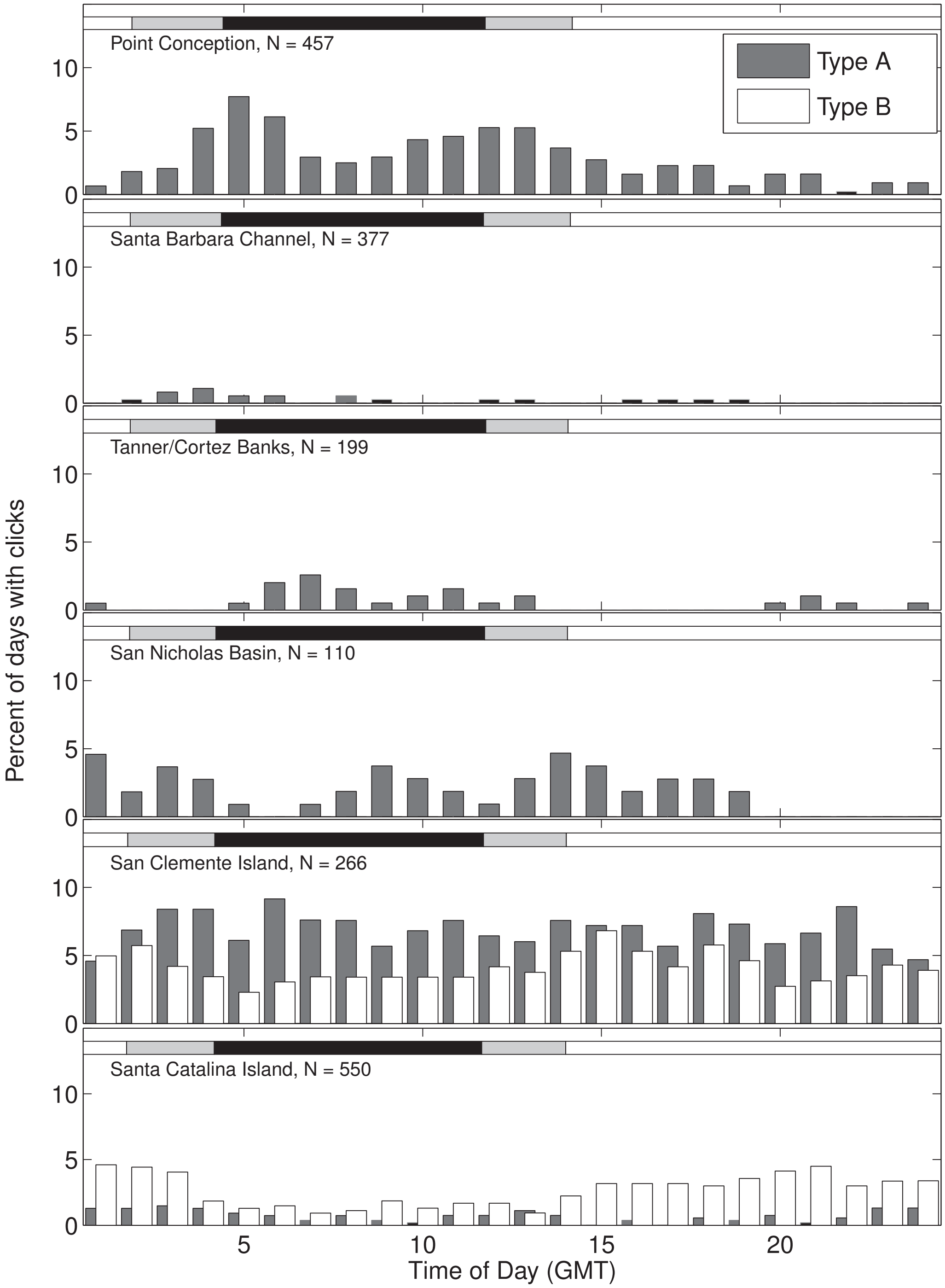

Figure 4.6. Diel patterns of Pacific white-sided dolphin echolocation click bouts at each of the six HARP locations. Vertical bars represent the percent of days that have clicks of each type (Type A: dark gray;Type B: white) present in each hour time bin. N represents the number of recording days at each site. Horizontal bar indicates periods of light (white) or darkness (black). Light gray areas represent periods that may be light or dark depending on time of year.

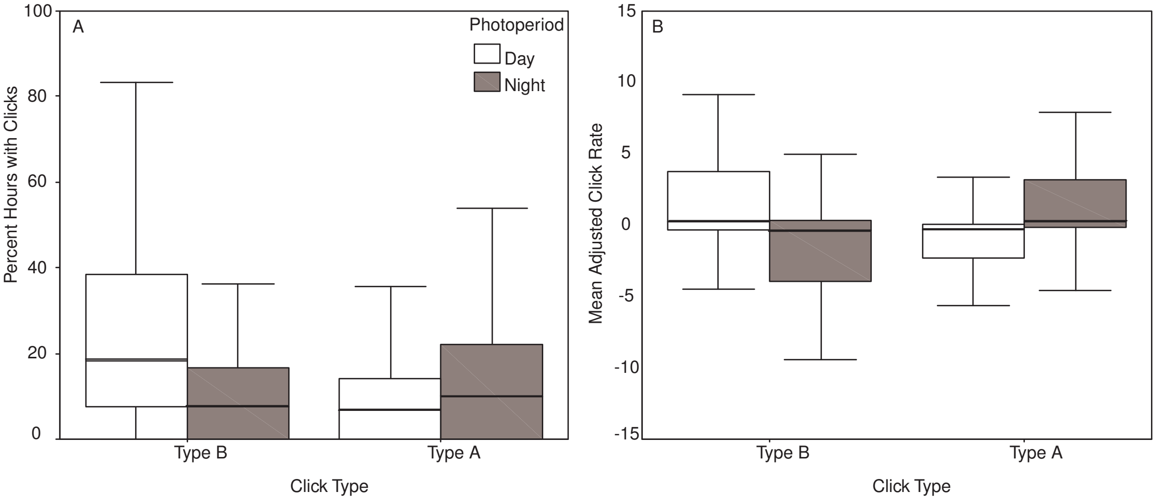

Figure 4.7. Variation in Pacific white-sided dolphin types A and B click bout occurrence (a) and daily click rate anomaly (b) between photoperiods. Central lines represent median value, boxes contain 25th to 75th percentiles and whiskers contain 5th to 95th percentiles of data. Click bout occurrence and daily click rate anomaly are both significantly higher during the night than during the day.

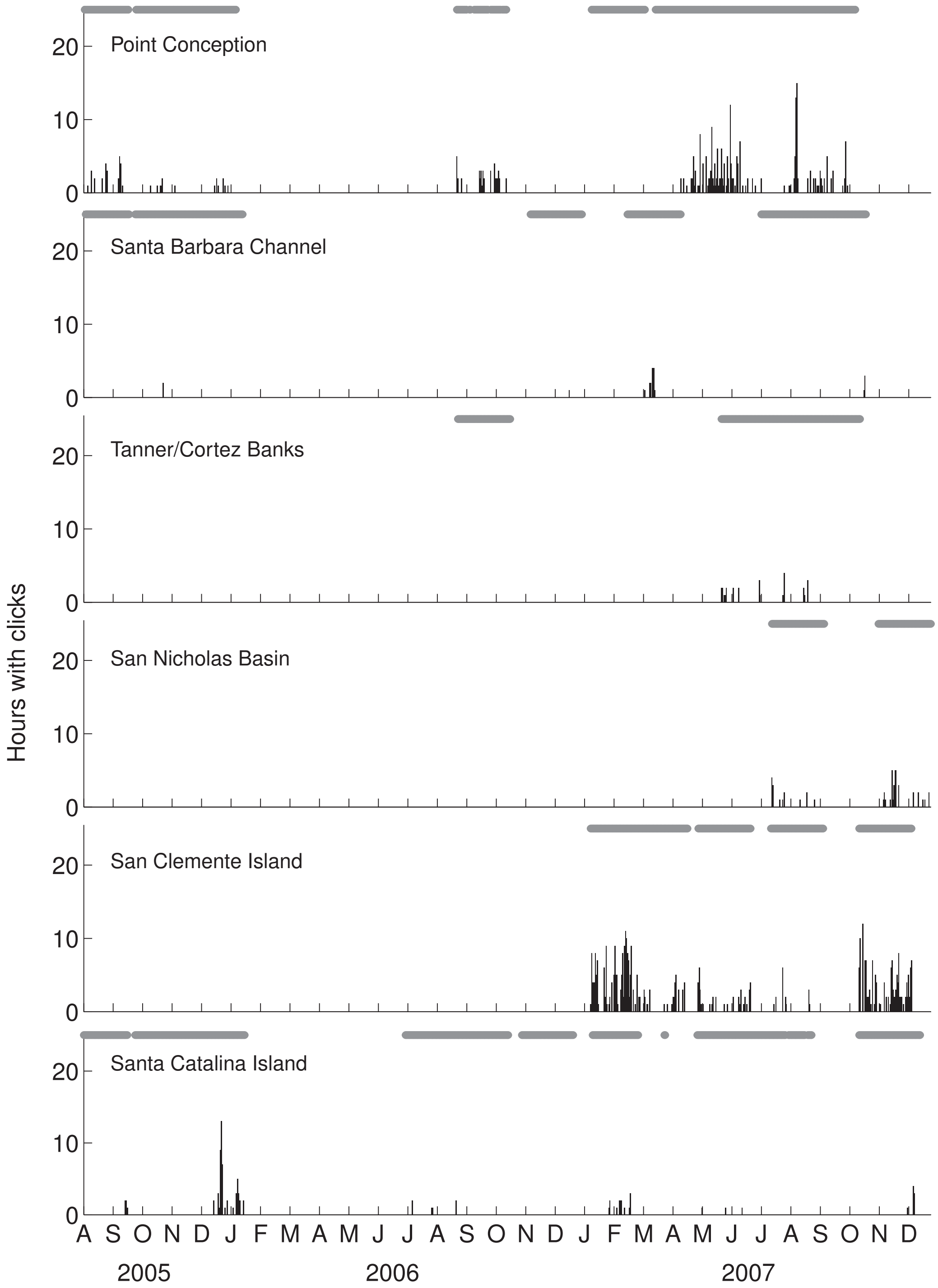

Figure 4.8. Time series representing presence of Pacific white-sided dolphin type A clicks at each of the six HARP sites. Plots represent the number of hour bins in which dolphin clicks were present each day. Gray bars at the top indicates times that data is available.

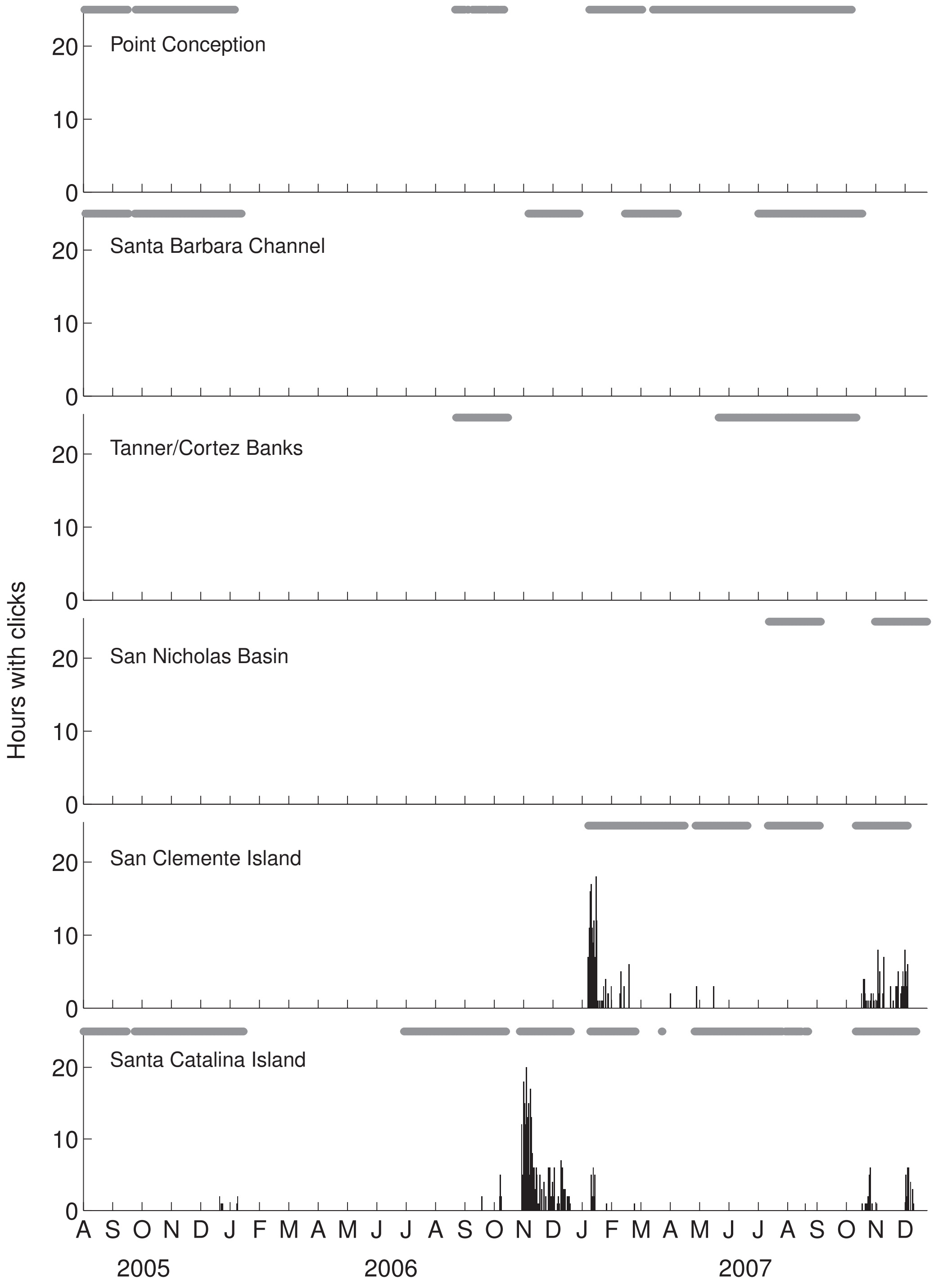

Figure 4.9. Time series representing presence of Pacific white-sided dolphin type B clicks at each of the six HARP sites. Type B clicks were only detected at the two southern inshore sites. Plots represent the number of hour bins in which dolphin clicks were present each day. Gray bars at the top indicates times that data are available.

