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Cetaceans in the Southern California Bight : behavioral, acoustical and spatio-temporal modeling

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Cetaceans in the Southern California Bight: Behavioral, Acoustical and Spatio-temporal Modeling

A dissertation submitted in partial satisfaction of the
requirements for the degree Doctor of Philosophy
in
Oceanography
by
E. Elizabeth Henderson

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2010

The Dissertation of E. Elizabeth Henderson is approved, and it is acceptable in quality and form for publication on microfilm and electronically:

Chair

University of California, San Diego

2010

DEDICATION

This dissertation is dedicated to my father, for inspiring me to be a scientist and for always knowing I could do it, and to my husband, for being my biggest fan and best friend for the last decade, and for standing by me and being an amazing support system through two of these. No more, I promise.

I am caught by the undertow
Within the heart of the sea
In all of the oceans beauty
It was only by your love
That I ever felt free
Force is not in need
To drag me any deeper
And in my hand I hold my heart
As I question to take it off my sleeve
Heaven has no greater beauty
Than this twisted sea

- Joseph Stotz

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Chapter 3, in full, is currently in preparation for submission. Henderson, E. E., Hildebrand, J.A., and Smith, M.H. Classification of Behavior Using Vocalizations of Pacific White-Sided Dolphins (*Lagenorhynchus obliquidens*). The dissertation author was the primary investigator and author of this material.

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PUBLICATIONS

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ABSTRACT OF THE DISSERTATION

Cetaceans in the Southern California Bight: Behavioral, Acoustical and Spatio-temporal Modeling

by

E. Elizabeth Henderson
Doctor of Philosophy in Oceanography
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Professor John A. Hildebrand, Chair

This dissertation examines the behavior, occurrence patterns, and distribution of small cetaceans in the Southern California Bight (SCB) across a variety of temporal and spatial scales in order to elucidate how they interact with their environment. I begin by correlating the surface behavior and vocalizations of two exemplar species, the common dolphin (*Delphinus* sp.) and the Pacific white-sided dolphin (*Lagenorhynchus obliquidens*). Surface behaviors of both species were classified based on their rates and types of vocalizations using random forest decision trees. Common dolphins were shown to travel predominantly throughout the day, with an off-shore movement at night and and in-shore movement in the morning, and are likely feeding at night on the scattering layer. Vocalizations were most abundant and complex in fast traveling, spread-out groups, and were lowest during foraging. The two Pacific white-sided dolphin "click type" groups demonstrated distinctly different behavioral patterns and vocalizations, with one foraging during the day and the other likely foraging at night. I go on to examine the occurrence patterns of all marine mammals encountered in the SCB in 2006, 2007 and 2008 from the R/P FLIP in relation to the local oceanography and biology. 2006 had warm ocean temperatures and the most encounters of all marine mammal species, while 2007 was the coolest, most stratified year with the highest chlorophyll levels, and had high baleen whale encounter rates but low delphinid encounter rates. 2008 was the warmest year with a deep mixed layer and deep chlorophyll maximum, and saw a moderate level of common dolphins, Pacific white-sided dolphins, and some baleen whales, but high numbers of California sea lions (*Zalophus californicus*). Also in 2008, net tows and sonar scans were added to examine the zooplankton and fish biomass around FLIP. Non-eucalanid copepods and siphonophores dominated the zooplankton biomass, while anchovy (*Engraulis mordax*) and jack mackerel (*Trachurus symetricus*) were presumed to dominate the fish biomass. Finally, I explore the distributions of eight species of small cetaceans throughout the SCB using a combined 30-year dataset from CalCOFI and SWFSC cruises. I model the distribution of each species against PDO, ENSO, and seasonal sea-surface temperature indices as well as depth metrics. All eight species demonstrated changes in their distributions relative to the three temperature shifts, offering insight into possible responses to future climate change shifts and ocean warming.

CHAPTER 1

Introduction

The distribution and abundance of marine mammals is often attributed to the movement patterns of their prey, and oceanographic proxies such as sea surface temperature, bathymetry, chlorophyll concentrations and thermocline depth have been used to estimate optimal marine mammal habitat (Au and Perryman 1985; Smith *et al.* 1986; Selzer and Payne 1988; Ballance *et al.* 2006). In addition, those oceanographic features have been incorporated into predictive models to approximate abundance patterns over time and space, and to understand the ecological niches that marine mammals fill (Forney 2000; Hastie *et al.* 2005; Ferguson *et al.* 2006; Redfern *et al.* 2006). For example, in the eastern tropical Pacific (ETP), the Costa Rica Dome is a region with a strong and shallow thermocline, increased upwelling associated with cyclonic circulation, and high zooplankton biomass. Both blue whales (*Balaenoptera musculus*) and short-beaked common dolphins (*Delphinus delphis*) have higher abundances in this region than in surrounding waters (Au and Perryman 1985; Reilly and Thayer 1990; Ballance *et al.* 2006). In fact, common and striped (*Stenella coeruleoalba*) dolphins were strongly associated with "upwelling-modified waters" throughout the ETP, including equatorial and coastal waters as well as the Costa Rica Dome; these areas were characterized by strong upwelling, a weak thermocline, and seasonal temperature fluctuations (Au and Perryman 1985). In contrast, spotted (*Stenella attenuate*) and spinner (*S. longirostris*) dolphins were associated with “tropical waters”, characterized by a strong thermocline and warm SST’s (Au and Perryman 1985). In the SCB, models predicting the distribution of short-beaked common dolphins included salinity, SST and depth, with an increase in abundance associated with warmer SST’s and an inshore/offshore presence that varied with year, while Dall’s porpoise (*Phocoenoides dalli*) distributions were associated with cooler SST’s, and were always located inshore (Forney 2000). These results demonstrate that even a single habitat can be shared by dissimilar species, and similar species can occupy different ecological niches; that those niches can vary across habitats for a single species; and that oceanographic parameters can vary across seasons or years, and marine mammal distributions can change as a result. Understanding those ecological niches, and how they change with regime shifts, is important as ocean temperatures rise with global climate change and important marine mammal habitats may shift or contract (Würsig *et al.* 2002; Learmonth *et al.* 2006; MacLeod 2009). While open water or coastally migrating species will not be as strongly impacted as those with limited ranges, they are still likely to be affected, either indirectly by shifts in the distribution or abundance of their prey, or directly by a change in the conditions that a species can physiologically tolerate (Learmonth *et al.* 2006; Simmonds and Eliott 2009).