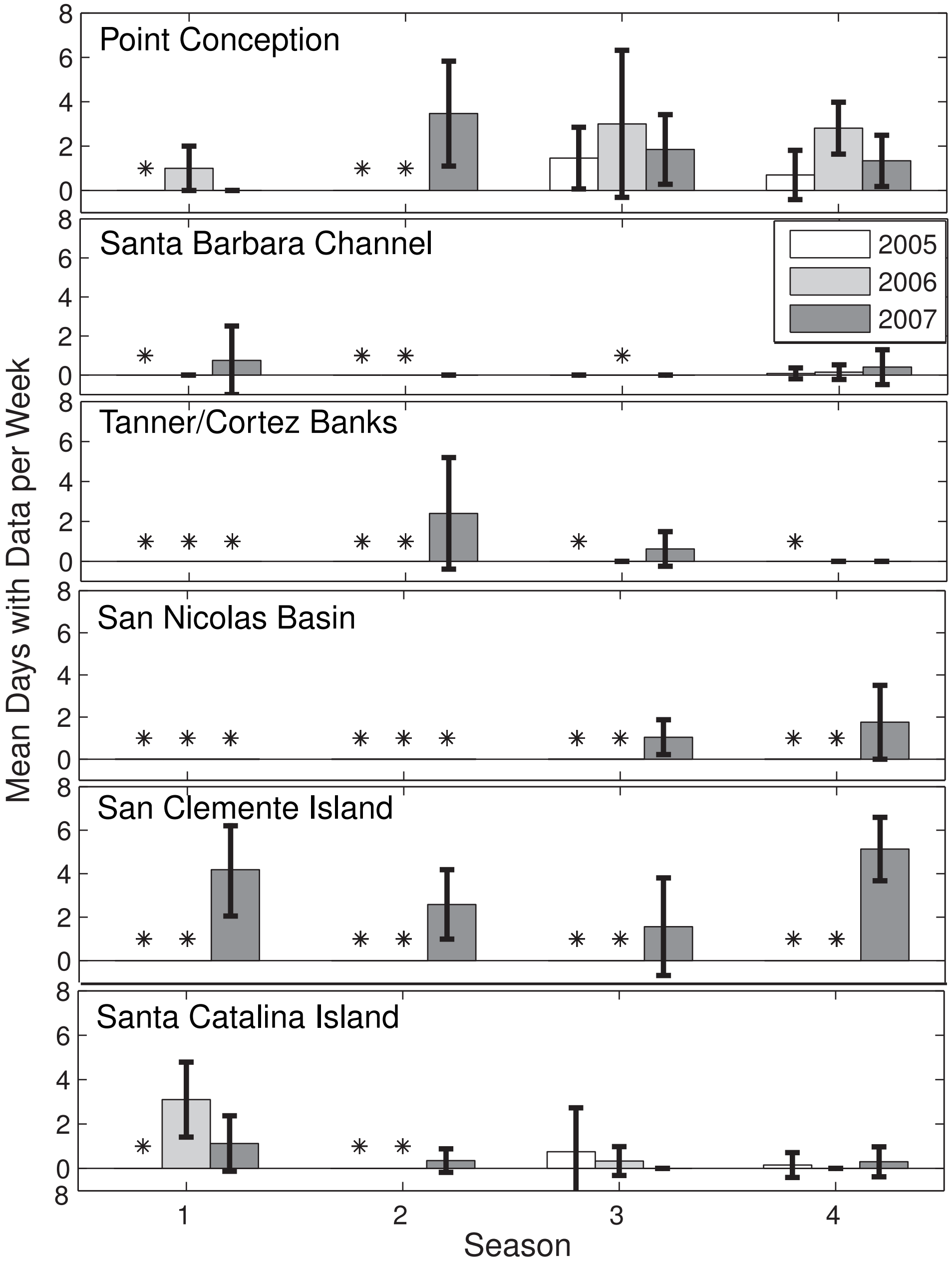

Figure 4.10. Seasonal and annual variation in mean days per week with Pacific white-sided type A click bouts across the six HARP sites. Bar are color coded by year. Error bars indicate standard deviation. Stars indicate no data available. Each plot represents a separate site:

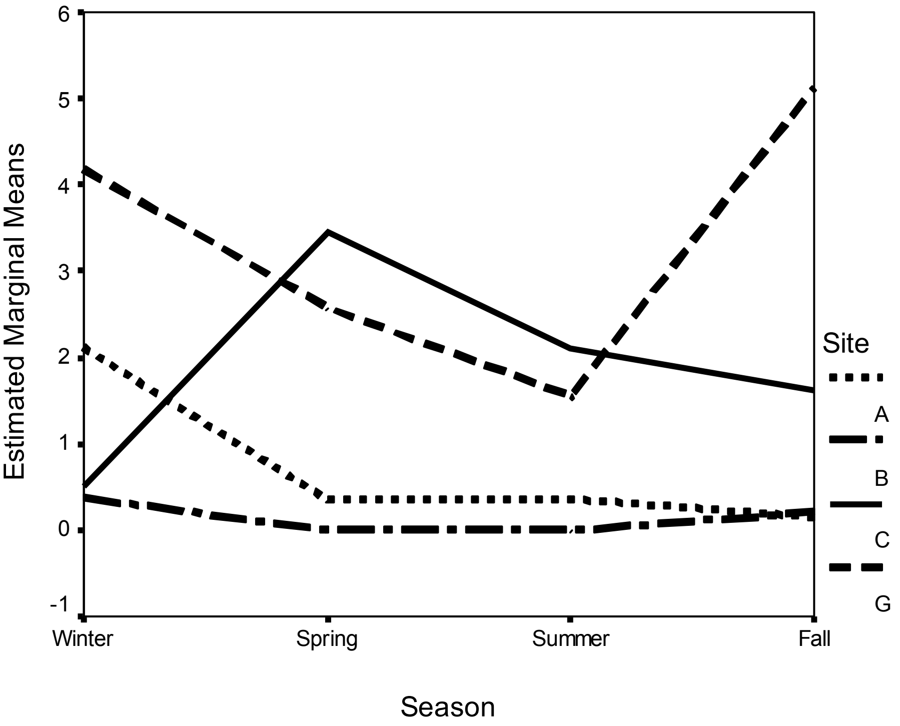

Figure 4.11. Seasonal by site interaction effects plot for Pacific white-sided dolphin type A click bouts. Sites: A = Santa Catalina Island, B = Santa Barbara Channel, C = Point Conception, and G = San Clemente Island

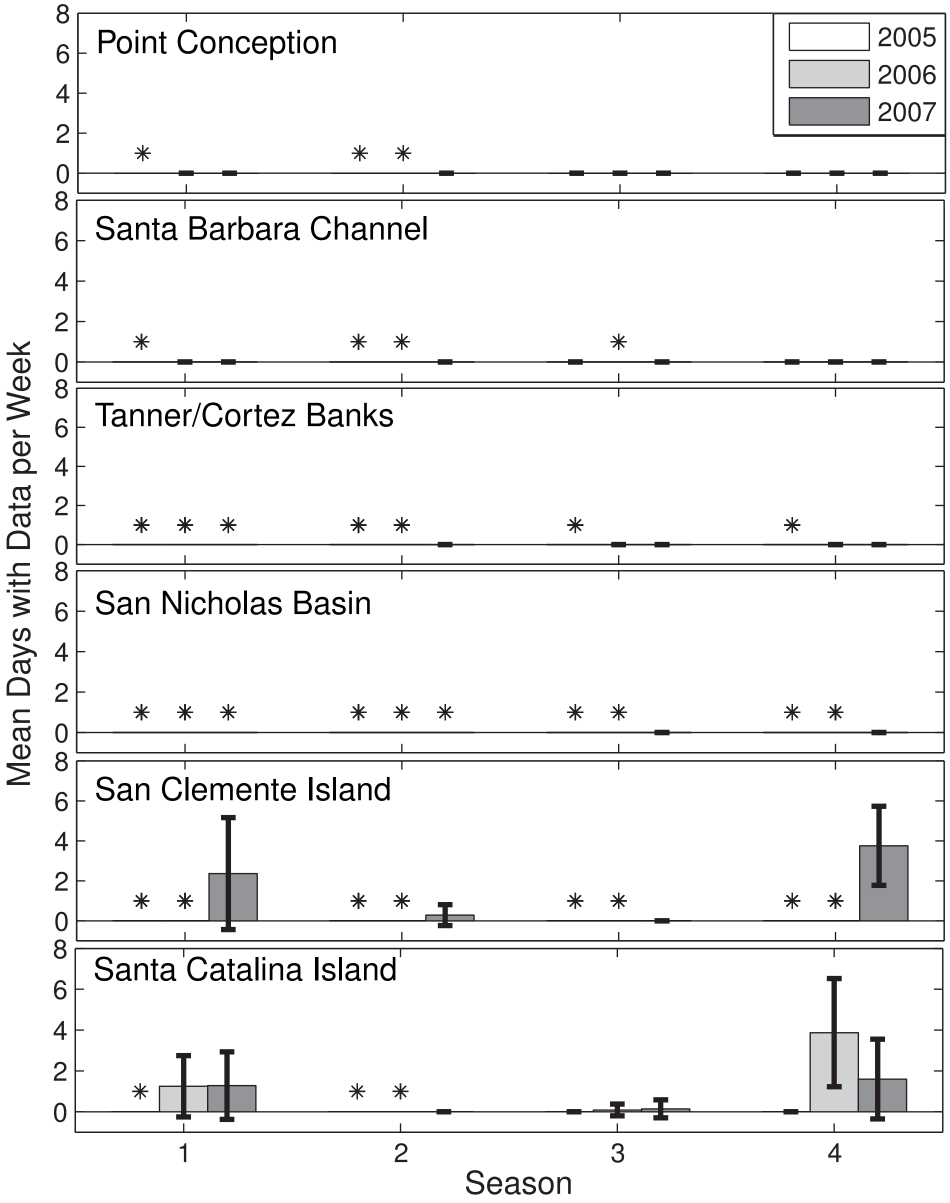

Figure 4.12. Seasonal and annual variation in mean days per week with Pacific white-sided type B click bouts across the six HARP sites. Bar are color coded by year. Error bars indicate standard deviation. Stars indicate no data available. Each plot represents a separate site:

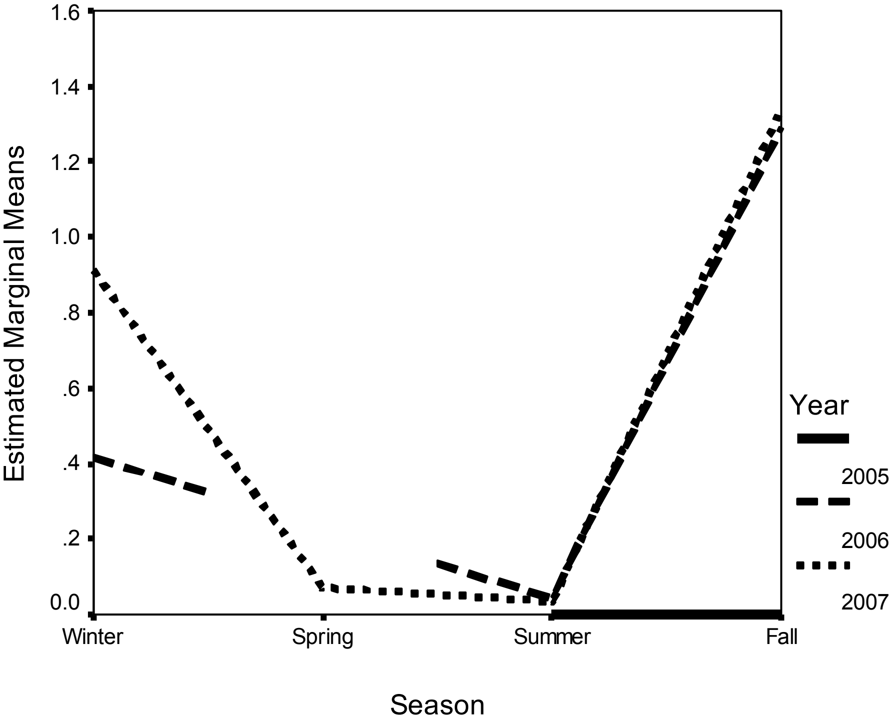

Figure 4.13. Season by year interaction effects plot for Pacific white-sided dolphin type B click bouts. Breaks in 2006 line at spring and before summer in 2005 indicate missing data.

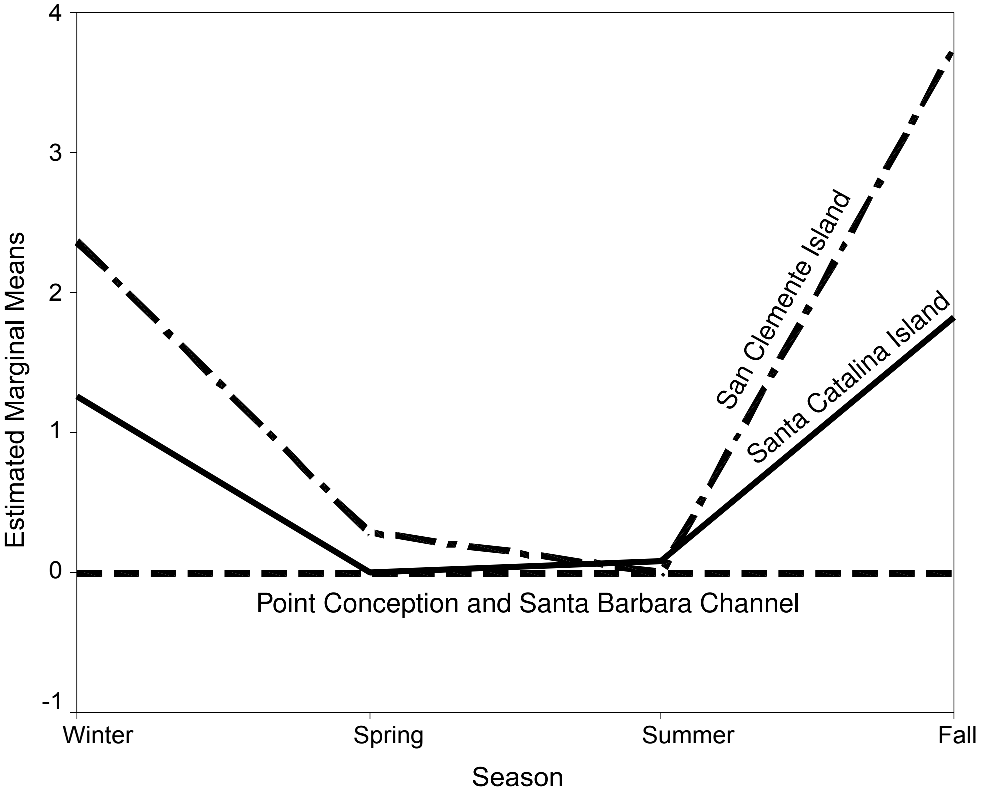

Figure 4.14. Seasonal by site interaction effects plot for Pacific white-sided dolphin type B click bouts. Both Santa Barbara Channel and Point Conception had zero click type B detections through all seasons.

TABLES

Table 4.1. Seasonal coverage at each site across three years of study. Cells represent the number of week-long samples. Site abbreviations: A = Santa Catalina Island, B = Santa Barbara Channel, C = Point Conception, and G = San Clemente Island. The remaining two sites were not included in the seasonal part of this study because they were only deployed during part of the year in 2007 and did not sample across all seasons.

	Winter			Spring			Summer			Fall			Total
Site	2005	2006	2007	2005	2006	2007	2005	2006	2007	2005	2006	2007	
A	0	4	8	0	0	9	7	12	10	13	12	10	85
B	0	4	8	0	0	3	7	0	12	13	7	5	59
C	0	3	10	0	0	13	7	5	13	13	4	3	71
G	0	0	11	0	0	12	0	0	9	0	0	8	40
Total	0	11	37	0	0	37	21	17	44	39	23	26	255
		48			37			82			88		255

Table 4.2. Summary of recording days, days with Pacific white-sided dolphin type A and B click bouts present, percent of days with Pacific white-sided dolphin type A and B click bouts present and mean instrument depth at each of the six HARP sites.

	Northern		Southern Offshore		Southern Inshore		
	Point Conception	Santa Barbara Channel	Tanner & Cortez Banks	San Nicholas Basin	San Clemente Island	Santa Catalina Island	Total
Recording Days	457	377	199	110	266	550	1959
Days with Type A click bouts	112	10	15	23	120	37	317
Percent Days with Type A click bouts	24.5	2.7	7.5	20.9	45.1	6.7	16.2
Days with Type B click bouts	0	0	0	0	55	75	130
Percent Days with Type B click bouts	0.0	0.0	0.0	0.0	20.7	13.6	6.6
Instrument Depth	787	585	1013	1316	435	351	

Table 4.3. Results of 3-way ANOVA for seasonal, annual and site effects on Pacific white-sided dolphin type A click bout occurrence. Stars indicate significant effects.

Source	Type IV Sum of Squares	df	Mean Square	F	Sig.	
Corrected Model	513.6	29	17.7	10.2	0.000	
Intercept	301.2	1	301.2	174.2	0.000	
SEASON	2.1	3	0.7	0.4	0.745	
SITE	207.1	3	69.0	39.9	0.000	*
YEAR	11.2	2	5.6	3.2	0.041	*
SEASON * SITE	124.2	9	13.8	8.0	0.000	*
SEASON * YEAR	1.9	3	0.6	0.4	0.783	
SITE * YEAR	13.0	4	3.2	1.9	0.115	
SEASON * SITE * YEAR	7.9	5	1.6	0.9	0.476	
Error	389.1	225	1.7			
Total	1260.7	255				
Corrected Total	902.7	254				

Table 4.4 Results of 3-way ANOVA for seasonal, annual and site effects on Pacific white-sided dolphin type B click bout occurrence. Stars indicate significant effects.

Source	Type IV Sum of Squares	df	Mean Square	F	Sig.	
Corrected Model	324.0	29	11.2	10.1	0.000	
Intercept	48.3	1	48.3	43.6	0.000	
SEASON	38.3	3	12.8	11.5	0.000	*
SITE	55.5	3	18.5	16.7	0.000	*
YEAR	6.1	2	3.0	2.7	0.067	
SEASON * SITE	50.2	9	5.6	5.0	0.000	*
SEASON * YEAR	11.0	3	3.7	3.3	0.021	*
SITE * YEAR	12.0	4	3.0	2.7	0.031	*
SEASON * SITE * YEAR	18.7	5	3.7	3.4	0.006	*
Error	249.1	225	1.1			
Total	649.5	255				
Corrected Total	573.1	254				

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CHAPTER 5

HABITAT MODELING FOR
RISSO'S DOLPHIN (*GRAMPUS GRISEUS*) AND
PACIFIC WHITE-SIDED DOLPHIN (*LAGENORHYNCHUS OBLIQUIDENS*)
USING ECHOLOCATION CLICK BOUT OCCURRENCE
IN THE SOUTHERN CALIFORNIA BIGHT

ABSTRACT

The Southern California Bight is a region of high productivity capable of supporting a variety of top predators such as dolphins. Delphinid habitat characterization offers the ability to predict distributions and abundances of species which respond to highly variable oceanographic processes. Remotely-sensed satellite data provide especially useful predictor variables for management and conservation as they are easily obtainable and available over broad spatial and temporal scales. Often, oceanographic processes that lead to productivity include a time delay due to ecological succession from nutrient-rich upwelled waters through phytoplankton and zooplankton blooms to abundance of fish, squid and their delphinid predators and the incorporation of time-lagged data into models may increase their predictive power. Generalized Additive Models (GAMs) were built to predict dolphin acoustic activity from long-term autonomous recording packages using time-lagged, remotely-sensed oceanographic variables including sea surface temperature (SST), SST coefficient of variation (CV), sea surface cholorphyll concentration (Chl), Chl CV, upwelling indices and solar and lunar temporal indices. Models were built using number of click bouts per week from Risso's dolphins and two Pacific white-sided dolphin click types. Best predictive models for Risso's dolphins and Pacific white-sided dolphin type A clicks included time-lagged variables, suggesting the importance of ecological succession between abiotic variables and dolphin occurrence, while best models of Pacific white-sided dolphin type B clicks were for current conditions, suggesting association with prey aggregating features such as fronts and eddies.

INTRODUCTION

For highly mobile species such as dolphins, estimates of abundance and distribution may be highly variable on seasonal and annual timescales (e.g. Forney and Barlow, 1998); habitat characterization can lead to improved distribution and abundance estimates (Forney, 2000; Ferguson et al., 2006; Becker, 2007). As top predators in marine ecosystems with requirements for daily feeding (Smith and Gaskin, 1974; Lockyer, 1981), their distribution is presumably determined by the distribution of their prey (Kenney and Winn, 1986; Gregr and Trites, 2001). Prey distributions are often patchy in the open ocean (Hutchinson, 1953) due to underlying dynamic oceanographic processes. The mechanisms relating marine predators to their prey and the underlying physical oceanography are often poorly understood, particularly for offshore species. Increasingly, researchers are developing quantitative habitat models using regression techniques to investigate the relationships between dolphin occurrence and measures of the surrounding environment (Redfern et al., 2006). Predictive habitat models can then be used by resource managers and conservation scientists to improve distribution and abundance estimates.

The choice of environmental predictor variables to incorporate into a model may depend on numerous factors. Explanatory models that seek to understand the mechanisms driving the relationship between dolphin occurrence and environmental variables should include variables that describe the relationship they are examining, such as prey biomass, abundance and diversity. However, for models developed for predictive purposes of management and conservation, it is important that environmental variables be easily accessible and available over a broad spatial and temporal scale (Hamazaki, 2002; Becker, 2007). Examples of such data include remotely sensed sea surface temperature, chlorophyll, and altimetry data, upwelling indices, and bathymetric descriptors. Increased sightings and numbers of odontocetes have been correlated with SST (Waring et al., 2001; Benson et al., 2002; 2002), chlorophyll concentrations (Smith et al., 1986), depth (Baumgartner et al., 2001; Hamazaki, 2002), bathymetric steepness (Baumgartner et al., 2001; Waring et al., 2001; Yen et al., 2004), and locations of SST or Chl fronts (Smith et al., 1986; Becker, 2007). It is unlikely that dolphins are responding directly to physical oceanographic variables such as these, but rather that their increased occurrence results indirectly from conditions that lead to increased prey abundance (Jaquet and Whitehead, 1996; Fiedler et al., 1998). For example, steep bathymetric slopes can lead to topographically-induced upwelling of nutrients leading to enhanced primary and secondary production (Baumgartner et al., 2001).

Aggregations of zooplankton and higher trophic levels may be due to either ideal conditions for primary production or concentrating mechanisms such as convergence zones where downwelling aggregates buoyant prey (Gregr and Trites, 2001). In the first scenario, a lag time may be present between the occurrence of the initial event and the development of phytoplankton and zooplankton blooms that lead to abundance of cetacean prey (Jaquet, 1996; Gregr and Trites, 2001; Croll et al., 2005). Vinogradov (1981) indicates a lag time as great as four months between initial oceanographic conditions and the abundance of fish and squid, the typical prey of dolphins. The inclusion of temporal lags into models incorporating abiotic variables may improve predictive power and lead to hypotheses about the mechanisms causing prey aggregation.

In addition to potential improvements in predictive power, the inclusion of temporal lags in predictive models can increase the utility to project managers by providing time to plan or cancel events that may impact the animals.

While quantitative models of cetacean habitat are becoming common, most of these models have been built from visual survey data (except Hastie et al., 2005). Long-term passive acoustic monitoring data offer higher resolution sampling than can be obtained from visual or acoustic shipboard surveys due to cruise, personnel and cost constraints and offer the added benefit of the ability to sample during poor visual conditions such as nighttime and rough weather. Additionally, Hamazaki (2002) notes the limitation of models of visual survey data to times when animals are at the surface, for example during rest behaviors such as logging, and the possibility that this may not therefore represent prime habitat. Recent advances allow Risso's and Pacific white-sided dolphin echolocation clicks off southern California to be classified by species (Soldevilla et al., 2008), providing the ability to study their ecology through passive acoustic monitoring techniques. Delphinid echolocation clicks are rarely produced while resting and are produced most frequently during foraging activities (Norris et al., 1994). Use of acoustic surveys based on delphinid echolocation clicks increases the likelihood that animals are both active and foraging and may increase the accuracy of habitat models.

This study investigates the utility of incorporating time-lagged oceanographic data into predictive habitat models of dolphin acoustic occurrence. Habitat models are built within a generalized additive model (GAM) framework and incorporate echolocation click occurrence from automonous recorders with remotely-sensed oceanographic variables, upwelling indices and solar and lunar temporal indices.

Generalized additive models (GAMs) offer a flexible regression technique for modeling the importance of environmental correlates for habitat prediction (Hastie and Tibshirani, 1990) and are increasingly being utilized in studies of dolphin habitat. We investigate the hypotheses that 1) the inclusion of readily available oceanographic predictor variables results in better predictive models of dolphin occurrence than the null model and 2) that the inclusion of time-lagged predictor variables results in better predictive models than those built on current time data. Forward-backward selection and cross-validation methods are used to select models with the best predictive power on data from an out-set.

METHODS

Study Area

The Southern California Bight (SCB) is a highly productive and complex oceanographic region. The dominant oceanographic feature offshore of Southern California is the equatorward flowing eastern boundary current, the California Current, (Reid et al., 1958; Wooster and Jones, 1970). The most prominent feature within the SCB is the Southern California Eddy, an offshoot of the California Current which breaks off at 32^{o}N to form a large counterclockwise gyre within the bight, entraining warm waters from Baja California as it heads inshore and poleward (Reid et al., 1958; Hickey, 1979). The unusually complex bathymetry within this region, described as the continental borderlands (Shepard and Emery, 1941), includes numerous high islands and banks and low troughs and basins that extend more than 80 km from the mainland coast before reaching the continental slope (Emery, 1960). These bathymetric features cause changes in current and wind flow around islands and banks resulting in the formation of mesoscale and sub-mesoscale eddies which then circulate through the bight (Kolpack, 1971; Brink and Muench, 1986; DiGiacomo and Holt, 2001; Caldeira et al., 2005). Mesoscale and sub-mesoscale eddies and the occurrence of seasonal wind-driven upwelling events result in alternating upwelling and relaxation events throughout the bight and are important sources of the high productivity of the region (Longhurst, 2007).

Study Animals

Risso's and Pacific white-sided dolphins are among the more abundant species of dolphins found in the Southern California Bight (SCB). Risso's dolphins are relatively large odontocetes which feed nearly exclusively on cephalopods (Clarke and Pascoe, 1985; Clarke, 1996). They are a tropical to temperate species that range from the Gulf of Alaska to the equator in the Eastern North Pacific (Leatherwood et al., 1980). Their role in the SCB ecosystem is not well understood. Extreme changes in distribution and abundance have been documented off the west coast of North America (Kruse, 1989; Green et al., 1992; Shane, 1995), but the cause of these movements and their habitat preferences remain unknown (Kruse et al., 1999). Previous studies indicate that steep bathymetry and warm waters (Dohl et al., 1983; Green et al., 1992; Baumgartner, 1997; Baumgartner et al., 2001) are important habitat features for Risso's dolphins around the world.

Pacific white-sided dolphins, on the other hand, forage opportunistically on epipelagic and mesopelagic schooling fish and cephalopods (Stroud et al., 1981) and their prey preferences typically reflect the most abundant prey in a region. Studies off southern California indicate that preferred prey include northern anchovy (*Engraulis* *mordax*), young Pacific hake (*Merluccius productus*), market squid (*Loligo opalescens*), jack mackerel (*Trachurus symmetricus*) and Pacific mackerel (*Scomber japonicus*) (Brown and Norris, 1956; Fitch and Brownell, 1968; Walker et al., 1986). They are a cold-temperate pelagic species endemic to the North Pacific Ocean (Leatherwood et al., 1984; Barlow and Forney, 2007). Similar to Risso's dolphins, Pacific white-sided dolphins exhibit high seasonal and interannual variability in occurrence and distribution off Southern California (Green et al., 1992; Shane, 1994; Forney and Barlow, 1998; Benson et al., 2002; Barlow and Forney, 2007) and their habitat preferences remain unclear, though they are frequently sighted in cooler waters near the shelf-break (Benson et al., 2002; Yen et al., 2004; Becker, 2007).

Acoustic Data Collection

Delphinid acoustic data used in the predictive models were collected using autonomous High-frequency Acoustic Recording Packages (HARPs) deployed at six locations throughout the Southern California Bight between August 2005 and December 2007 (Figures 5.1 & 5.2). A brief description of these autonomous seafloor-mounted recorders is provided here for clarity; see Wiggins and Hildebrand (2007) for a detailed description of HARP design and capabilities. The HARP data-logging systems include a 16-bit A/D converter, up to 1.9 TB of storage capacity, a hydrophone suspended 10m above the seafloor, a release system, ballast weights, and flotation. The data-loggers are capable of sampling up to 200 kHz and can be set to record continuously or on a duty cycle to accommodate variable deployment durations. This study includes data from 30 HARP deployments each lasting between 1-4 months duration. Temporal coverage at each of the six sites is variable due to cruise timing constraints and occasional instrument failures, as illustrated in Figure 5.3. Data from all deployments included in this study were sampled at 200 kHz, resulting in a recording bandwidth of 100 kHz.

A variety of duty cycles were used across deployments ranging from continuous recording to recording as little as 25% of the time. The majority of the deployments recorded acoustic data continuously, however nine of the deployments contained data recorded on a duty cycle to allow a longer duration deployment due to recovery scheduling constraints. Three duty cycle sampling schemes were used such that the duration that recordings were on each cycle was consistently 5 minutes, but the duration that recording was off was 5, 10, or 15 minutes for a given deployment. Figure 5.3 illustrates the duty cycle coverage of the various deployments. The use of a duty cycle affects the probability of detecting calling bouts; our method of accounting for this sampling scheme will be discussed in Section II.C.

Acoustic Data Analysis

Acoustic data were analyzed with a custom program, *Triton*, using a MATLAB interface. Raw acoustic HARP data were converted to XWAV format, a format similar to WAV format that incorporates metadata in an expanded header file, including recording start and stop times. This timing information is crucial when analyzing duty-cycled data. Each HARP deployment resulted in 1.6 - 1.9 TB of data which are impractical to analyze manually in original form. Therefore, these data were compressed for visual overview by creating long-term spectral averages (LTSAs, Wiggins and Hildebrand, 2007) from the XWAV files. LTSAs are effectively long-term spectrograms created using the Welch algorithm (Welch, 1967) by coherently averaging 4000 spectra created from 1000 point, 0% overlapped, Hann-windowed data and aligning the resulting averaged spectra over time. The resulting LTSAs had resolutions of 100 Hz and 5 seconds in the frequency and time domains, respectively.

The method of spectral-averaging has proven effective for visually examining large acoustic data sets (e.g. Burtenshaw et al., 2004). At the described resolution, delphinid whistling and echolocation clicking bouts, rain bouts, ship passings, and other acoustic phenomenon can easily be distinguished from background noise. Soldevilla et al. (2008) describe distinct spectral patterns found in individual echolocation clicks of Risso's and Pacific white-sided dolphins. One distinct click type was found for Risso's dolphins, while two distinct click types were found for Pacific white-sided dolphins, denoted types A and B. These spectral patterns are found in autonomously recorded HARP data (Soldevilla et al., 2008) and are particularly striking as visualized in LTSAs (Figure 5.4). By visually examining thirty minute long LTSA segments, start and end times of click bouts exhibiting the described spectral patterns were located, logged, and assigned to the appropriate species and species subgroups. Click bouts from mixed-species groups that included Risso's or Pacific white-sided dolphin clicks were often distinguishable and were noted as such. These occurred in 15-25% of occurrences and usually involved unidentifiable click types (Soldevilla et al. 2008). For each click type, presence or absence of click bout detections was determined for hour-long time bins and both the total number of hours with acoustic detections per week as well as the total hours with recordings per week were calculated such that a new week started on the first day of each year. The incorporation of data into week-long samples resulted in the loss of one day per year.

Duty Cycle Corrections

The incorporation of a duty cycle into our sampling scheme reduces the probability of detecting acoustic occurrence of the three dolphin click types. A sub-sampling experiment was conducted on all continuous data to estimate the probability of detecting clicks under each of the three different duty-cycle sampling schemes. For each hour of continuous data, 60 permutations were conducted in which the start of a five minutes on / X minutes off (where X = 5, 10 or 15 minutes) sampling scheme was applied such that the cycle started at each possible minute of the hour. The presence or absence of at least one detection within the hour was noted for each of the 60 permutations and the probability of detection for that hour was calculated as the average of the 60 permutations. For each species, hourly probabilities were averaged across all hours at all sites to obtain a single detection probability for the species at the specified duty cycle (Table 5.1). The reciprocal of this detection probability is used within the GAMs as a correction factor for duty cycled data as described in section IIG.