While predictive models of marine mammal distribution created from multi-year datasets are an excellent method of assessing long term trends in distribution and movement patterns, the best approach to understanding a species’ ecological niche is to examine their behavior in relation to their habitat. Many examples exist of behavioral studies for a variety of species, particularly bottlenose dolphins (Shane *et al.* 1986; Wells 1991; Hanson and Defran 1993; Henderson and Würsig 2007), killer whales (*Orcinus orca*) (Hoelzel 1993; Nichol and Shackleton 1996; Simon *et al.* 2007b), spinner dolphins (Norris *et al.* 1985; Benoit-Bird and Au 2001), humpback whales (*Megoptera novaeangliae*) (Baker and Herman 1984; Silber 1986; Clapham 1996; Craig and Herman 2000) and sperm whales (*Physeter macrocephalus*) (Whitehead and Weilgart 2000; Christal and Whitehead 2001; Davis *et al.* 2007). These in-depth behavioral studies have led to great insights into the habitat use patterns, foraging behavior and social structure of these species. However, behavioral studies are constrained because cetaceans spend most of their time underwater, the cost of spending enough time at sea to gather good behavioral data, or the opportunistic presence of some species close enough to land to conduct shore-based observations. Passive acoustic monitoring of cetaceans using autonomous instruments to record vocalizations can be conducted for long periods of time at relatively low cost (Wiggins 2003; Mellinger et al. 2007; Wiggins and Hildebrand 2007), but thus far has been largely limited to confirming the presence or absence of animals and some species identification (Oswald et al. 2003; Soldevilla et al. 2008; Baumann-Pickering 2009). Additional work has been conducted to combine visual and acoustic sampling in wild populations of a few delphinoid species (Ford 1989; Weilgart and Whitehead 1990; Dawson 1991b; Herzing 1996; Van Parijs and Corkeron 2001b), but recording and analysis techniques have varied and results differ across species, making inferences for other species difficult. If behavior could be correlated with vocalizations, then autonomous recording packages could be deployed across a broad spatial range and subsequent acoustic data could be analyzed to assess marine mammal behavior and habitat use. This has been successfully demonstrated with blue whales, which have been shown to produce distinct feeding and social calls; long-term recordings have demonstrated seasonal and multi-year changes in blue whale foraging behavior (Oleson 2005; Oleson *et al.* 2007a), but has not been attempted with delphinids.

BACKGROUND

Southern California Bight

The Southern California Bight (SCB) is an ideal region to examine the behavioral ecology of marine mammals, as it a region of complex bathymetry, oceanography and biology, and is part of the range of a broad array of marine mammal species. The SCB is defined as the region south of Point Conception, where the California land mass curves eastward, north of approximately 30° N, and including the Channel Islands, and is the southern part of the California Current System (CCS). The dominant current is the equatorward flowing California Current, a cool, low saline, subarctic water current, with its strength mediated by the Aleutian Low and North Pacific High pressure systems (Checkley Jr. and Barth 2009). There are also two poleward flowing currents; the California Countercurrent, also called the Inshore Countercurrent or the Davidson Current north of Point Conception (Strub and James 2000), and the California Undercurrent, both of which bring warm, saline Equatorial waters north (Reid *et al.* 1958; Hickey 1993). The California Current is strongest and closest to shore in spring, when there is predominantly equatorward flow in the SCB. In contrast, in summer and fall the California Countercurrent dominates, bringing warmer water further north and west into the SCB and pushing the California Current further offshore (Hickey 1993; Hickey *et al.* 2003; Caldeira *et al.* 2005). The meeting of these currents forms strong mesoscale eddies, which have been shown to play an important role in zooplankton and fish larvae retention (Logerwell *et al.* 2001; Logerwell and Smith 2001), creating hotspots for predators. Eddies and other mesoscale features are strongest in summer and fall (Strub and James 2000; Checkley Jr. and Barth 2009). Finally, productivity in the SCB is high due to equatorward winds in the summer that force an offshore flow and create upwelling of cold, nutrient-rich water near the coast (Checkley Jr. and Barth 2009). The complex bathymetry of the region, with deep submarine canyons, sea mounts, and a steep slope along the 2000 m isobath, also creates areas of entrapment for phyto- and zooplankton that attract fish and top predators like marine mammals (Hui 1979; Selzer and Payne 1988; Baumgartner 1997).

In addition to seasonal variations in temperature, upwelling and productivity, the SCB experiences interannual variability through temperature fluctuations such as the El Niño Southern Oscillation (ENSO), the North Pacific Gyre Oscillation (NPGO), and the Pacific Decadal Oscillation (PDO) (Mantua and Hare 2002; Wang and Fiedler 2006; Di Lorenzo *et al.* 2008). Strong El Niño years bring higher sea surface temperatures (SST) and increased downwelling to the SCB region (Norton *et al.* 1985) resulting in a depression of the thermocline, decreases in nutrients, a subsequent reduction in zooplankton abundance and an increase in zooplankton, fish, and marine mammals normally found further south (Sette and Isaacs 1960; McGowan 1985; Smith 1995; Defran *et al.* 1999). The PDO pattern is similar to ENSO, but longer-lived, occurring over decades rather than years (Mantua and Hare 2002). During the warm, positive PDO phase, the California Current is weakened and the Countercurrent is strengthened, bringing warmer waters further north and west into and beyond the SCB and creating anomalously warm SST's along the California coast. In contrast, during the cool, negative PDO phase the California Current is stronger, bringing cool water further south and east into the SCB (Mantua and Hare 2002).

The high productivity of the region has led to diversity and species richness in zooplankton, fish and squid (Star and Mullin 1981; Cross and Allen 1993; Checkley Jr. and Barth 2009), as well as marine mammals, including at least ten species of small cetacean, seven mysticete species, several beaked whale species, and four pinniped species. The small cetaceans include cool temperate water species, such as Pacific white-sided dolphins (*Lagenorhynchus obliquidens*), northern right whale dolphins (*Lissodelphis borealis*), and Dall's porpoise (*Phocoenoides dalli*), warm temperate and tropical species, including short-beaked common dolphins (*Delphinus delphis*), long-beaked common dolphins (D. *capensis*), striped dolphins (*Stenella coeruleoalba*), and Risso's dolphins (*Grampus griseus*), and the cosmopolitan bottlenose dolphin (*Tursiops truncatus*), found in oceans and bays worldwide.

Dolphin vocalizations

Dolphins produce a variety of vocalizations (Watkins and Wartzok 1985), broadly characterized as clicks, burst pulses, and whistles (Au 1993; Richardson *et al.* 1995a), although these calls fall more along a gradient than in distinct categories (Fristrup and Watkins 1994; Murray *et al.* 1998). Clicks are short duration, broadband pulsed calls used in echolocation and navigation, and can range from less than 20 kHz to over 100 kHz in frequency (Au 1993; Au 2004; Li *et al.* 2005; Verfuss *et al.* 2005; Soldevilla *et al.* 2008). The inter-click interval (ICI) between clicks is considered the two-way transit time such that the returning echo from one click is received before the next click is produced (Au 1993). When this interval becomes much shorter (e.g. less than 5 ms), individual clicks within a click train become difficult to perceive, and the call is classified as a terminal buzz or burst pulse (Murray *et al.* 1998; Johnson *et al.* 2006), depending on the context. Terminal buzzes have been recorded for foraging beaked whales, and occur at the end of an echolocation click train, as the whale approaches their target (Madsen *et al.* 2005; Johnson *et al.* 2006; Johnson *et al.* 2008). Burst pulse calls are a series of rapidly produced clicks perceived as tonal sounds and occur both in echolocation and communication (Watkins 1964; Dawson 1991a; Richardson *et al.* 1995a; Lammers *et al.* 2003). Whistles are frequency-modulated, long duration tonal calls, typically produced between 5 kHz and 20 kHz, used for communication and often have harmonic structure (Richardson *et al.* 1995a). Harmonics may be a result of the intensity of the call and could be received only when the calls occur on-axis (Evans *et al.* 1964; Au 1993); however they likely also impart spacing or other information to other group members (Lammers and Au 2003) and could be deliberately produced. Not all species produce whistles, including porpoises and species of the *Cephalorhynchus* genus (Herman and Tavolga 1980); there is also debate whether or not Pacific white-sided or northern right-whale dolphins produce whistles (Caldwell and Caldwell 1971; Whitten and Thomas 2001; Rankin *et al.* 2007). In species without whistles, burst pulse calls may play an even greater role in communication (e.g. Rankin *et al.* 2007).