Oceanographic Data

As part of the CalCOFI / CCE-LTER oceanographic program, composites of sea surface temperature (SST) and chlorophyll concentration (Chl) satellite data are readily available for the SCB. Values of SST and Chl were obtained from 7-day composites of 1 km resolution satellite images created by Mati Kahru of the Integrated Oceanography Department at Scripps Institution of Oceanography (http://spg.ucsd.edu/Satellite_Data/California_Current/). Composites averaged over 7 days represent a compromise that allows high temporal resolution of oceanographic changes while minimizing missing data due to cloud coverage (e.g. Becker, 2007). At each site, 20 km radius masks were created centered on each of the HARP sites using the software WIM (www.wimsoft.com). Time-series of SST and Chl values were then obtained for each site using the automated program wam-statist which obtains statistics including area with valid data, mean and standard deviation values of the areas covered by the masks. Coefficients of variation (CVs), based on values within each 20 km radius, were calculated for both SST and cChl and were included in the model as proxies for temperature and productivity fronts. Weekly samples with greater than 95% cloud cover were omitted from the analyses to prevent use of non-representative data.

Additional environmental data obtained for inclusion in the model were the upwelling index for the SCB and a proxy variable to represent lunar phase (nighttime lunar duration). Lunar data was obtained from the U.S. Naval Observatory website (http://aa.usno.navy.mil). Nighttime lunar duration, a continuous proxy for lunar phase, was calculated as the duration that the moon was above the horizon while the sun was below the horizon each day. These values were then summed over the week-long sample. Lunar duration and lunar phase are closely correlated but a weekly average of phase was difficult to represent due to the shifting nature of 7-day samples and a 29-day lunar cycle. The coastal upwelling index, an index of the strength of the wind forcing on the ocean that forces water away from the coast, was obtained from the Pacific Fisheries

Environmental Laboratory Environmental Research Division website at the National Oceanographic and Atmospheric Association (http://www.pfeg.noaa.gov/products/PFEL/modeled/indices/upwelling/upwelling.html). A single index was available for the SCB which represented the average upwelling over a 3^o region centered at 33^oN and 119^oW.

Temporal Lags

Vinogradov (1981) and Gregr and Trites (2001) described the importance of the temporal relationship between oceanographic variables such as SST, chl a and upwelling and note that there may be a time-lag between conditions favorable to primary productivity and the accumulation of higher trophic level prey that whales and dolphins feed on. Lag times may be as short as several weeks for baleen whales that feed on zooplankton (trophic level = 3.2) (Pauly et al., 1998) or as high as four months for sperm whales (Vinogradov, 1981) which are feeding on upper trophic level squid (trophic level = 4.4) (Pauly et al., 1998). Risso's and Pacific white-sided dolphin are also high-trophic level foragers (trophic levels = 4.3 and 4.1, respectively) (Pauly et al., 1998), therefore, depending on the mechanisms of prey aggregation, one might expect a lag time between physical oceanographic and primary productivity descriptors and the occurrence of dolphins. Consequently, weekly lag times ranging from 0 to 16 weeks were incorporated into the models to investigate the effect of prey accumulation mechanisms on dolphin occurrence patterns. As inclusion of a large number of hypothesis tests increases the chance of significant results due to random causes, the number of lag models was reduced by including only weeks that were a power of 2 to allow investigation of multiple scales. Therefore, individual models were created for 0, 1, 2, 4, 8, and 16 week lagged data.

Quotient Analysis

An exploratory analysis of the relationships between occurrence of dolphin click bouts and environmental variables was carried out using quotient curves. Quotient curves represent the relative occurrence of click bouts in the environment over the full spectrum of measured environmental variables (Drapeau, 2004). Each environmental variable was split into about 30 categories and the frequencies of occurrence of weekly samples of each variable were calculated. Similarly, hours with dolphin click bouts present were summed for each category. Percent occurrence of click bouts per category were divided by percent occurrence of environmental variables, effectively weighting the preferred habitat characteristics by those that were available for sampling. Quotient values greater than one indicate significant selection for those values of the environmental variables.

Habitat Modeling

The relationships between dolphin acoustic activity and dynamic oceanographic predictor variables were investigated within a generalized additive model framework (Hastie and Tibshirani, 1990). A GAM, a nonparametric extension of the generalized linear model (GLM), may be represented as

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

in which $g(\mu)$, the link function (the mean of the response variable (μ) with a given distribution function), is related to functions of the additive predictor variables, $\alpha + \sum f_j(X_j)$. The link function allows specification of alternative distributions for non-normally distributed response data. The functions of the predictor variables may incorporate nonparametric forms such as smoothing splines, allowing greater flexibility in fitting the relationships than with GLM's.

Separate GAMs were built to describe and predict acoustic detection rates for each of the three click types (Gg, LoA, LoB). Discrete count data errors are often well approximated with a Poisson error distribution (McCullagh and Nelder, 1999); but behavioral data, such as number of hours with detections per week, are typically clumped leading to over-dispersion of errors and are therefore more appropriately modeled with a quasi-likelihood distribution (McCullagh and Nelder, 1999). In this study, the number of hours with detections per week was modeled using a quasi-likelihood error distribution with a logarithmic link function and variance proportional to the mean to approximate an over-dispersed Poisson distribution.

The variables included in a GAM model should be independent and orthogonal (Hastie and Tibshirani, 1990). Tests of correlations between variables revealed that sea-surface temperature and chlorophyll are highly correlated, likely as a result of increased productivity associated with cold, nutrient rich upwelled waters. To prevent the model from fitting correlated predictor variables, $\log_{10}$Chl was regressed against SST (Figure 5.5) and the residual log Chl values were included in the model terms instead.

To ensure the models contained only significant terms, model development incorporated the forward/backward stepwise selection of variables using the step.gam.off function in SPlus 6.0 (Insightful Corp.). Models were constructed with options for linear terms and smoothing splines with 2 or 3 degrees of freedom. This allowed the flexibility of incorporating non-linear effects while restricting unrealistic complexity that might be difficult to interpret ecologically (Forney, 2000; Ferguson et al., 2006). In addition to the variables described above, a temporal variable of week was included to account for seasonal effects. Weeks were numbered sequentially from 1 to 52 starting with the first day of the year. This term was included with a factorial interaction for region (north vs south) due to known differences in seasonal occupation within the SCB (Soldevilla, 2008, Chapter 4). Splus does not accommodate factorial spline interaction terms, therefore week was modeled as a 1, 2 or 3 degree polynomial fit. Some weeks did not contain a complete week of data. To standardize the expected detection rate to account for this and duty cycle variability, an offset term was included that accounted for both number of hours per week with recordings and duty cycle. Akaike's Information Criterion (AIC) was used to determine the best model at each step of the forward/backward selection process. To improve estimation of the dispersion parameter and allow selection of higher order spline fits when appropriate, stepwise selection of variables occurred twice for each model, following Ferguson et al. (2006). The first call to the stepwise selection process started with the null model and excluded linear terms while the second call to the selection process began with the best model from the first call and included linear functions.

The use of AIC can result in over-fitting a model to the data at hand thereby leading to lower predictive ability. A cross-validation approach was used to assess the predictive power of a number of models. Studies that incorporate spatially-rich surveys over several years typically assess predictive power through a pseudo-jackknife approach by leaving out survey data from a single year and testing the model on this novel dataset (e.g. Forney, 2000; Hastie et al., 2005; Ferguson et al., 2006; Becker, 2007). In contrast, this study is temporally-rich at several sites which would suggest that a pseudo-jackknife approach could be used in which one site is left out for model testing. Removal of a large block of related data (a year or a site) would result in stronger tests than removal of randomly selected samples. However, Soldevilla (2008, Chapters 3 and 4) found site specific and seasonal differences which, given the uneven sampling effort across sites, seasons and years may result in low predictive power of these tests. Therefore a compromise was developed in which 20% of the data were removed as a series of four randomly selected smaller blocks ensuring that no more than 13 consecutive weeks at a single site were removed at a time. In this manner, a pseudo-jackknife approach was incorporated that used 80% of the data to develop models and removed 20% of the data for use in cross-validation testing. Therefore, for each click type, the stepwise building procedure was performed on all combinations of data with a different 20% of the data left out, resulting in five best models. The best model of these five was selected by comparing cross-validation performance using predict.gam and selecting the model with the lowest average squared prediction errors (ASPEs) on its novel dataset.

After the best model was selected using cross-validation and the above criteria, this model was fit to the entire dataset to obtain final parameter estimates.

RESULTS

HARP recordings contained 251 week-long samples from the six instruments deployed in the SCB (Table 5.2). Of these 251 samples, Risso's dolphin, Pacific white-sided dolphin type A and Pacific white-sided dolphin type B clicks were detected in 101, 71, and 30 weeks, respectively. Over 80% of the weeks contained complete recordings with 168 hours, and all weeks contained at least 6 full days (144 hours) of recorded time. The maximum hours per week containing Risso's dolphin and Pacific white-sided dolphin types A and B clicks were 84, 54, and 98 hours, respectively, while mean hours per week with click detections were 12.4, 4.4 and 2.1 hours, respectively.

With respect to sampled oceanographic variables, Risso's dolphin click bouts occurred more often in warmer waters with low variability and less in low Chl waters (Figure 5.6, Table 5.2). Pacific white-sided type A click occurred more often in waters with moderate SST and Chl variability and less often in warm and low Chl waters (Figure 5.6, Table 5.2). Water properties with Pacific white-sided type B occurrence were the most dissimilar from those of the total recording set such that they occurred more often in mid-temperature waters (14-19^{o}C) with high Chl and upwelling indices and low SST and Chl variability (Figure 5.6, Table 5.2).

Of the six time-lagged models produced for each of the five Risso's dolphin pseudo-jackknife cross-validation datasets, the best models (lowest AIC) are presented in Table 5.3. Of the five best models, 2-week lagged models were selected for two datasets, while 4-week lagged models were selected for three datasets. The forward-backward selection algorithm resulted in inclusion of two to five of the seven possible oceanographic variables across the five best models. Average SST was selected in the best models of all five datesets, while SST CV was selected in four of the five. Chlorophyll variables and the interaction between Week and Region were selected in two to three of the models, while moon duration and upwelling were selected in one and zero models, respectively. The model with the best predictive power, as indicated by the lowest ASPE value on the out-data, included the 4-week lagged oceanographic data with 3 df spline fits to residual chlorophyll and average SST and linear fits to the CVs of both chlorophyll and SST (Table 5.3, Figure 5.7). Positive relationships exist between the number of hours with clicks present per week and average SST, log chlorophyll residual and chlorophyll CV, while a negative relationship is present for SST CV. The spline fit for log chlorophyll residual exhibits a slight dip around -2, while the spline fit for SST reaches a maximum around 20^{o}C before leveling out. The final model had a moderate goodness of fit to the data the model was built upon, explaining 47% of the deviance. The moderate goodness of fit and predictive power are illustrated in Figure 5.8a which plots observed and predicted hours with detections as a function of sample number such that the out-data is denoted by light grey boxes. By sorting observed data by hours with detections (Figure 5.8b), it becomes clearer that there is a slight increasing trend in model predictions with increasing observed values, but there remains a lot of variability to be explained. The final best predictive model equation includes a log link function with a 13.70 dispersion factor; coefficient values are reported in Table 5.4.

Of the five best Pacific white-sided click type A models, the 2 week lagged model was selected for one data set, while the 4 and 16 week lagged models were each selected for two datasets (Table 5.3). The forward-backward selection algorithm resulted in inclusion of two to five of the seven possible oceanographic variables across the five best models. The interaction between region and week was included in all five models, while each of the SST variables were included in three of the five models. Log chlorophyll residual and upwelling indices were selected in two of the five models and moon duration and chlorophyll CV were each included in only one model. The model with the best predictive power on the out-dataset incorporated the 4-week lagged oceanographic data with a linear term for average SST, a 3df spline fit for SST CV and the interaction term of region with a 2 degree polynomial fit to week (Table 5.3, Figure 5.9). The relationships between number of hours with Pacific white-sided type A clicks and SST variables were generally negative. In the northern regions, the relationship indicates a peak in hours per week with detections during the summer, while in the southern regions, the relationship indicates a peak during the fall - winter. The final model had a relatively low goodness of fit to the data the model was built upon, explaining 24% of the deviance. The low goodness of fit and predictive power are illustrated in Figure 5.10a. The sorted data (Figure 5.10b) does not indicate an increasing trend in model predictions with increasing observed values and suggests that a lot of variability remains to be explained. The final best predictive model equation includes a log link function with a 13.14 dispersion factor; coefficient values are reported in Table 5.4.

Pacific white-sided click type B models had the least consistency in temporal lag selection: the 0 week (current conditions), 1 week and 8 week lag models were each selected for one data set, while the 16 week lag model was selected for two datasets (Table 5.3). The forward-backward selection algorithm resulted in inclusion of three to five of the seven possible oceanographic variables across the five best models. There was greater consistency in which variables were included with SST CV and the interaction between region and week being included in all five models, and average SST being included in four of the five. Chlorophyll CV was never selected and log chlorophyll, upwelling index, and moon duration residual were each selected in two to three of the five models. The model with the best predictive power on the out-dataset incorporated the 0-week lagged oceanographic data with 3 df spline fits for upwelling index, average SST, and SST CV and the interaction term of region with a 2 degree polynomial fit to week (Table 5.3, Figure 5.11). The relationship between number of hours with Pacific white-sided type B clicks and average SST variables exhibited a peak at 18^{o}C and fell off rapidly at lower temperatures. The relationship with upwelling is generally positive and levels off at high upwelling indices (>150). The relationship between hours with type B detections and SST CV was generally negative. The relationship to week indicates low detections during summer and a seasonal peak in late fall to early winter. The final model had a high goodness of fit to the data the model was built upon, explaining 82% of the deviance. The high goodness of fit and predictive power are illustrated in Figure 5.12a. The sorted data (Figure 5.12b) also clearly indicates an increasing trend in model predictions with increasing observed values. The final best predictive model equation includes a log link function with a 9.20 dispersion factor; coefficient values are reported in Table 5.4.

DISCUSSION

Predictive models of Risso's dolphin occurrence indicate that a four week lag is important and that temperature variables are the most important predictors, while chlorophyll predictors were also important. On the other hand, seasonal and lunar periods were not important, nor were upwelling indices. Numerous studies off of southern California have indicated that while Risso's dolphins may be found in waters as cold as 10^{o}C, they generally exhibit a preference for higher temperature waters (Kruse, 1989; Tynan, 1997; Benson et al., 2002), and have been shown to expand their range into northern territories during extended warm bouts (Leatherwood et al., 1980). Our results indicate that detections of Risso's dolphin click bouts increase with increasing temperature up to 20^{o}C above which they remain constant, in support of previous findings. However, the model results indicate a negative relationship to SST CV, suggesting a preference for waters that are homogenous in temperature. Given the 4 week lag time associated with these variables, this finding may corroborate the findings of Leatherwood *et al.* (1980) indicating the importance of extended warm bouts. Generally positive relationships were found to the 4-week lag of both log chlorophyll residuals and chlorophyll CV, indicating that highly productive regions are important habitat predictors. The 4 week lag time may be due to successional changes from lower tropic level phytoplankton up through zooplankton followed by the aggregation of higher-trophic-level necktonic cephalopods, the preferred prey of Risso's dolphins (Clarke, 1996). Previous studies have indicated that deep warm waters with steep bathymetry are important predictors of Risso's dolphin habitat (Kruse, 1989; Baumgartner, 1997; Baumgartner et al., 2001; Hamazaki, 2002; Yen et al., 2004; Tynan et al., 2005), and steep bathymetry has been explained as an indicator of high productivity caused by fronts where offshore waters meet shelf waters (Baumgartner, 1997; Baumgartner et al., 2001). While bathymetric indices were not included in this study due to the limited spatial resolution, the model results suggest the importance of fronts and high productivity.

The models for the two click types of Pacific white-sided dolphins had some similar features and some interesting differences. Seasonal and SST variables were important in models for both click types. The seasonal relationship for both click types at the southern sites indicated an increase in detections during late fall to winter and the relationship to SST CV indicated a high response in homogenous temperature conditions with decreasing detections as heterogeneity increased. On the other hand, the response to average SST was opposite for the two click types, with click type A being detected more frequently in cooler waters; while click type B was generally detected in warmer waters, with a peak at 18°C. A positive relationship existed for click type B and upwelling indices, while this term was not significant enough to be included in the best click type A model. In the northern regions, click type A had a peak during the summer, but type B was not heard in this region. A final difference is that the model for click type A was based on data with a 4-week time lag while the model for click type B included current data (0 lag). Results of average SST suggest distinctly different water temperature preferences between the two click types. Soldevilla (2008, Chapter 4) suggests that the two most likely hypotheses for significance of click types are that they represent the northern and southern dolphin populations or foraging on different prey types which exhibit northern and southern distributions. These average SST results support both hypotheses if click type B is related to either the southern Baja dolphin population or a southern prey type, and if click type A is related to either the northern CA/OR/WA dolphin population or northern prey types with cooler water preferences. Previous studies of Pacific white-sided dolphins mainly encompass the northern populations' range and indicate cooler water preferences as well (Benson et al., 2002; Becker, 2007). Seasonal patterns were described by Soldevilla (2008, Chapter 4) and are included as important predictors in these models. Interestingly, SST CV showed a negative relationship for both click types, indicating a preference for more homogenous waters, rather than frontal locations. Becker (2007) found the opposite result with more encounters in regions with high SST CV. This may represent regional differences in preferred habitat between the SCB and the entire California coast, differences in behavior state of dolphins sampled visually compared to acoustically, or it could be related to differences in spatial scale of the studies. Finally, a positive relationship to the upwelling index was an important predictor for type B click detections, which seems counter-intuitive given the negative relationship to SST CV. This discrepancy may be a result of use of local data for SST while the upwelling index is general to the entire SCB. Both upwelling and click type B occur seasonally in the SCB, and this general term may be included in the model due to this relationship. While the correlation between week and upwelling index was low, a strong correlation may exist if a phase shift is considered.

The differences in lag times found across the best models for the three click types may suggest differences in the prey aggregating mechanisms of the dolphin prey types. Processes that occur at 0-lag at a fixed location would indicate that the ecosystem has already been built up and the process is acting as an aggregating mechanism, such as downwelling convergence zones or eddies that are moving past the location. Processes that might include a lag-time include coastal upwelling and eddies that are just forming. The best model chosen for Pacific white-sided dolphin type B clicks was the 0-lag model.

This suggests that the dolphins and their prey are responding to conditions that already contain higher trophic levels. The best models for both Risso's dolphin and Pacific white-sided dolphin Type A clicks included four week lagged data. This suggests the important predictive features are ones that are building up over time. High predictions occur for both dolphins in waters with low temperature variability four weeks ago, while predictions for Risso's dolphins were also high in conditions of high chlorophyll biomass and frontal regions. Studies of coastal upwelling systems indicate that while upwelling brings high nutrients to the surface enhancing the productivity of the waters, calm relaxation periods are necessary to allow stratification to develop and phytoplankton to bloom (Huntsman and Barber, 1977; Jones and Halpern, 1981) which may then result in abundant food for higher trophic level predators (Lasker, 1975; 1978). This type of ecosystem build up may be what is driving the conditions for increased prey of Risso's and Pacific white-sided dolphins. In particular, the high chlorophyll productivity and low SST frontal structure may indicate waters in an early stage of relaxation and rapid phytoplankton growth four weeks prior. One concern with this hypothesis is that one would expect these productive waters to move over time (Vinogradov, 1981), so the temporal lag at a fixed location is difficult to explain. Within the SCB, high amplitude current fluctuations exhibit 20-30 day periodicity at a given basin which may be attributable to eddy advection or freely propagating waves, such as coastally trapped waves (Hendricks, 1977; Hickey, 1992). An alternative hypothesis to explain the time lag of 4 weeks may be that it indicates prey moving with these periodic features.

The goodness of fit of the Pacific white-sided type B click detections was especially high, with an explained deviance of 82%. Explained deviances in habitat studies by Becker (2007) ranged from 1-43% over a wide variety of species, while Ferguson’s (2005) explained deviances for beaked whales and delphinids ranged between 5-15%. Does the high explained deviance of this model indicate that this model includes some of the most important variables needed to explain dolphin presence? Or is this a byproduct of the low number of detections and the high number of zeros included in the model? This study examines both spatial and temporal prediction, simultaneously while the other studies were based only on spatial prediction. Seasonal variables were important terms which may indicate that seasonal occurrence is fundamentally easier to predict than spatial occurrence. Alternatively, if predictions remained close to zero when observations were high, this might indicate that the model was good only because it predicts such low values regardless of oceanographic conditions. While the model does in fact have high predictions during times when observations were high, the data included in the out-set for the predictive part of the study has very few observed detections and the predictions at these times were typically close to zero (Figure 5.12). This suggests that the latter may be the case. However, most of the best models included similar terms suggesting the validity of the model. As mentioned above, the type B click may represent the southern Baja California population of Pacific white-sided dolphins or foraging on a specific prey with a southerly distribution. In either case it is likely that the study area incorporates the northern extreme of the dolphin or prey habitat. It is possible that this high degree of fit is real and that that the inclusion of oceanographic variable values from non-habitat regions results in a better fit by distinguishing between habitat and non-habitat. Analyses of continued time-series data from this region should investigate whether this model continues to have high predictive and explanatory power over time.

On the other hand, the Risso's dolphin and Pacific white-sided type A models had moderate to low goodness of fit (49% & 23%, respectively) with much more variability remaining to be explained (Figures 5.8 & 5.10). The area sampled in this study is a portion of the overall range of the dolphins. As mentioned above, the inclusion of data from a larger area that extends beyond the viable habitat of the species being modeled might result in more accurate description of habitat. It is also possible that the models were limited by the predictor variables included such that closer indicators of prey abundance might be important. Another possibility is that other time lags than the ones included in this model may be better indicators of habitat. Suggestions to improve studies due to each of these points are discussed in further detail below. Other possible reasons for the low predictive ability may be that Pacific white-sided dolphins are opportunistic foragers on variable prey types which may lead to multiple habitats being modeled. Becker (2007) notes that complex habitat models require large sample sizes, so more data may be necessary to improve these models. Another factor that may be important is that this study only samples a small portion of the habitat and while conditions may be good here, highly mobile animals such as dolphins may be actively selecting regions of better habitat outside the sampled region or selecting this region as the best of bad options. Future studies should extend the spatial range covered to include both a greater part of the animals' known range and to extend beyond their range into non-habitat.

Although the predictive models presented here cannot be used to determine the mechanisms behind dolphin occurrence, they provide information to allow appropriate hypothesis to be developed and tested. Among the larger gaps in understanding the mechanisms are a thorough understanding of both what prey these dolphins are feeding on and how the prey are responding to the environment. Risso's dolphins are known to feed primarily on cephalopods (Clarke, 1996), yet many species of squid are found off California (Okutani and McGowan, 1969; Roper and Young, 1975) and stomach content analyses are available for only one Risso's dolphin off California almost 50 years ago (Orr, 1966). On the other hand, Pacific white-sided dolphins are opportunistic foragers and feed on the most abundant, appropriately sized prey so their prey types likely change over time. Habitat models of potential prey species (e.g. Schismenou et al., 2008), could be compared with habitat models for dolphin to help determine which prey species are most important in their diets during the study period. Concurrent sampling of dolphins and their prey would be important as well.

While remotely sensed SST and Chl data can indicate the presence of fronts and areas of high productivity, the ecological structure of the regions, including the make-up of phytoplankton, zooplankton and fish assemblages, can only be determined through in situ oceanographic sampling including species composition from water samples, net tows and multi-frequency acoustic backscatter. Southern California has one of the richest and longest time series of oceanographic data available; however, CalCOFI surveys only occur 4 times per year and therefore were not of high enough temporal resolution to include in this study. Marine mammal surveys occurring in conjunction with CalCOFI oceanographic sampling may be a better venue for exploring mechanisms affecting prey and dolphin abundance. In situ sampling of some properties could be incorporated into moorings at the HARP location, including temperature, salinity, current meters, fluorescence and multi-frequency active acoustics. Concurrent dolphin acoustic and environmental sampling of this sort would allow finer resolution of prey field and water properties resulting in a better indication of water mass and frontal structure allowing mechanistic questions to be asked from autonomous acoustic data. However, these properties would be less useful for resource managers who do not have easy access to this type of data in real-time.

This study indicates the importance of temporal variability in predicting dolphin occurrence. While this study was limited to incorporating the same lag time for all oceanographic variables, it seems likely that in fact there may be several different lag times that are important, both because succession processes might result in abiotic and different levels of biotic variable to have different lags, but also because these dolphin species feed on a variety of prey each of which may be represented by different time lags. Numerous methods for analyzing time-series are available and these could be used to identify a greater variety of temporal correlations and phase shifts (ie lag times) than this method could. Temporal cross-correlation techniques can incorporate multiple variables and relate both frequency of occurrence and phase shifts more easily that the lagged GAM models described here. Unfortunately these techniques were not feasible due to the large gaps present in our time series. Future studies should attempt to minimize gaps in the timeseries, especially large gaps. Data with smaller gaps may be analyzable using techniques such as ARIMA or Kalman filtering.

An important caveat to predictive modeling that Hamazaki (2002) notes is that the statistical significance of terms included in predictive habitat models does not necessarily imply the ecological significance of those variables to the dolphins. It is important to form hypothesis about the potential ecological relationships described in models and develop appropriate tests of to determine ecological significance.

CONCLUSIONS

Temporal predictive models of cetacean habitat provide researchers and managers the ability to examine how dynamic ocean processes affect the occurrence of cetaceans in a specific area of interest. The combination of remotely-sensed oceanographic data and long-term acoustic sampling of acoustically classifiable cetaceans such as Risso's and Pacific white-sided dolphins offer potential to examine these temporally changing patterns and understand the time-scales of importance. The models presented here for Risso's and Pacific white-sided dolphins indicate that process occurring as much as 16 weeks prior may explain or predict dolphin occurrence, although the models with best predictive power were based on 0-week and 4-week lagged oceanographic data. The ability to predict dolphin occurrence with time lagged data is especially pertinent for managers who wish to minimize the impact of anthropogenic events by enabling them to plan events several weeks in advance.

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Chapter 5, in full, is currently being prepared for submission for publication of the material. Soldevilla, Melissa; Wiggins, Sean; Hildebrand, John. The dissertation author was the primary investigator and author of this material.

FIGURES

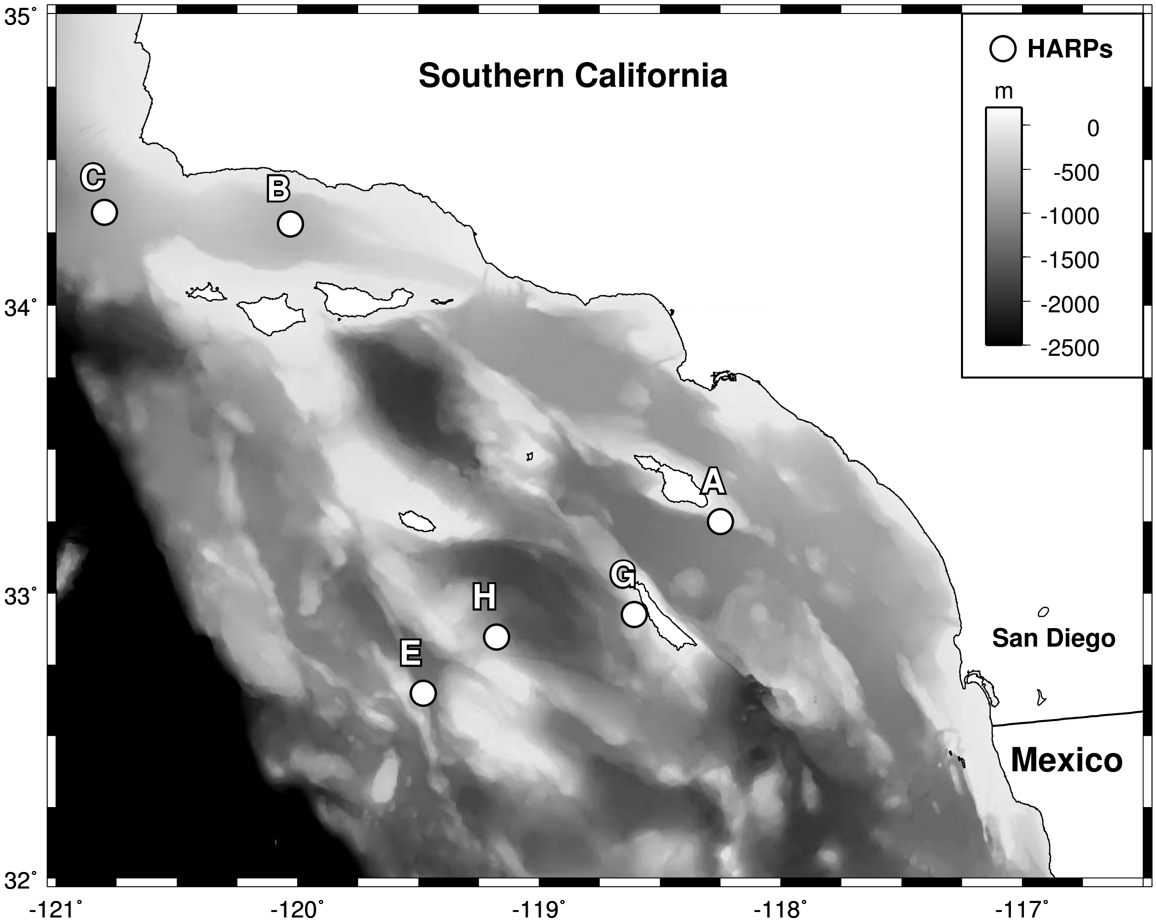


Figure 5.1. Map of study area including locations of HARP deployments. Depths are indicated by colorbar. Sites: A = Santa Catalina Island, B = Santa Barbara Channel, C = Point Conception, E = Tanner/Cortez Banks, G = San Clemente Island, and H = San Nicholas Basin.

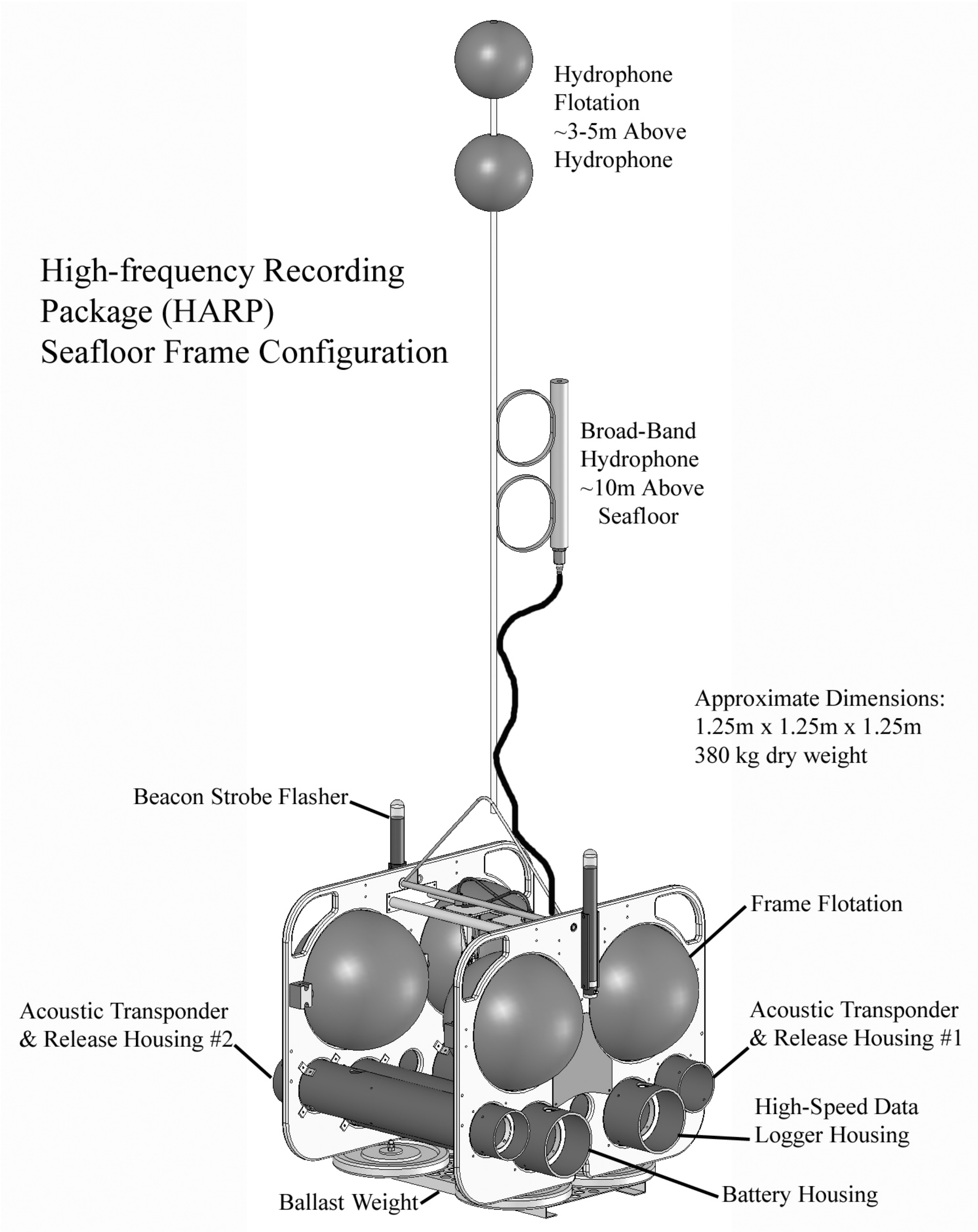


Figure 5.2. HARP schematic representation of sea-floor recording package.