Focal Species

Two of the most frequently observed species in the SCB are common dolphins and Pacific white-sided dolphins. These species provide an interesting contrast, as Pacific white-sided dolphins are a cool temperate water species predominantly distributed north of 23°N along the California coast (Walker *et al.* 1986; Brownell *et al.* 1999), while common dolphins are a warm temperate and tropical species, distributed south of 36°N off California (Evans 1982; Perrin 2002). The majority of their overlap occurs in the SCB, but their use of this shared habitat is markedly different. Common dolphins are found in the region year-round, but short-beaked common dolphins demonstrate a seasonal inshore/offshore movement (Dohl *et al.* 1986), expanding their range and moving offshore in warm summer months, and restricting their range to the eastern coastal portion associated with the California Countercurrent. Long-beaked common dolphins have a strong inshore distribution, occurring within approximately 150 km of the coast (Heyning and Perrin 1994). Pacific white-sided dolphins are associated with the colder California Current, and are generally observed in the SCB from November through April when the California

Current is at its strongest and the waters of the SCB are cooler (Leatherwood *et al.* 1984). While both species have been shown to feed on both epipelagic schooling fish and mesopelagic fish and squid (Stroud *et al.* 1981; Walker and Jones 1993; Heise 1997; Ohizumi *et al.* 1998; Osnes-Erie 1999), prey preferences differ throughout their range. In the SCB, Pacific white-sided dolphins primarily consume epipelagic schooling fish and squid, including northern anchovy (*Engraulis mordax*), Pacific hake (*Merluccius productus*), Pacific saury (*Cololabis saira*), and market squid (*Loligo opalescens*) (Brownell *et al.* 1999), while short-beaked common dolphins seem to feed primarily on myctophids and various squid species (e.g. *Abraliopsis felis*), and long-beaked common dolphins seem to prefer Pacific hake and market squid (Osnes-Erie 1999).

Limited behavioral or acoustic work has been conducted on common dolphins or Pacific white-sided dolphins. Common dolphin whistles have been well characterized (Moore and Ridgway 1995; Ansmann *et al.* 2007), and attempts have been made to classify clicks and whistles to species (Oswald *et al.* 2003; Roch *et al.* 2007). Although the distribution and abundance of common dolphins is well understood in the SCB (Dohl *et al.* 1986; Forney and Barlow 1998; Barlow and Forney 2007), there has been little effort to study their behavior, and work that has been done in other regions has been shown to be habitat-specific (e.g. Neumann 2001a; MacLeod *et al.* 2008; Stockin *et al.* 2009). For example, foraging behavior in the Bay of Plenty, a deep bay adjacent to the open ocean, occurred in 17% of observations (Neumann and Orams 2003), while in the nearby Hauraki Gulf, a semi-enclosed shallow gulf, foraging occurred in 61.8% of observations (Burgess 2006). Recent work on Pacific-white sided dolphin clicks has shown distinct peak-and-notch patterns that are species-specific and also identified two distinct click types based on differences in the peak-and-notch structure (Soldevilla *et al.* 2008) that may correlate with the two populations identified through genetic and morphological evidence (Walker et al. 1986; Lux et al. 1997). In addition, Soldevilla *et al.* (2010) showed that the diel pattern of the two click types were different, with "Type A" clicks recorded throughout the SCB and predominantly at night, while "Type B" clicks were only recorded at southern and inshore locations, and largely occurred during the day. No behavioral work has been conducted on free-ranging Pacific white-sided dolphin populations.

Dissertation Outline

The goals of this study are to examine the distribution patterns and identify the ecological niches of marine mammals of the SCB using both large-scale habitat modeling and behavioral and acoustic analysis. By assessing these trends across varying temporal and spatial scales, we achieve a better understanding of how species partition resources and respond to changes in their habitat, which will help inform management decisions in terms of anthropogenic impacts and global climate change.

My first goal was to correlate the surface behavior and vocalizations of the two exemplar taxa of delphinid in the SCB, common dolphins and Pacific white-sided dolphins. Through those correlations I hoped to identify the ecological niches of each species, and to determine the level of overlap or resource partitioning between the two.

Behavioral focal follows were conducted on groups from both species with concurrent acoustic recordings of their vocalizations. Time budgets of behavior were created, and classification models were constructed using call features to classify and predict surface behavioral patterns. Chapter two, entitled "The Behavioral Context of Common Dolphin (*Delphinus* sp.) Vocalizations", describes the results for common dolphins, and includes an analysis of the relationship between surface behavior, group size, group spacing, and rates of vocalizations. The dominant behavior recorded for common dolphins was traveling, as groups traveled offshore in the afternoon and onshore in the morning. The highest number of clicks, pulsed calls, and complex whistles were produced during fast travel, while during foraging there were few pulsed calls and whistles produced, and the whistles were simple with narrow bandwidths and few harmonics. In addition, while little daytime foraging was observed, night-time vocalization patterns strongly suggest that common dolphins were foraging nocturnally in offshore waters.

Chapter three, "Classification of Behavior Using Vocalizations of Pacific White-Sided Dolphins", examines the behavioral patterns and vocalizations of the two populations of Pacific white-sided dolphins, and demonstrates the strong differences between them. "Type A" click groups were observed slow traveling and milling during the day, while "Type B" click groups spent much of their time foraging and traveling. In addition, call patterns varied between the two groups, with more clicking during milling and foraging for "Type A" click groups and more clicking during mixed forage and slow travel for "Type B" click groups. Finally, call features differed significantly across behavioral categories, and classification models using random forest decision trees showed strong potential for using vocalizations to predict behavior.

My second goal was to examine patterns of marine mammal occurrence and distribution related to oceanographic features across different temporal and spatial scales. Chapter four, “The Role of Marine Mammals as Top Predators: A Multi-Step Analysis of Marine Mammal Occurrence Patterns in the Southern California Bight”, examines the occurrence patterns of all marine mammals in the SCB across three years, using a point-sampling method. The Floating Instrument Platform (R/P FLIP) was deployed off San Clemente Island in the fall of three consecutive years. All marine mammals were recorded, along with multiple oceanographic features. Marine mammal sightings were then correlated with biotic and abiotic parameters, including SST, thermocline depth, chlorophyll concentrations, zooplankton abundances and estimated fish biomass, to look for occurrence patterns across time. 2006 was the most speciose year, with multiple dolphin and whale species present in high numbers, along with warm SST’s and a possible front between water masses located nearby. Fin whale (*Balaenoptera physalus*) and northern elephant seal (*Mirounga angustirostris*) sightings peaked in 2007, a cooler year with more stratification and higher chlorophyll concentrations. 2008 was also warm, with a deep thermocline and deep chlorophyll maximum depth, but had the fewest sightings of dolphins and whales, although high numbers of California sea lions (*Zalophus californianus*) were recorded. Zooplankton abundances and fish biomass were also estimated in 2008, with non-eucalanoid copepods and siphonophores dominating the zooplankton, and northern anchovy (*Engraulis mordax*) and jack mackerel (*Trachurus symetricus*) presumed to dominate the fish biomass aggregated around FLIP.