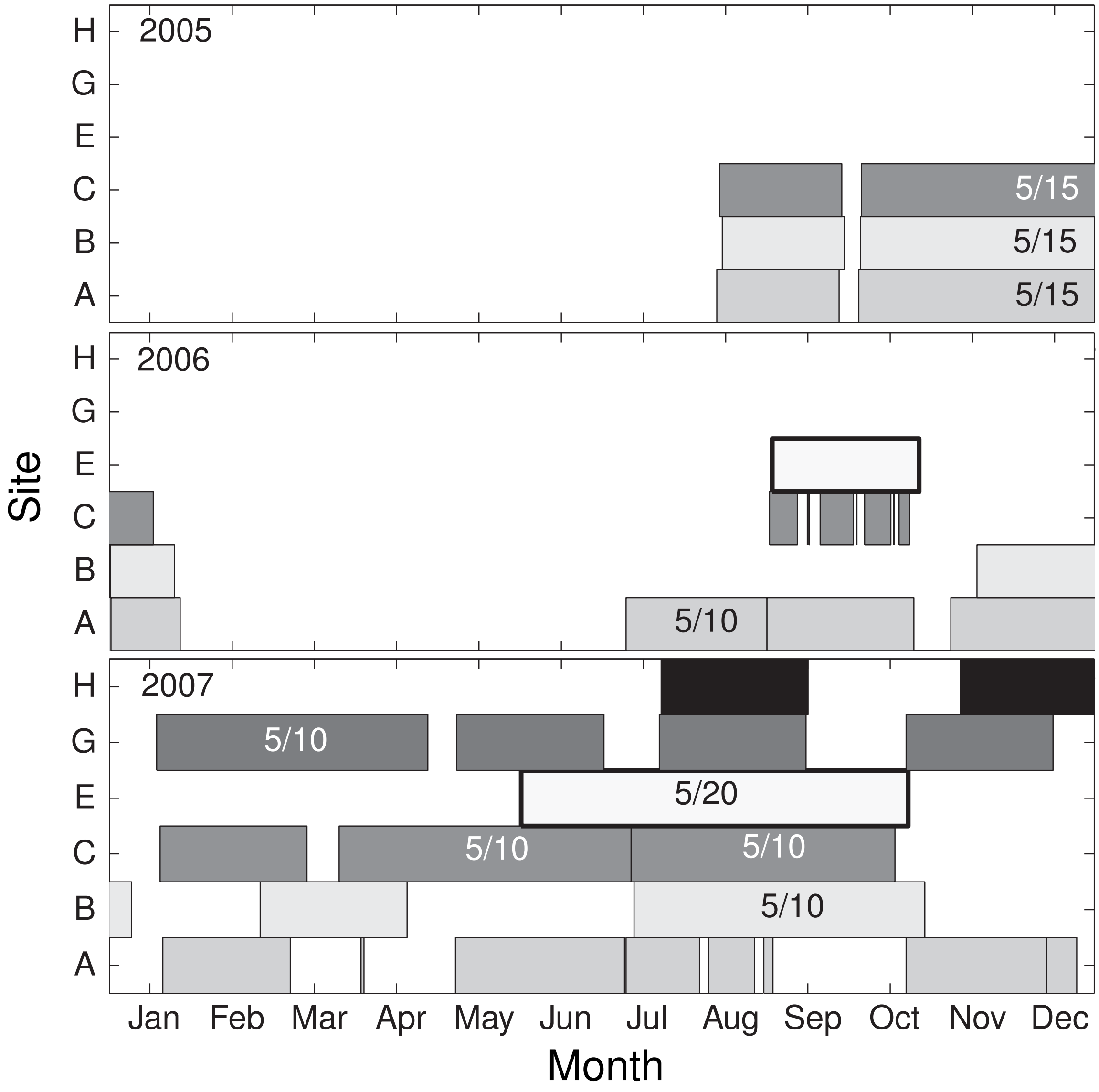


Figure 5.3. HARP data and duty cycle information at each of six sites in the SCB. A = Santa Catalina Island, B = Santa Barbara Channel, C = Point Conception, E = Tanner/Cortez Banks, G = San Clemente Island, and H = San Nicholas Basin. Shading represents dates when data is available at each site. Numbers within shaded regions represent the specified duty cycle as minutes on / minutes of total cycle. Shaded regions without numbers represent continuous data. Data spanning year boundaries follow the previous duty cycle.

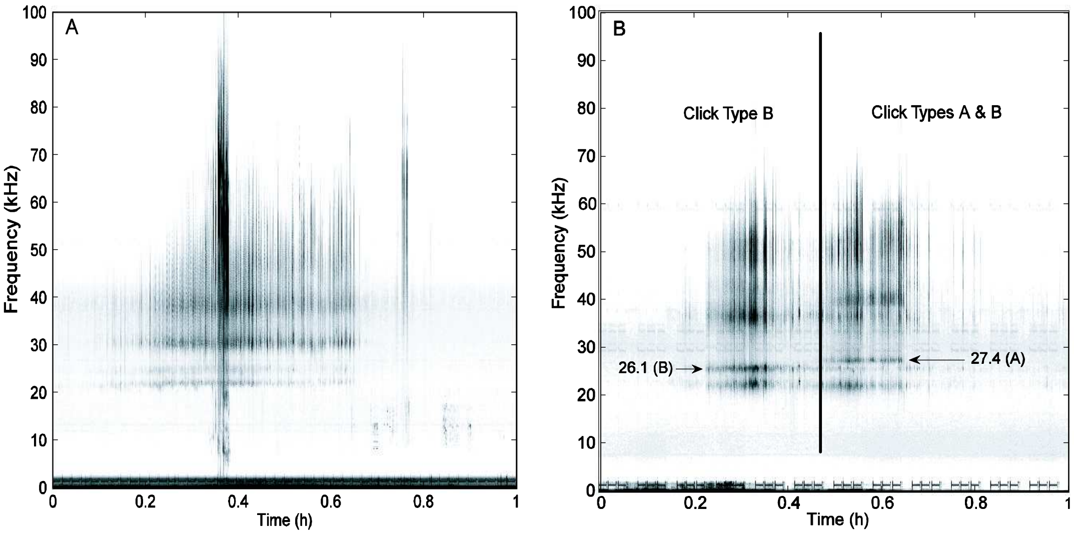


Figure 5.4. Click bouts in HARP long term spectral averages. A) Clicks with the Risso's dolphin spectral pattern. B) Overlapping Pacific white-sided click bouts that transition from subgroup B to a mix of subgroups A and B. The concurrent occurrence of both Pacific white-sided dolphin click types is unusual; typically only one type is present at a time

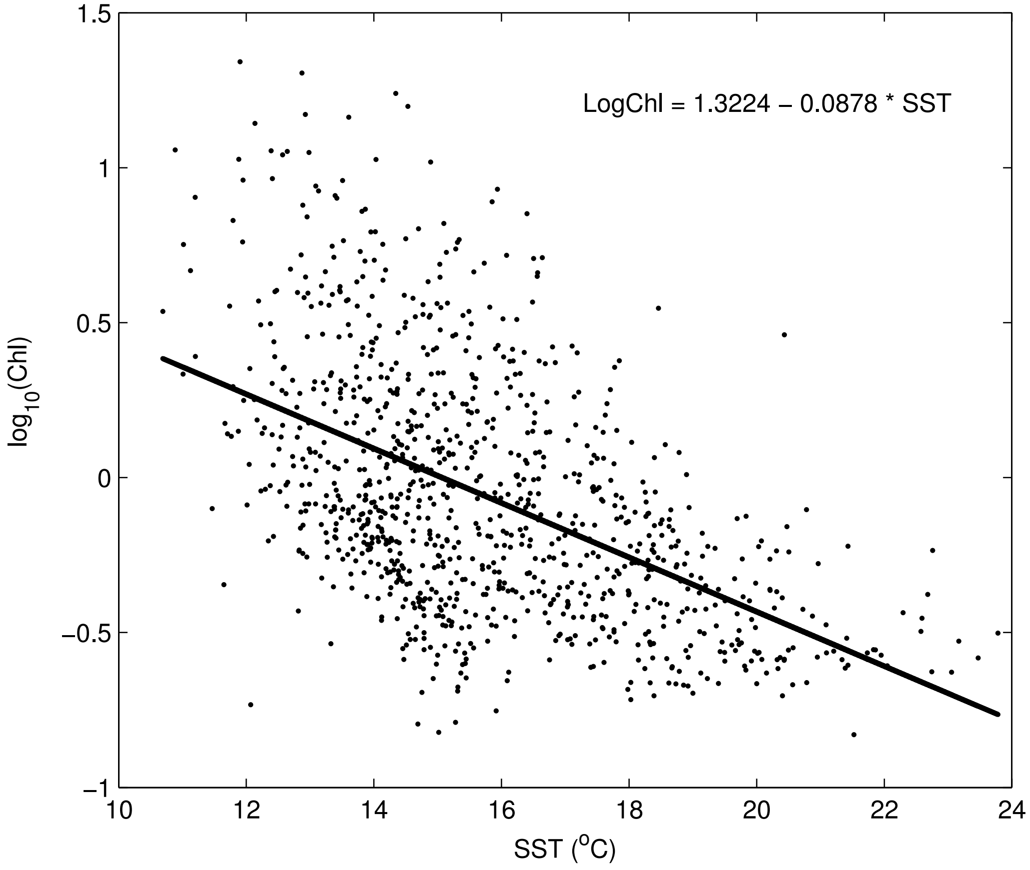
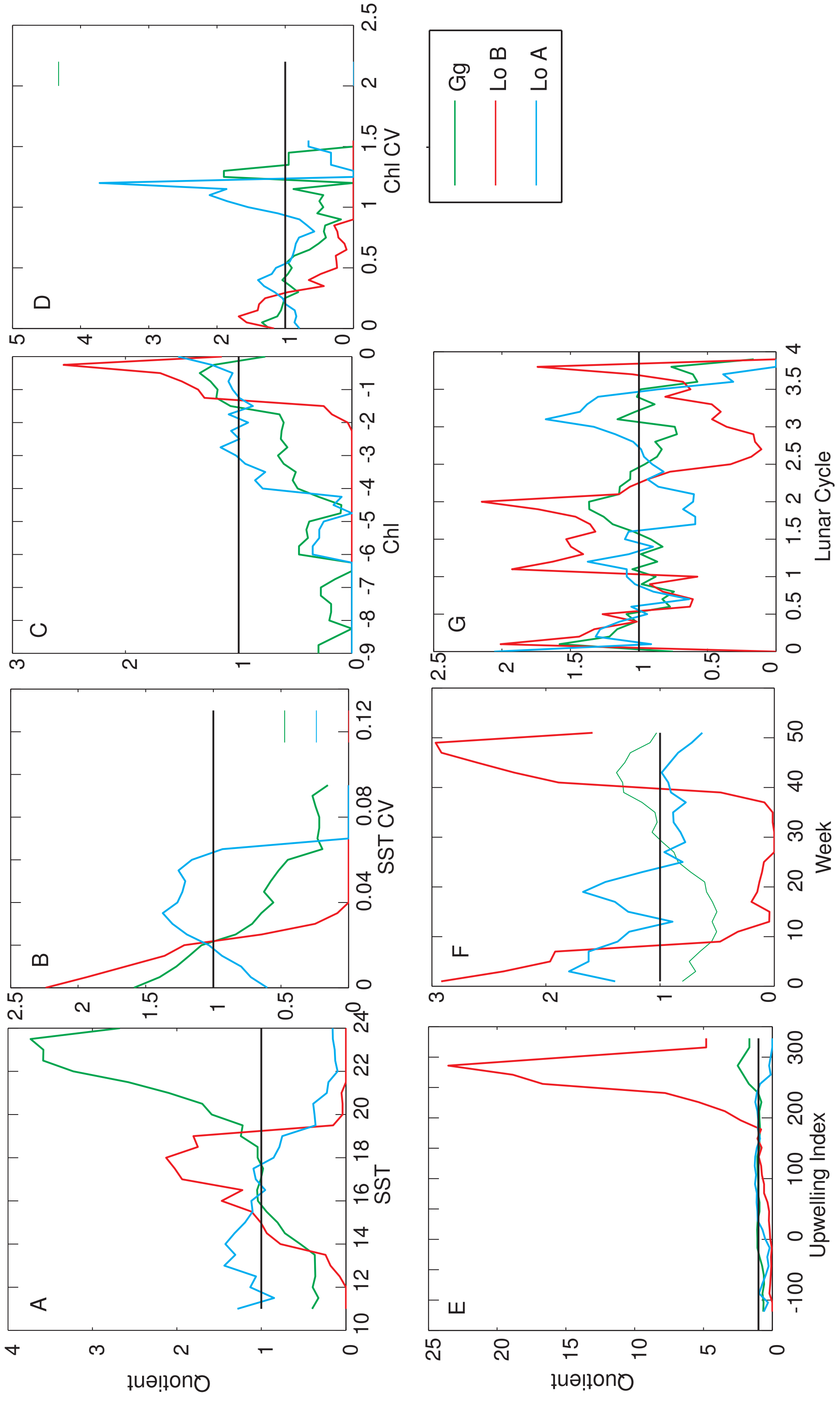


Figure 5.5. Regression of the log of Chl on SST to remove correlative effects from the model. Residual values of Chl were calculated and included in the model.

Figure 5.6. Quotient curves of the relationship between dolphin click occurrence and environmental variables. A) SST (^{o}C), B) SST CV, C) Chl, D) Chl CV, E) Upwelling index, F) Week, G) Nighttime lunar duration. The horizontal black line at quotient value 1 indicates where dolphin habitat is the same as the available environmental conditions. Higher values indicate selection for environmental variable range while lower values indicate avoidance. Occurrence of Risso's dolphin clicks and Pacific white-sided dolphin click types A and B were analyzed.