Finally, in chapter five, "Effects of Sea Surface Temperature Variation on the Distribution of Small Cetaceans in the Southern California Bight: Implications for Climate Change", I modeled the distribution patterns of eight dolphin species in the SCB across temperature fluctuations on three different temporal scales using a 30-year dataset of observations. Changes in distribution were examined across seasonal temperature fluctuations on an annual scale, El Niño/Southern Oscillations (ENSO) on a 2-7 year time scale, and Pacific Decadal Oscillations (PDO) on a decadal time scale. Model results varied among species, but each included at least one SST variable and one depth variable, indicating changes in distributions correlated with SST fluctuations. Implications of the results are considered in light of changing ocean temperatures and the potential impact on the species investigated here.

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 two, entitled "The Behavioral Context of Common Dolphin (*Delphinus* sp.) Vocalizations", has been submitted to Marine Mammal Science and is presented as part of this dissertation with acknowledgement to the co-authors in the study.

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CHAPTER 2

The Behavioral Context of Common Dolphin (*Delphinus* sp.) Vocalizations

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Abstract

Correlations between surface behavior and concurrent underwater vocalizations were modeled for common dolphins in the Southern California Bight over multiple field seasons. Clicks, pulsed calls, and whistles were examined, with a total of 50 call features identified. Call features were used to classify behavior using random forest decision trees. Common dolphins spent most of their time traveling. The highest number of clicks, pulsed calls, and complex whistles were produced during fast travel. In contrast, during foraging there were few pulsed calls and whistles produced, and the whistles were simple with narrow bandwidths and few harmonics. Behavior and vocalization patterns suggest nocturnal foraging in offshore waters as the primary feeding strategy. Group size and spacing were strongly correlated with behavior and rates of calling, with higher call rates in dispersed traveling groups and lower call rates in loosely aggregated foraging groups. These results demonstrate that surface behavior can be classified using vocalization data.

Introduction

Vocal communication plays a vital role in behavior and social interactions across a broad array of species. An examination of the behavioral context of vocalizations has been conducted for numerous taxa, ranging from crickets (Thorson *et al.* 1982); amphibians (Wells 1977; Krishna and Krishna 2005); and fish (Crawford *et al.* 1986; Bass *et al.* 1997); to birds (Roberts 2003; Mennill and Vehrencamp 2008; Naguib and Janik 2009) and mammals (Belwood and Fullard 1984; Clarke 1990; Crockford and Boesch 2003; Simeonovska-Nikolova and Bogoev 2008; Naguib and Janik 2009). Many of these studies have focused on the behavioral context of specific call types, such as distress or contact calls (Richman 1980; Clarke 1990; Vergne *et al.* 2009), calls that signal aggression (McCowan and Rommeck 2006), or calls that contain information about body size or fecundity (Charlton *et al.* 2009). For marine mammals, there has also been much research identifying the behavioral context of specific calls, particularly for foraging (Janik 2000a; Leighton *et al.* 2004; Simon *et al.* 2006). In addition to examining calls with a specific function, several studies have examined acoustic behavior across broad behavioral states (Taruski 1979; Sjare and Smith 1986; Dawson 1991a; Simon *et al.* 2007b), demonstrating that the types and rates of calls produced vary with behavioral state.

Common dolphins (*Delphinus* sp.) are found throughout the world's oceans, in coastal and inshore warm tropical and temperate waters (Reeves *et al.* 2002). They have been shown to prefer water ranging from approximately 10°C to 28°C (Evans

1982; MacLeod *et al.* 2008) and to migrate seasonally inshore and offshore as temperatures change (Dohl *et al.* 1986; Forney and Barlow 1998; MacLeod *et al.* 2008). In addition, they seem to be sensitive to sea surface temperature changes related to El Niño/Southern Oscillation (ENSO) events, as evidenced by their following warmer water masses and avoiding cooler water (Tershy *et al.* 1991; Neumann 2001b; Benson *et al.* 2002). They are also associated with upwelled, more saline waters with weak thermoclines (Au and Perryman 1985; Reilly 1990). Prey species include epipelagic schooling fish as well as myctophids and squid (Ohizumi *et al.* 1998; Osnes-Erie 1999; Neumann and Orams 2003; Meynier *et al.* 2008), and foraging behavior appears to be dependent upon the region or prey availability (Gallo-Reynoso 1991; Neumann and Orams 2003). Some behavioral work has been conducted to examine diel behavior patterns of common dolphins off New Zealand (Neumann 2001a; Stockin et al. 2009); however behavior, particularly foraging, may be habitat-specific. In addition, some limited work on vocalizations has been conducted, principally on the characterization of common dolphin whistles (Moore and Ridgway 1995; Ansmann *et al.* 2007) and attempts to classify clicks and whistles to species (Oswald *et al.* 2003; Roch *et al.* 2007). However, the present study is the first to examine both behavior and vocalizations of common dolphins, and to attempt to utilize vocal data to classify and predict behavior as a means to better understand habitat use.

Common dolphins produce a number of vocalizations, including whistles, clicks, and burst pulse calls (Moore and Ridgway 1995; Richardson *et al.* 1995b;

Soldevilla *et al.* 2008). Whistles are frequency-modulated, long duration tonal calls used for communication and often have harmonic structure as well (Richardson *et al.* 1995b). Harmonics may be a result of the intensity of the call and may be received only when the calls occur on-axis; however they may also impart spacing or other information to other group members (Lammers and Au 2003) and therefore may be deliberately produced. Clicks are short duration, broadband pulsed calls used in echolocation and navigation, and range from 23 kHz to over 100 kHz (Richardson *et al.* 1995b; Au 2004; Soldevilla *et al.* 2008). Burst pulse calls are a series of rapidly produced clicks perceived as tonal sounds and occur both in echolocation and communication (Richardson *et al.* 1995b). Common dolphins also produce buzzes (Moore and Ridgway 1995) and other non-whistle pulsed sounds, occasionally referred to as barks, yelps or squeals (Caldwell and Caldwell 1968; Ridgway 1983).

The western North Pacific common dolphin population, found off the coast of California, was split from the single species *Delphinus delphis* into two species, *D. delphis and D. capensis*, based on morphological and genetic distinctions (Heyning and Perrin 1994; Rosel *et al.* 1994). However, external features vary across a wide spectrum even within these species (e.g., Farley 1995), and at-sea identifications to the species level are often difficult. Unlike Pacific white-sided dolphins (*Lagenorhynchus obliquidens*), which have been shown to have distinctive clicks that may be population or sub-species specific (Soldevilla *et al.* 2008), common dolphins do not seem to have species-specific calls. Therefore, for purposes of this analysis the genus will be considered as a whole.

The objectives of this study were to (1) create a behavioral time budget for common dolphins from the Southern California Bight, (2) to create a model of surface behavior based on acoustic data, and (3) to utilize that model to classify and predict behavior based on only acoustic data.

Methods

Study Area and Survey Platforms

This research was conducted in the Southern California Bight (SCB) near San Clemente Island, about 60 miles offshore of San Diego (Figure 1). Data were obtained in seven field seasons from August 2006 through November 2008 using two types of research vessel. The primary survey platform was the Scripps Institution of Oceanography R/P FLIP (Floating Instrument Platform), a live-aboard stationary moored platform from which visual and acoustic observations were conducted (Fisher and Spiess 1963). FLIP was deployed northwest of San Clemente Island from October 2 – November 3 in 2006 in 637 m water depth; October 30 – November 29 in 2007 in 840 m water depth; and October 17 – November 14 in 2008 in 347 m water depth (Figure 1, inset).

The secondary research method used small boat-conducted surveys within the Naval Southern California Offshore Range (SCORE). This work was done in conjunction with the Naval Undersea Warfare Center's Marine Mammal Monitoring on Navy Ranges (M3R) program (Jarvis *et al.* 2003; Moretti *et al.* 2004; Falcone *et al.* 2009). The M3R system uses seafloor hydrophones to detect and localize vocalizing marine mammals; small boats with experienced observers were utilized to verify the location and species for M3R acoustic detections. Rigid-hulled inflatable boats (RHIBs, 5.3 m to 5.9 m in length) were used for these surveys. Four week-long surveys were conducted, from August 14-20 in 2006, April 13-22 and October 22-26 in 2007, and August 2-10 in 2008.

Behavioral and Acoustic Sampling

Observers in the crow's nest of FLIP, located 26.5 m above the waterline, monitored the ocean 360° around FLIP using both the naked eye and 7x50 Fujinon binoculars, containing a reticle scale to estimate distance and a magnetic compass to estimate bearing. These observers recorded all marine mammal and vessel sightings throughout daylight hours in Beaufort sea state 5 or less. Dolphin groups that were first identified by crow's nest observers and that approached the face side of FLIP within 1 km were selected for group focal follow observations, which were conducted from the top deck level, 15.24 m above the waterline. Groups were defined as animals in apparent association, moving in the same direction and generally carrying out the same activity, following Shane (1990). Group focal follows were conducted using the instantaneous sampling method (Altmann 1974; Mann 1999), whereby the behavioral states and pertinent activities (e.g. high arch dives, tail slaps) of the majority of the group were recorded every 1 to 3 minutes, or upon the next surfacing if the group was underwater. Behaviors were recorded within each group focal follow at as consistent an interval period as possible (e.g. 1 minute); however that interval varied slightly between groups depending on the surfacing period of the animals, the size of the group, or due to inter-observer differences. In addition, bearing, distance, group size, group spacing, orientation towards FLIP, and direction of travel were also recorded for each behavioral sample. Group spacing considered the overall position of animals relative to each other, defined as less than one body length apart (tight), approximately one body length apart (loose), or greater than one body length apart (dispersed), as well as the formation of the group as a whole (clustered, in a line, or spread out). Focal follow behavioral sampling continued while the group remained on the face side of FLIP and within 1 km.

There were 6 behavioral states recorded: slow, moderate or fast travel, mill, forage, and social/surface active (see Table 1 for behavior descriptions); these could also be recorded simultaneously if the group as a whole was doing more than one behavior at a time, or if portions of the group were doing different behaviors (Shane 1990; Hanson and Defran 1993; Henderson and Würsig 2007). The primary behavior was defined as the ongoing behavior and/or the dominant behavior of the group. For example, if the ongoing behavior of the group was travel and then surface activity commenced while still traveling, the primary activity was considered travel and the secondary behavior surface active. If the dominant behavior was travel and some individuals engaged in brief milling, travel was the primary behavior with mill secondary. However, if a portion of the group broke off and changed behavior or direction of travel permanently, they were then counted as a separate group and the focal follow continued on the original group. However, neither of those daughter groups was included in subsequent acoustic analyses.

Focal follows were also conducted on delphinid groups from the small boats on the SCORE range. Many of the dolphin groups encountered resulted from M3R acoustic detections, and were therefore biased towards larger, more active groups easily sighted from the RHIBs. When groups were sighted, the vessel would attempt to approach the group without disrupting their behavior. Once the initial sighting data, including species, group size, and group spacing, were gathered, instantaneous sampling protocol was implemented every 1 to 3 minutes using methods comparable to those used on FLIP, except without the use of binoculars. After the group appeared acclimated to the presence of the vessel, the boat would maneuver ahead of the group, turn off the engine, and deploy a drop hydrophone. Behavioral sampling would continue as the group passed the boat; once they had passed, the hydrophone was retrieved and the process repeated until several recordings had been obtained or until the group was out of sight. Finally, environmental data (Beaufort sea state, swell height, cloud cover, and visibility) were collected hourly, or when conditions changed.

FLIP hydrophones were deployed at depths ranging from 30 to 50 m and recorded continuously 24 hours a day. Small boat hydrophones were deployed at depths ranging from 20 to 30 m, and were deployed and recovered for each group encounter. Both AQ-1 (Teledyne Benthos, North Falmouth, MA) and HS150 (Sonar

Research and Development Ltd, Beverly, UK) hydrophones were used. These were connected to custom built preamplifiers and bandpass filtered electronic circuit boards designed to flatten ambient noise over all frequencies (Wiggins and Hildebrand 2007). All hydrophones had a 2 kHz high pass filter and were sampled to192 kHz with 24 bits. Analog data received on FLIP hydrophones were digitally converted using a MOTU 896HD firewire audio interface (Mark of the Unicorn, Cambridge, MA) with gain on all channels set to maximize signal input while avoiding clipping. Since potential differences in gain between recordings could bias results, in all cases only data with a high signal-to-noise ratio (at least 6 dB SNR) were used to minimize bias. In the 2006 and 2007 FLIP deployments, the sound analysis and recording software program Ishmael (Mellinger 2001) was used to record the signal to computer hard-drive. In 2008, the data were recorded to computer hard-drive using a program written in MATLAB® (Mathworks, Natick, MA). The analog-to-digital converter used on board the small boats was the two-channel Fostex FR2 field memory recorder (Fostex America, Foster Electric, USA, Inc., Gardena, CA).

Call Selection

To ensure that vocalizations could be attributed to a single group, common dolphin focal follow groups selected for analysis were the only group present both acoustically and visually. In addition, each group was located within 1 km of the vessel so behavior could be consistently observed, and the acoustics team could reliably detect all vocalizations produced. All acoustic data were cut into 30-second intervals based on focal follow time stamps. Each of these 30-second files was tagged with a behavioral category and was associated with supplemental sighting data, including group size, group orientation (towards the vessel), group spacing and sighting distance. Each 30-second file was examined using spectrograms created in a customized MATLAB® program (Wiggins 2003). A 1024-point Fast Fourier Transform (FFT) with a 50% overlapping Hann window was used to transform time series of the data into the frequency domain.