A
SST
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B
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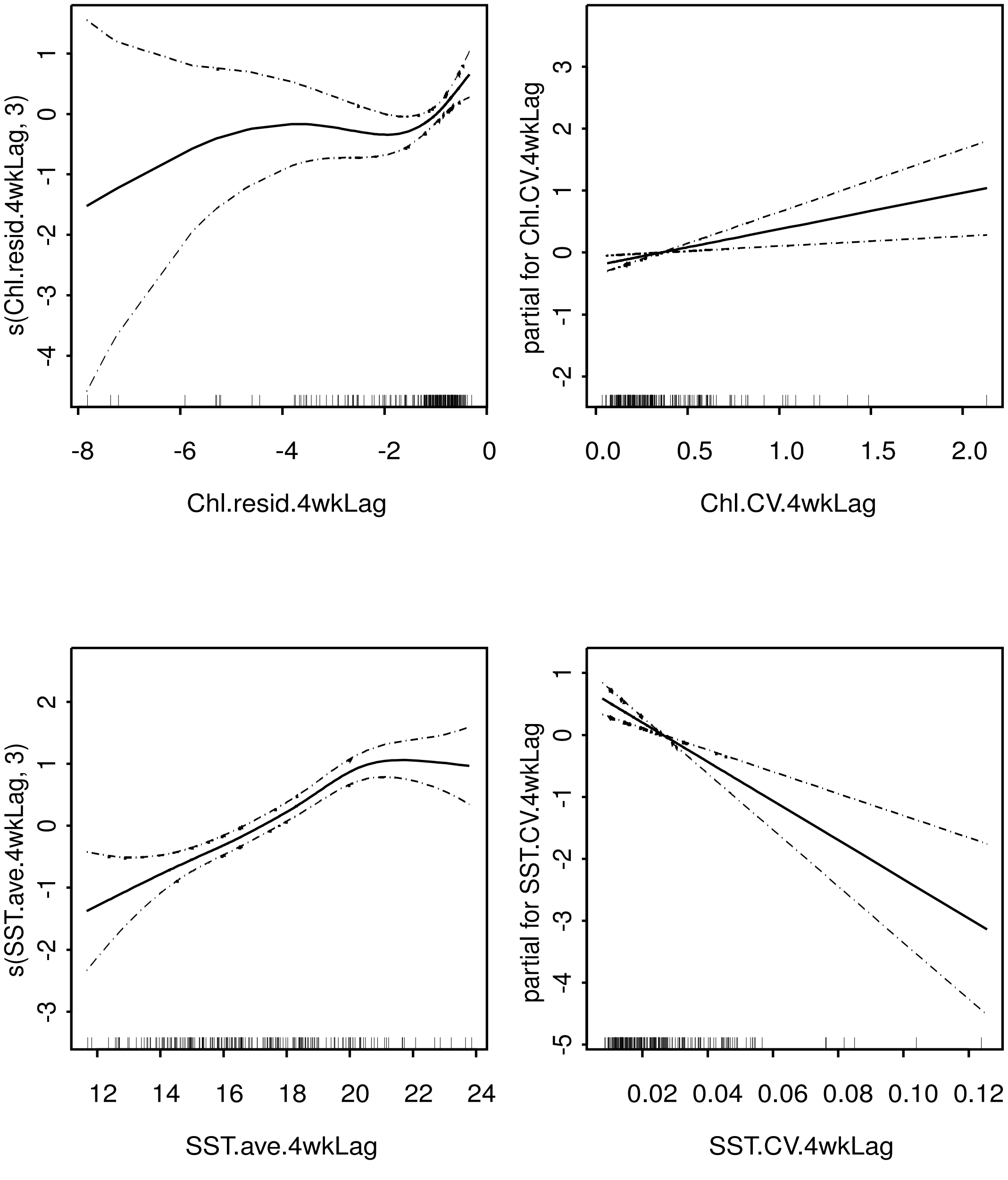

Figure 5.7. **Modeled partial fits of oceanographic variables to Risso's dolphin hours detected per week. Solid line represents the best fit while dotted lines represent the confidence intervals. All plots are plotted on the same scale so that the strength of the slope indicates the importance of the variable in the model. The y-axis label indicates the fit type (partial = linear, poly(.) = polynomial, s(.) = spline) and the degrees of freedom. Rugplot at the bottom indicates location of sample values.**

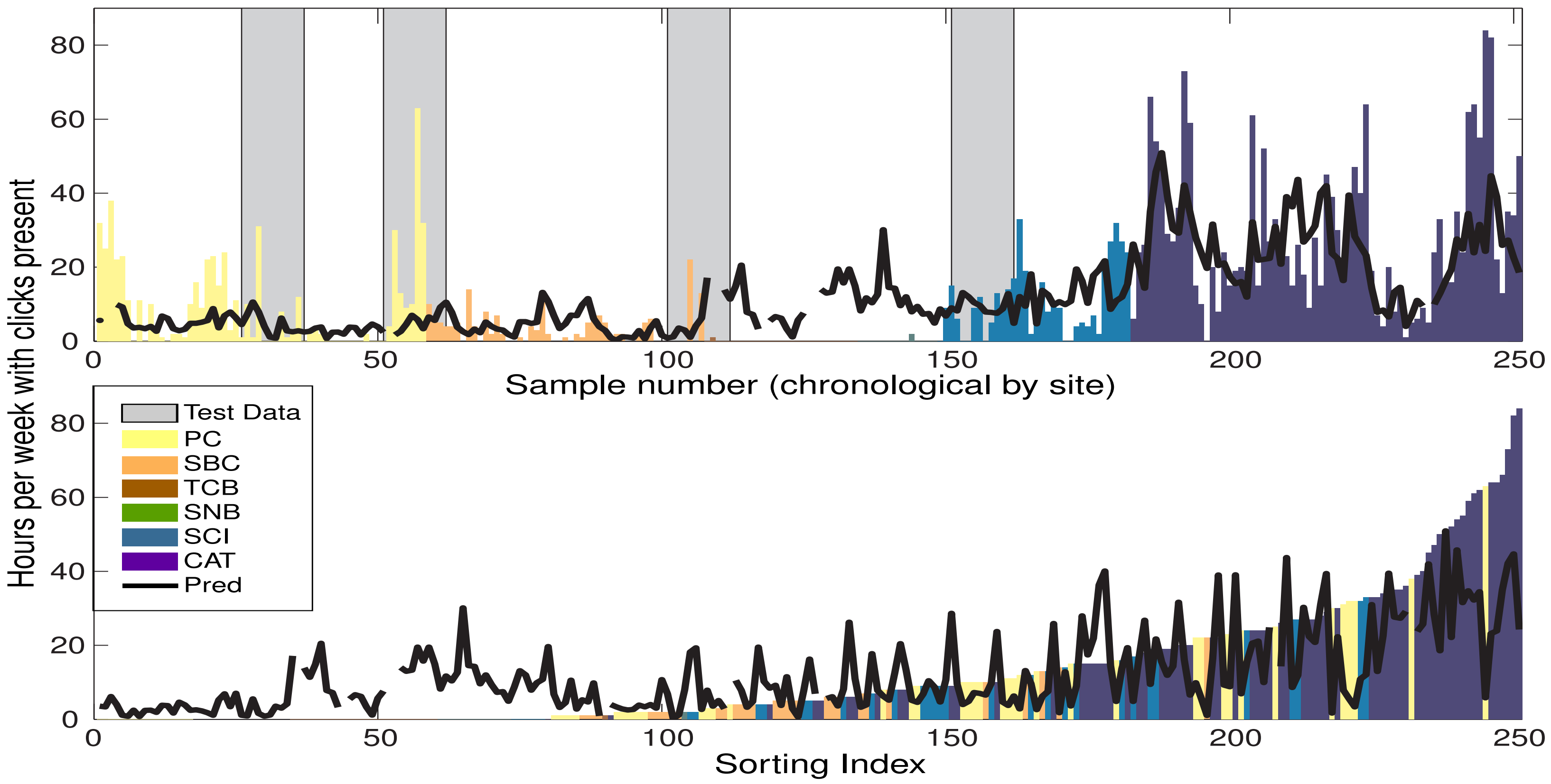

Figure 5.8. Risso's dolphin observed and predicted values from the best model. Observed values are plotted by sample number chronologically by site (A) and sorted from low to high values of hours per week (B) and are represented by colored bars where the color indicates the site. PC = Point Conception; SBC = Santa Barbara Channel; TCB = Tanner/Cortez Banks; SNB = San Nicholas Basin; SCI = San Clemente Island ; CAT = Santa Catalina Island. Black line represents predicted values from the model. Breaks in the prediction line indicate the presence of missing environmental data. These samples were not included in models. In the top plot, the data which was removed during model building and used to test predictive power is highlighted by light grey boxes.

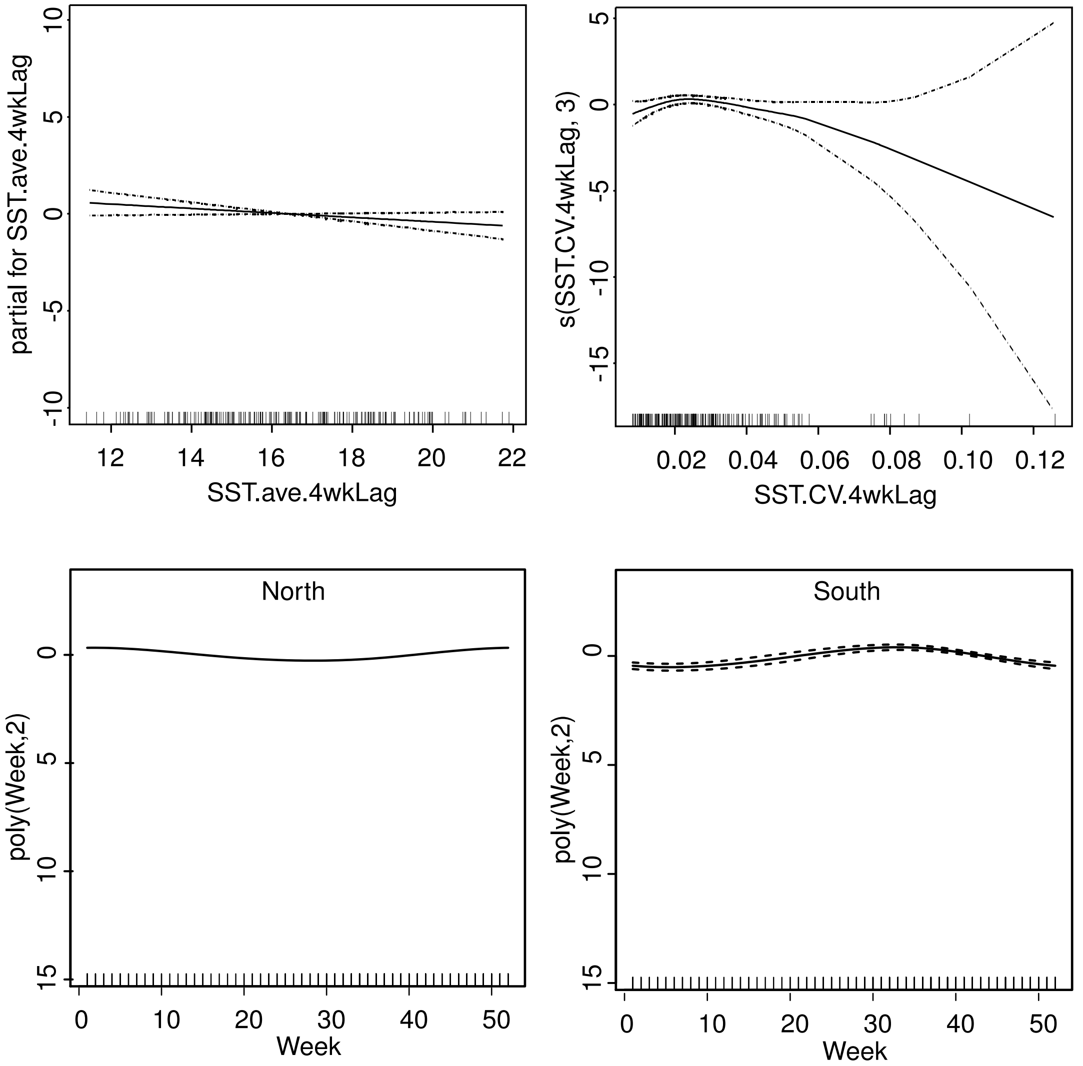

Figure 5.9. Modeled partial fits of oceanographic variables to Pacific white-sided dolphin click type A hours detected per week. Solid line represents the best fit while dotted lines represent the confidence intervals. Plots are plotted on the same scale so that the strength of the slope indicates the importance of the variable in the model. The y-axis label indicates the fit type (partial = linear, poly(.) = polynomial, s(.) = spline) and the degrees of freedom. Rugplot at the bottom indicates location of sample values. Note: The lower two plots represent the interaction between region and week such that left and right plots are for the northern and southern regions, respectively. The interaction plots were created with R using mgcv because SPlus was not able to plot interactions terms. The two algorithms produced similar model fits for SST and SST CV which suggests that these interaction plots are valid for the SPlus algorithm.

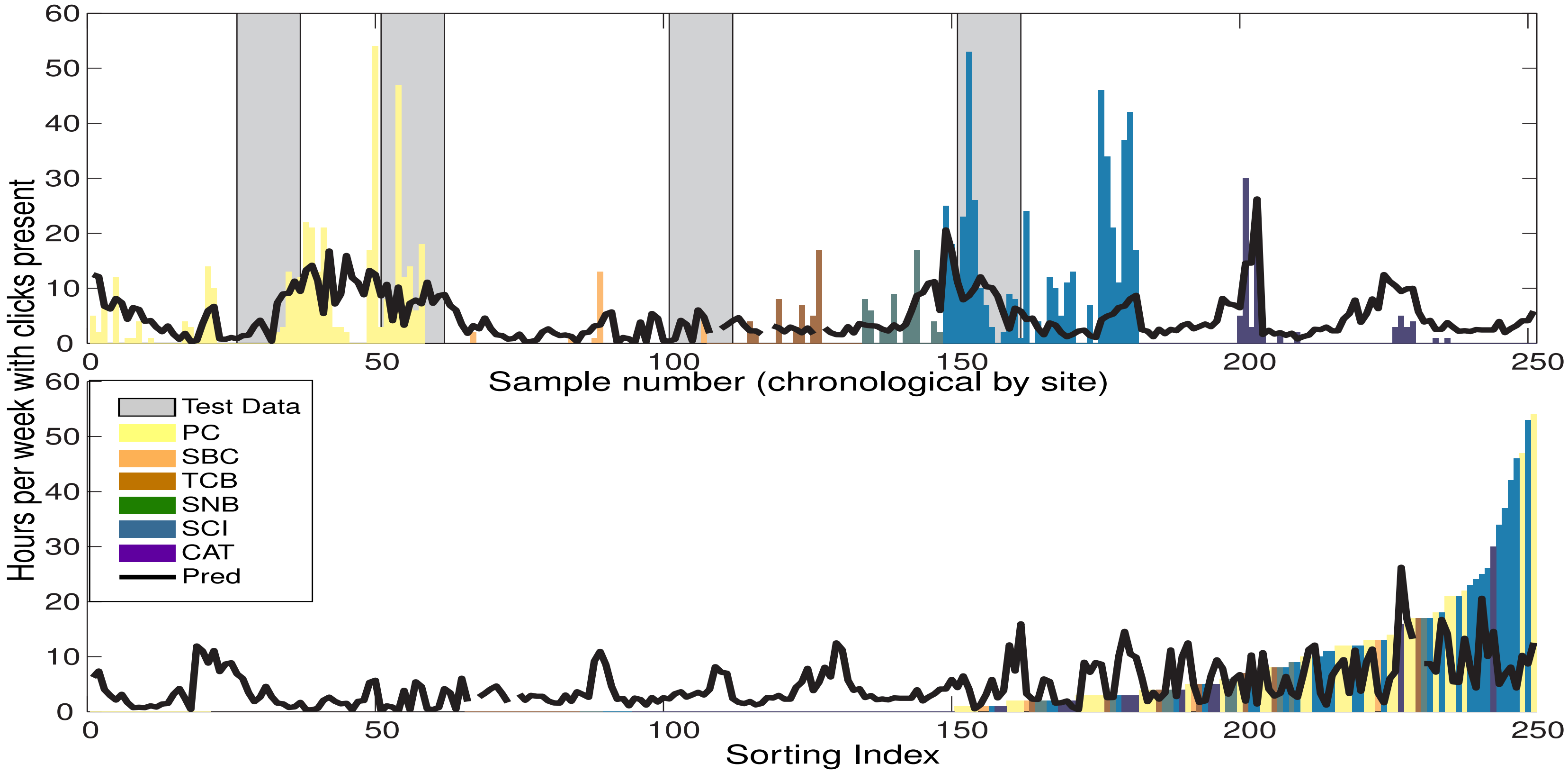

Figure 5.10. Pacific white-sided dolphin type A observed and predicted values from the best model. Observed values are plotted by sample number chronologically by site (A) and sorted from low to high values of hours per week (B) and are represented by colored bars where the color indicates the site. PC = Point Conception; SBC = Santa Barbara Channel; TCB = Tanner/Cortez Banks; SNB = San Nicholas Basin; SCI = San Clemente Island ; CAT = Santa Catalina Island. Black line represents predicted values from the model. Breaks in the prediction line indicate the presence of missing environmental data. These samples were not included in models. In the top plot, the data which was removed during model building and used to test predictive power is highlighted by light grey boxes.