A total of 6 vocalization types were counted using both automated and manual techniques: clicks; click trains; pulsed calls; single whistles; whistles with harmonics; and whistle bouts. Each vocalization type had a suite of 7-9 call features that were calculated, including minimum and maximum frequencies; bandwidth; length; and total duration of each type for each 30-second interval. For whistles, the start and end frequencies, the number of steps or turns and, if applicable, the number of harmonics were counted. This led to a total of 50 call features available for analysis.

Clicks were detected automatically (Roch *et al.* 2007), using bandwidth filters and threshold levels appropriate for each recording session such that the majority of clicks were detected while false positives were minimized. In most cases, this method was sufficient to count all high-quality clicks (e.g., above a 6-7 dB signal-to-noise threshold); however, in some cases there were high numbers of clicks present that could not all be counted due to click envelope length constraints. Therefore the total number of clicks detected should be viewed as a minimum estimate rather than an absolute count. Inter-click interval (ICI), click length, and number of bouts (defined as a sequence of clicks spaced less than 0.4 s apart) were also calculated from automatic detections.

All files were also manually examined for burst pulses, whistles, and click trains. All burst pulse and buzz-type calls were lumped for analysis as pulsed calls (Figure 2d). The start and end frequencies, bandwidth, call length, and total call duration for each 30-second interval were calculated for all pulsed calls. Click trains that were still distinct as clicks, but were obviously produced by a single animal based on their ICI, were also counted, with minimum and maximum frequency, bandwidth, and click train length also recorded. Due to a high degree of variation among whistles, these were broken down into three categories for analysis. The first category was single whistles with no harmonics and with distinct start, end, minimum and maximum frequencies (Figure 2a). The numbers of steps or turns per whistle were also calculated, along with bandwidth, individual whistle length and total duration for each 30-second interval. The second category of whistles included those that were still distinct, but contained harmonics (Figure 2b). As with single whistles, the start, end, minimum and maximum frequencies were recorded, along with bandwidth, whistle length, total whistle duration for each 30-second interval, number of steps or turns, and, finally, the number of harmonics present. The last whistle category was that of overlapped whistles, where the start and end frequencies of individual whistles were no longer distinguishable (Figure 2c). In this case, the start and end times, minimum and maximum frequencies, and bandwidth of each whistle bout were documented, along with the duration of the bout for each 30-second interval.

Analysis

Chi-square analyses were conducted on behavior data to examine differences across time-of-day categories, group size, and group spacing. Acoustic detection results (including median call counts, start, end, minimum and maximum frequencies, bandwidth, call length and durations per 30-second interval) were first resampled with replacement 1000 times in order to increase sample size, as some calls were produced infrequently. Kruskal-Wallis nonparametric tests were then used, followed by Tukey-Kramer multiple comparison tests, to examine whether any of the 50 call features were significantly different for each behavioral category (Kruskal and Wallis 1952; Jaccard *et al.* 1984).

To examine the ability to classify behavior based on vocalizations, random forest decision trees were created using call feature and associated behavioral data (Brieman 2001; Siroky 2008). Random forest models are a series of unpruned classification trees, with 5000 bootstrap samples taken from the original dataset. Two-thirds of the predictor variables were then randomly selected at each node and the best split was chosen among those. Behaviors were then classified based on a majority vote from the 5000 trees. An estimate of the error rate was obtained using the data not used in each bootstrap iteration, termed the “out-of-bag” (OOB) data, as a test dataset.

Classifications based on the OOB data were then aggregated and used to calculate an error rate, called the OOB error estimate (Brieman 2001; Liaw and Wiener 2002). Random forest models were created using the entire dataset to look at rates of correct classification for each behavior. Initially, this was conducted with only the 50 call features, and then group size and spacing data were included to determine their contribution to the model. Next, the Gini variable importance measure was implemented to reduce the number of call features included in the model. This metric is based on a weighted mean of the improvement of individual trees based on the inclusion of each variable as a predictor. Finally, a five-fold cross validation procedure was conducted, with the dataset randomly divided without replacement such that 80% of the data were used for training and 20% were used for testing five times. Since individual 30-second segments were not independent of each other when they came from the same group, the division of data was based on number of groups rather than segments. Thus 30-second files from one group were always included in the training or testing datasets together. Group size and spacing information were excluded from this procedure as they would not be known from acoustic data alone.

Results

A total of 61 common dolphin groups were selected for analysis from 97 days of effort (Table 2), with 670 30-second intervals evaluated. Group size varied from 2 to 1000, with a median size of 100 (mean = 205 ± 9). Focal follow duration ranged from 2 to 70 min, with a mean of 21 minutes.

While multiple behaviors were counted simultaneously, the primary behavior of common dolphins was almost always traveling, with other behaviors (e.g. social/surface activity or milling) counted as secondary. In addition, there were too few instances of travel/mill or travel/surface active to be considered as separate categories. Therefore, a "mixed travel" category was created for observations of travel as the primary behavior when a secondary behavior was also occurring. Additionally, surface active/social behavior always co-occurred with travel, and was never observed as the primary behavior. Therefore no separate social behavior category was used for analysis, and all social behavior was included in the mixed travel category. Ultimately six behavioral categories were utilized: forage, mill, slow travel, moderate travel, fast travel and mixed travel (summarized in Figure 3).

Moderate travel was the dominant behavior (28.0%), with foraging the least frequent (7.5%). When the data were divided into four time-of-day categories (early morning, mid-morning, mid-afternoon and late afternoon), the observed rates of each behavior in each time period were highly significantly different ($X^2_{15} = 9.76$ E-18, p <<< 0.001). The little foraging that was observed largely occurred in the morning, with a peak at mid-morning. Slow travel also peaked at mid-morning and decreased throughout the day, while moderate and fast travel increased throughout the day, indicating an increase in activity and travel speed throughout the day. Finally, milling and mixed travel peaked during the mid-afternoon period (Figure 4), possibly indicating an increase in social behavior after the mid-morning period of foraging.

Group size varied significantly across behavioral categories (X^2_{20} = 2.47 E-47, $p << 0.001$; Figure 5). Fast traveling occurred in larger groups (66% of groups had 101-500 animals) while slow travel mainly occurred in mid-size groups (47.6% of groups had 51-100 animals). Foraging groups were mostly comprised of both smaller and larger groups; 40% of groups had 11-50 animals and 56% of groups had 101-500 animals. Finally, while milling occurred in groups of all sizes, it dominated the smallest size class (≤ 10 animals). Overall, fast travel involved the largest groups (median = 140) and milling involved the smallest groups (median = 70). Group spacing also varied significantly across behavioral categories (X^2_{20} = 1.38 E-19, $p << 0.001$; Figure 6). While traveling groups tended to be spread out, particularly at slower swimming speeds (fast travel = 37.1%; moderate travel = 42.9%; slow travel = 58.5%), the animals appeared to come closer together as travel speed increased, with 30.1% of fast travel groups tightly spaced, compared to 10.7% of moderate travel and only 4.6% of slow travel groups. In contrast, foraging groups were predominately loosely spaced (40.8%); mixed travel groups were most often observed in clusters (32.9%); and milling groups were observed in all formations.

Kruskal-Wallis nonparametric tests and Tukey-Kramer multiple comparison tests indicated that differences across each behavioral category for all 50 call features were significant; for each call feature there was at least one behavior that ranked outside the confidence intervals of the other behaviors. The highest number of clicks and pulsed calls were recorded during fast travel behavior, with median values of 388 clicks and 3 pulsed calls per 30-second interval (mean = 464 ± 35.3 and 5.5 ± 0.6, respectively), whereas the fewest clicks were recorded during moderate travel (median = 203.5, mean = 421 ± 40.7) and slow travel (median = 210, mean = 293 ± 26.4). The fewest pulsed calls were recorded during foraging (median = 0, mean = 1.2 ± 0.2) and slow travel (median = 0, mean = 1.7 ± .2).

The highest number of single whistles were recorded during fast travel (median = 5.5, mean = 6.8 ± 0.6) and moderate travel (median = 7, mean = 7.9 ± 0.6); the highest number of whistles with harmonics also occurred during fast travel (median = 4, mean = 5.0 ± 0.4). In addition, both single whistles and whistles with harmonics were the most complex and had the most harmonics during fast travel (single whistles: median = 0.5, mean = 0.7 ± 0.1 number of steps; whistles with harmonics: median = 2, mean = 2.1 ± 0.2 number of steps, and median = 1, mean = 1.1 ± 0.1 number of harmonics). The fewest number of both types of whistles occurred during slow travel (single whistles: median = 1, mean = 4.6 ± 0.6; whistles with harmonics: median = 0, mean = 2.0 ± 0.3). Additionally, fast travel, moderate travel and mixed travel exhibited the longest duration and bandwidth of whistle bouts. Mean whistle bout duration was 11.3 s (± 0.9 s) for fast travel, 10.4 s (± 0.9 s) for moderate travel, and 9.7 s (± 1.0 s) for mixed travel, while mean whistle bout bandwidth was 20.6 kHz (±1.5 kHz) for fast travel, 15.2 kHz (±1.2 kHz) for moderate travel, and 19.5 kHz (±19.7 kHz) for mixed travel. In contrast, during foraging mean whistle bout duration was only 3.8 s (±0.6 s), and mean whistle bout bandwidth was only 9.4 kHz (±1.1

kHz), less than half the bandwidth recorded during fast travel. Individual whistles were shortest during foraging (median = 0.2 s, mean = 0.2 s ± 0.02 s), and were almost the least complex, only above slow travel in the fewest number of steps (forage: mean = 0.4 ± 0.1; slow travel: mean = 0.3 ± 0.1) and fewest number of harmonics (forage: mean = 0.8 ± 0.1; slow travel: mean = 0.8 ± 0.1).

Random forest models were initially created using all 50 call features. Additional models were then created using the top 30 ranked call features (Gini > 10), and using the top 10 ranked call features (Gini > 20). This was done to remove potentially spurious or auto-correlated data, improving model performance. Ultimately included in the model were: all click variables (click length, ICI, click count per 30-second interval, and number of click bouts per 30-second interval); pulsed call bandwidth; single whistle length and duration; the count of single whistles per 30-second interval; the count of whistles with harmonics per 30-second interval; and the duration and bandwidth of whistles with harmonics.

Rates of correct classification of behavioral state by random forest models changed notably with the inclusion of group size and group spacing. In Table 3, results are presented both with and without the inclusion of group size and group spacing. When group size and spacing were excluded from the model with all 50 call features, the OOB error rate was 56.9%. With group size and spacing data included, the OOB error dropped to 43.1%. When only the top 30 call features were included, as well as group size and spacing data, the OOB error rate dropped further to 40.3%. Finally, when only the top ten call features, group size, and group spacing data were included, the OOB error rate was only 32.7%. Classification rates increased for all behaviors across each of the four model iterations, with improvement more than double in some cases.

The cross validated predictive random forest models were created using both the top 30 call feature dataset and the top ten call feature dataset; both excluded group size and group spacing data, as these would not be known from an acoustic recording. Results were better than expected by chance for both datasets for all behaviors except mill (Table 4), although no behaviors were predicted as successfully as they had been classified in the original Random Forest models. The OOB error rate for the top 30 call feature dataset was 39.9%, and was 35.8% for the top 10 call feature dataset.

Discussion

Common dolphins encountered in the region off San Clemente Island in the SCB were most often observed to be traveling. A distinct diurnal movement pattern has been observed, with common dolphins moving offshore into deeper waters in the late afternoon and evening, and returning inshore at dawn (Frasier, personal communication). This movement, coupled with the low rate of observed daytime foraging, suggests that this population is foraging at night, likely on the rising Deep Scattering Layer (DSL) present in deeper waters, which supports the findings of Ohizumi (1998). In addition, daytime foraging was primarily observed in the morning, and may represent opportunistic feeding on epipelagic schooling fish. Morning foraging was followed by a period of increased milling and mixed travel/social behavior. This pattern is similar to those observed for other dolphin species. In dusky dolphins (*Lagenorhynchus obscurus*) in Argentina that feed on schools of anchovy (*Engraulis anchoita*), morning foraging bouts are followed by a period of rest and then an increase in social behavior. Dusky dolphins in New Zealand, on the other hand, feed on the rising DSL at night, and tend to remain near land in the morning, then move offshore into deeper water in the afternoon and evening (Würsig *et al.* 1991). Hawaiian spinner dolphins (*Stenella longirostris*) also feed on the DSL, and follow an inshore-offshore diurnal pattern. Alternating rest and social behavior, they remain in shallow bays during the day, and then move offshore in the late afternoon to begin foraging (Norris and Dohl 1980; Norris *et al.* 1994; Benoit-Bird and Au 2003).

Common dolphin night-time vocalization data had numerous call periods with patterns similar to daytime foraging vocalization patterns: discrete click bouts and few whistles or pulsed calls, with whistles frequently occurring at the start and end of click bouts. Further analysis of these nocturnal call patterns is needed, but the qualitative pattern supports the idea that this population of common dolphins is feeding at night on the DSL. This is similar to the pattern found by Goold (2000), who recorded common dolphin vocalizations off the British Isles and found peaks in “acoustic contact” (the number of call bouts) in early morning and late evening that were presumed to correspond with feeding behavior. In addition, Goold found a call rate minimum in the early afternoon period, corresponding in this study to the peak in mill and slow travel behaviors, both of which had fewer calls. Osnes-Eire (1999) found that the stomach contents of short-beaked common dolphins caught as fisheries by-catch off California were dominated by myctophid and squid species, and the stomach contents of long-beaked common dolphins had myctophid, epipelagic fish, and squid remains. These findings also lend support to the hypothesis that common dolphins in this region are primarily engaged in night-time feeding.