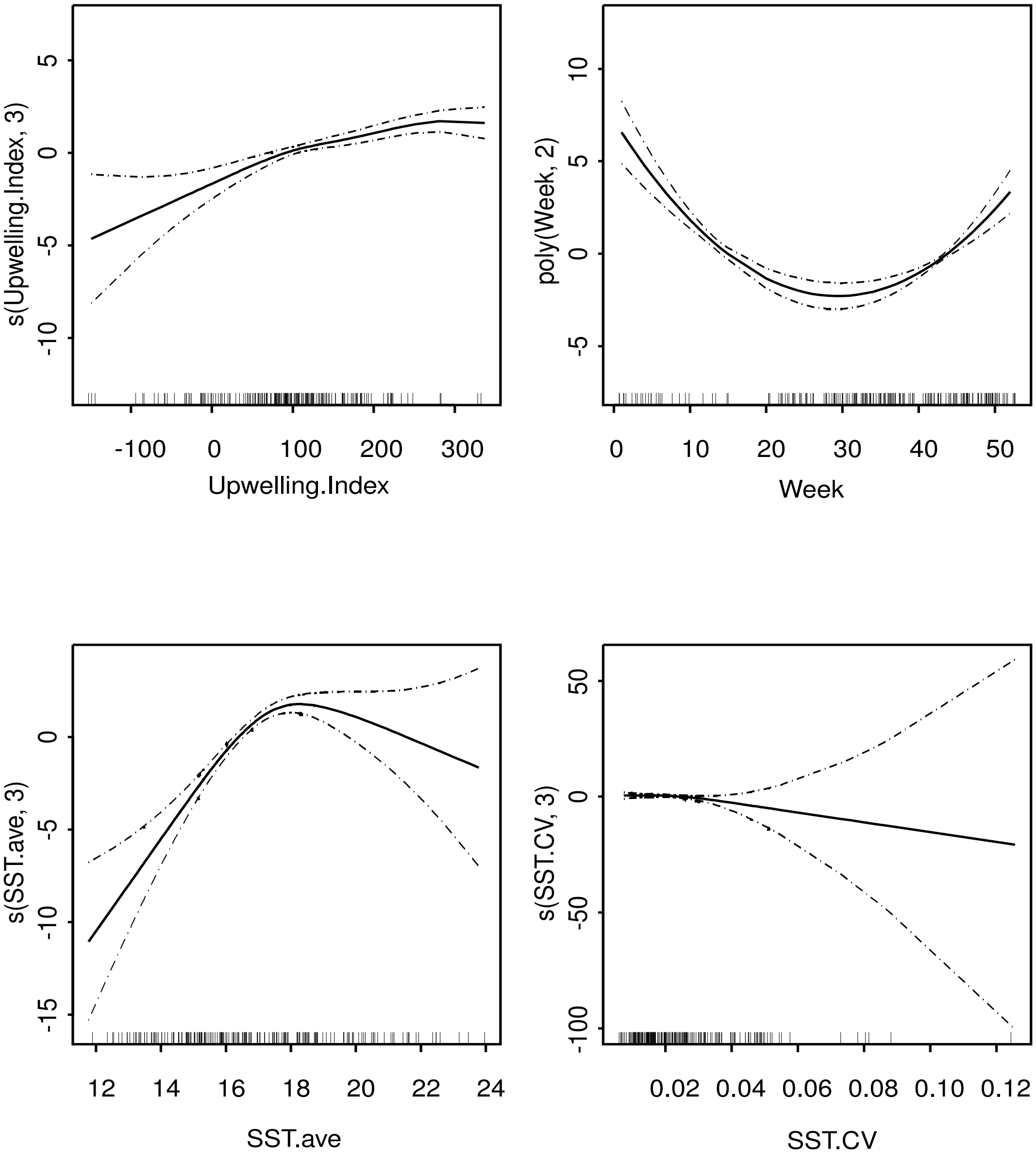

Figure 5.11. Modeled partial fits of oceanographic variables to Pacific white-sided dolphin click type B hours detected per week. Solid line represents the best fit while dotted lines represent the confidence intervals. Plots are plotted on the same scale so that the strength of the slope indicates the importance of the variable in the model, with the exception of SST CV which had large confidence intervals. The y-axis label indicates the fit type (partial = linear, poly(.) = polynomial, s(.) = spline) and the degrees of freedom. Rugplot at the bottom indicates location of sample values.

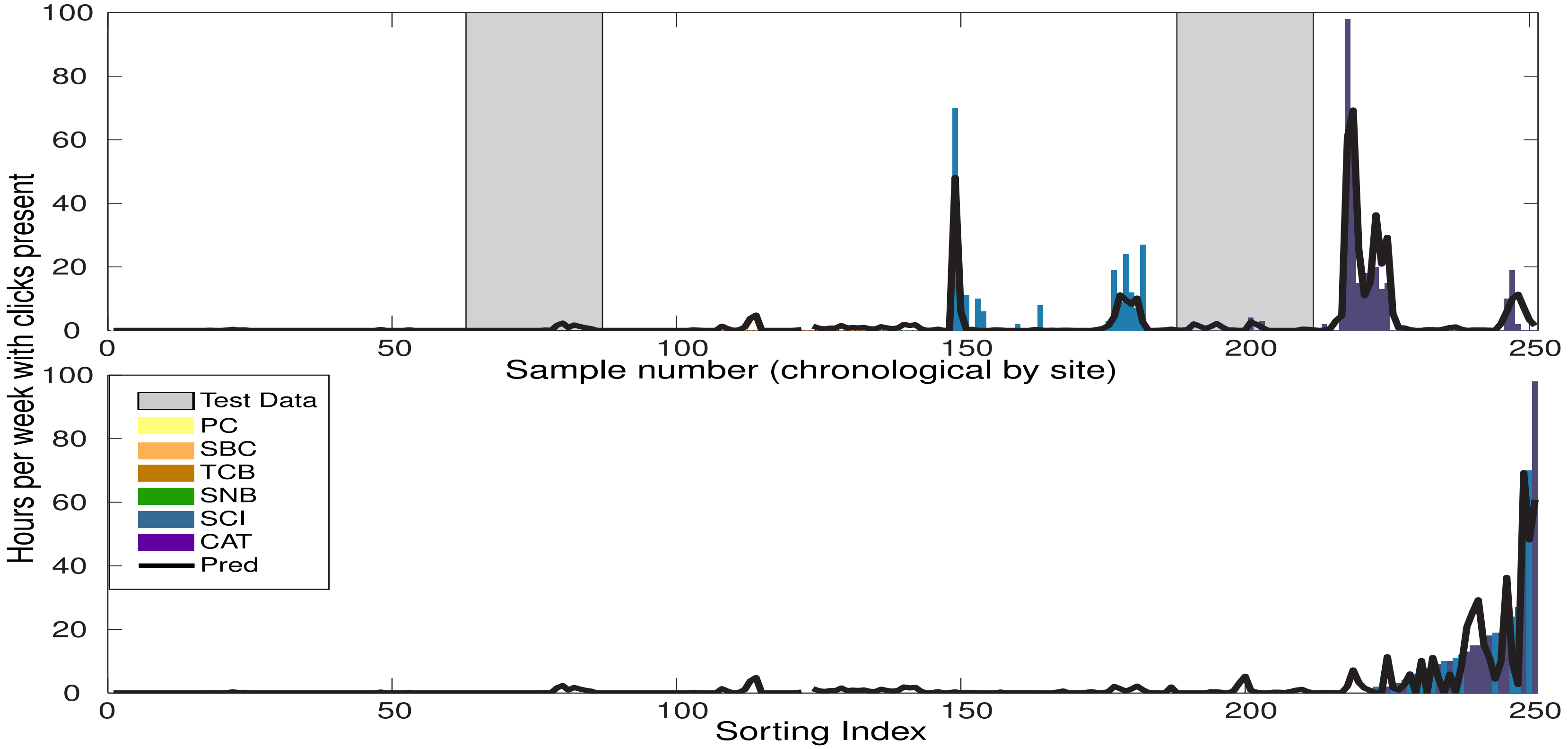

Figure 5.12. Pacific white-sided dolphin type B observed and predicted values from the best model. Observed values are plotted by sample number chronologically by site (A) and sorted from low to high values of hours per week (B) and are represented by colored bars where the color indicates the site. PC = Point Conception; SBC = Santa Barbara Channel; TCB = Tanner/Cortez Banks; SNB = San Nicholas Basin; SCI = San Clemente Island ; CAT = Santa Catalina Island. Black line represents predicted values from the model. Breaks in the prediction line indicate the presence of missing environmental data. These samples were not included in models. In the top plot, the data which was removed during model building and used to test predictive power is highlighted by light grey boxes.

TABLES

Table 5.1. Results of sub-sampling of continuous HARP data to develop detection probabilities and their inverse correction factors for three duty-cycles. Correction factors are included as an offset in models for each click type. The duration (min) between starts of 5 min recordings are indicated by the column dc off. The remaining columns indicate percent detections and correction factors for the three click types: Gg = *Grampus griseus*; Lo B = *Lagenorhynchus obliquidens* type B; and Lo A = *L. obliquidens* type A.

Percent detections

dc off	Gg	Lo B	Lo A
5	0.97	0.97	0.94
10	0.93	0.93	0.89
15	0.88	0.88	0.83

Correction factor

dc off	Gg	Lo B	Lo A
5	1.03	1.03	1.06
10	1.08	1.08	1.13
15	1.13	1.13	1.20

Table 5.2. Summary of available data and zero-lag oceanographic variables for the entire recording dataset (Total) and for subsets that include the presence of each of the three click types: Gg = *Grampus griseus*; Lo A = *Lagenorhynchus obliquidens* type A; and Lo B = *L. obliquidens* type B.

		Total	Gg	Lo A	Lo B
Hours Per Week					
	Min.:	145	0	0	0
	Max.:	168	84	54	98
	Mean:	165	12.4	4.4	2.1
	Std Dev.	5.5	16.9	9.1	9.3
	Median	168	5	0	0
	N:	251	171	101	30
Upwelling					
	Min	-149	-149	-87	-51
	Max	337	337	282	337
	Mean	90.3	83.5	97.7	128.5
	Std Dev.	77.2	79.5	64.7	82.4
	Median	95	87	98	108
SST.ave					
	Min	11.5	11.5	11.5	14.0
	Max	23.8	23.8	23.1	20.4
	Mean	16.5	16.7	15.9	16.5
	Std Dev.	2.6	2.7	2.3	1.6
	Median	16.3	16.2	15.6	16.7
SST.CV					
	Min	0.007	0.008	0.009	0.010
	Max	0.126	0.126	0.126	0.029
	Mean	0.027	0.027	0.028	0.017
	Std Dev.	0.016	0.017	0.016	0.006
	Median	0.022	0.022	0.026	0.016
Chl.resid					
	Min	-9.0	-9.0	-5.5	-1.3
	Max	-0.3	-0.3	-0.3	-0.3
	Mean	-1.5	-1.4	-1.2	-0.6
	Std Dev.	1.4	1.4	1.0	0.2
	Median	-0.9	-0.8	-0.9	-0.6
Chl.CV					
	Min	0.06	0.06	0.06	0.11
	Max	2.13	2.13	1.50	0.77
	Mean	0.34	0.34	0.35	0.26
	Std Dev.	0.26	0.25	0.23	0.14
	Median	0.27	0.27	0.30	0.21

Table 5.3. Terms included in best models. The best models are presented for each of the five cross-validation datasets of each click type. Best AIC values are presented from the training data and ASPE values are presented from the test data. Lag times indicate which week model was chosen as the best for each cross-validation model. Environmental variables which were included in the model are indicated and represent the best fit that was chosen followed by the selected degrees of freedom (L = linear, p# = polynomial, s# = spline). The inclusion of the interaction term of region (north or south) by week is indicated by R*. No interaction term was included for L. obliquidens type B as they were only detected at the southern sites. Terms that were not included in the best models are indicated by a dash. The percent of models that included each environmental variable is presented to indicate the importance of that variable across different cross-validation datasets. Variables included in more models are likely to be important indicators of dolphin occurrence.

	AIC	ASPE	Lag	Upwelling	Moon Duration	Chl residual	Chl CV	SST mean	SST CV	Region:Week
Grampus griseus										
Group 1	2563.71	190.14	4	-	-	-	-	s3	L	-
Group 2	**2470.91**	**169.37**	**4**	**-**	**-**	**s3**	**L**	**s3**	**L**	**-**
Group 3	2464.85	392.98	4	-	s2	-	-	s3	-	R*p3
Group 4	2776.46	414.54	2	-	-	s3	s2	L	s2	R*W
Group 5	2706.06	208.87	2	-	-	L	-	s2	s2	-
% Models including term				0	20	60	40	100	80	40
Lagenorhynchus obliquidens A										
Group 1	1682.13	186.98	2	s3	-	-	-	-	s3	R*p2
Group 2	1743.90	130.37	4	-	-	L	L	L	s3	R*p3
Group 3	2004.64	51.56	16	s3	-	-	-	-	-	R*p2
Group 4	**2109.05**	**18.77**	**4**	**-**	**-**	**-**	**-**	**L**	**s3**	**R*p2**
Group 5	1285.12	174.32	16	-	s3	L	-	L	-	R*p2
% Models including term				40	20	40	20	60	60	100
Lagenorhynchus obliquidens B										
Group 1	367.09	500.31	8	s3	-	-	-	-	s3	p2
Group 2	**563.13**	**5.39**	**0**	**s3**	**-**	**-**	**-**	**s3**	**s3**	**p2**
Group 3	695.75	5.65	1	s3	s2	-	-	s3	s3	p2
Group 4	529.54	111.00	16	-	L	L	-	L	s3	L
Group 5	507.25	30.57	16	-	L	s3	-	L	s3	p2
% Models including term				60	60	40	0	80	100	100

Table 5.4. Values of coefficients from the best predictive models fit to the entire dataset. Dispersion parameter was estimated for a quasi-Poisson distribution of the response variable. Environmental variables which were included in the model are indicated and represent the best fit that was chosen followed by the selected degrees of freedom (l(.) = linear, p(.) = polynomial, s(.) = spline). The inclusion of the interaction term of region (north or south) with week is indicated by region:week. No interaction term was included for L. obliquidens type B models as they were only detected at the southern sites. Only terms that were included in the model are presented.

	Terms	Coefficient
Grampus griseus		
	Dispersion	13.70
	Intercept	-5.73
	s(Chl.resid.4wkLag,3)	0.18
	l(Chl.CV.4wkLag)	0.52
	s(SST.ave.4wkLag,3)	0.22
	l(SST.CV.4wkLag)	-25.30
Lagenorhynchus obliquidens Type A		
	Dispersion	13.14
	Intercept	-1.77
	l(SST.ave.4wkLag)	-0.10
	s(SST.CV.4wkLag,3)	-11.59
	South poly(Week,2) 1	-3.79
	South poly(Week,2) 2	7.98
	North poly(Week,2) 1	3.62
	North poly(Week,2) 2	-15.58
Lagenorhynchus obliquidens Type B		
	Dispersion	9.20
	Intercept	-21.67
	s(Upwelling.Index,3)	0.01
	poly(Week,2) 1	-6.87
	poly(Week,2) 2	30.53
	s(SST.ave,3)	0.95
	s(SST.CV,3)	-26.18

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