Vocalization patterns during travel are markedly different than during foraging, with rates of clicks, whistles, and pulsed calls increasing as travel speed increases. In addition to a higher overall call rate during fast travel, whistle bouts were longer and more broadband (indicating the presence of harmonics), and individually distinguishable whistles were more complex and had more harmonics. Ansmann *et al.* (2007) described common dolphin whistles from the Celtic Sea and examined whistle parameters against behavior and group size. While harmonics were not recorded in this case, the authors did find whistles to be more complex when dolphins were traveling. North Atlantic pilot whales (*Globicephala melaena*) also produced more whistles during "transiting" behavior, although the whistles were less complex than in other behavior categories. However, the other behavior categories included being herded and hunted by whalers, and so in this case transit behavior had a lower level of stress or excitement than other categories (Taruski 1979). Weilgart and Whitehead (1990) also recorded North Atlantic pilot whale calls and looked at more comparable behavioral categories. They also found an increase in whistling with increased travel speed, and recorded less complex whistles during milling. More whistles and pulsed calls were also recorded during "directive swimming" in beluga whales

(*Delphinapterus leucas*) than during most other behavioral states except social interactions (Sjare and Smith 1986).

There are no studies correlating common dolphin clicks or pulsed calls with behavior; however a comparison with other species shows mixed results. In a study similar to this one, few whistles and pulsed calls, and fewer than expected echolocation clicks were recorded during foraging bouts of Hawaiian spinner dolphins (Benoit-Bird and Au 2009). Also similar to this study, Brownlee (1983) recorded the most clicks and whistles during travel for Hawaiian spinner dolphins, and the fewest clicks, whistles or burst pulses during milling behavior. However, Brownlee (1983) found a high rate of clicks during foraging. Furthermore, high click rates were recorded during foraging for Pacific humpback dolphins (*Sousa chinensis*); during "surface activity" (which was attributed to foraging in this study) for pilot whales; and during feeding bouts of killer whales (Weilgart and Whitehead 1990; Van Parijs and Corkeron 2001a; Simon *et al.* 2007b). Burst pulses were also associated with foraging and social behavior in Pacific humpback dolphins (Van Parijs and Corkeron 2001a) and with foraging in killer whales (Simon *et al.* 2007b).

An increase in echolocation clicks may be expected during foraging as the dolphins detect and localize prey targets, and an increase in communicative calls anticipated as dolphins forage cooperatively. Therefore, it may be that the multi-directional nature of foraging behavior, coupled with the strong directionality and rapid attenuation rates of clicks (Au 1993) are leading to clicks and pulsed calls being missed as the dolphins turn away from the hydrophone. However, Benoit-Bird and Au

(2009) recorded more clicks during the transitions between foraging stages than during discrete foraging bouts. While they attributed some of that difference to missed clicks, they also theorized that clicks may be used to coordinate the group or even as a form of communication, and therefore fewer clicks may be produced during discrete bouts. In addition, whistles or pulsed calls may be used to signal the start and end of foraging bouts, but may not be produced during discrete periods of foraging (unpublished data). To investigate this further, work is being conducted in the SCB using a suite of widely spaced (~1 km) hydrophones to determine if calls are being produced but missed on a single hydrophone, or if call rate estimation by a single hydrophone is accurate.

Group size and spacing data were strongly correlated with behavior and seemed to influence call rates as well. While call rates of common dolphins generally increase with group size it is not a linear relationship; in addition, call rates were highest in dispersed groups followed by tightly clustered groups, with the fewest calls in loosely aggregated groups. Weilgart and Whitehead (1990) also did not find a correlation between the numbers of whistles produced and group size for pilot whales. Rather, they recorded more whistles when more subgroups were present. These relationships are likely tied to behavior; fast traveling groups had the highest call rates of all types of calls and were predominantly spread out in large groups or were tightly clustered. In contrast, foraging groups produced fewer calls and were most often loosely aggregated in both small and large groups. Therefore the role of behavior is important to call production rates, and an increase in group size alone can not predict an increase in calls without additional information.

There were very positive results in the use of vocalization data to classify behavioral states, and classification rates improved as only the most important call features were included in the random forest model. While some behaviors such as fast and moderate travel were classified very well, at 81% and 85% respectively, other behaviors were not as well classified. Still, all behaviors were classified far better than by chance. When the 5-fold cross validation was performed, correct prediction rates were lower than the original classification rates; however all behaviors, except for mill, were still predicted better than by chance.

These results may reflect the limitations of this dataset, since the behaviors that were classified most successfully were also those that dominated the behavioral budget of this population. It may be that as additional focal follow data are collected with a broader range of behaviors, the classification models will improve. It could also be that behavioral states may not have been correctly identified and therefore calls were incorrectly categorized and the models were corrupted. This caveat is particularly salient for observations made from the RHIBs, where behavior may still be impacted by the presence of the boat even after a period of acclimation, and where perspective of the whole group may be limited in rough conditions or for very large groups. There could also be too much overlap in the types and rates of vocalizations produced in certain behaviors to discretely classify them. Despite these possible limitations, this modeling technique was also applied to Pacific white-sided dolphin vocalization and behavioral data, with comparable classification success (unpublished data). In that case, forage and mill were the top predicted behaviors at 78% and 75%

correct classification, respectively. Therefore, these results support the idea that this technique is limited by lack of data, not by poorly categorized behavior or overlap in call types with behavior. Further work with more species and additional data will help to strengthen these models and reduce uncertainty. These more robust models can eventually be used to predict the behavior of animals from vocalizations recorded at night or from autonomous instruments. This will permit greater insight into dolphin habitat use across longer spatial and temporal scales than can be learned from visual observations alone. These models can also be used as a baseline of vocal and surface behavior to compare against observations from impacted areas, allowing for a greater understanding of the effect of vessel traffic and other anthropogenic noise, prey reduction through over-fishing, and habitat changes through ocean acidification and warming.

Conclusions

Daily behavioral patterns of common dolphins in the SCB are dominated by inshore/offshore travel. A small amount of foraging was observed during the morning, but most foraging is occurring at night, likely on the deep scattering layer, after the dolphins have moved further offshore into deeper waters. Surface behavior, group size and group spatial configurations are all correlated, with the largest groups engaged in traveling while milling and foraging occurred in smaller groups; foraging groups were also spaced more loosely, while traveling groups were either very spread out or were tightly clustered. Analyses of vocalizations indicate an increase in the number of clicks, pulsed calls and whistles, as well as an increase in the complexity of whistles with travel speed; most vocalizations were recorded during fast travel and the fewest clicks, pulsed calls and simplest whistles were recorded during slow travel and forage. Models of call features have proven to be capable of classifying and predicting surface behavior, and could be used to classify behavior when visual data are not available.

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Table 2.1 - Descriptions of the group behavioral categories used for analysis.

Behavior	Description

Travel	• Categorized by speed
	  • Slow: low to the water, little leaping, slow moving, no white water
	  • Moderate: increased directional leaping, faster swim speeds, some white water
	  • Fast: rapid movement, mostly directional leaping, lots of white water
	• Move in same direction
	• Move steadily and/or rapidly
	• Often synchronous and/or frequent surfacings

Forage	• Variable direction of movement by individuals within the group • Generally remain in same area but can be spread out • May have high arching dives/leaps • Visible fish chasing/tossing or bursts of rapid directed swimming
Mill	• Variable direction of movement by individuals within the group • Remain in one area in close proximity • Slow swimming speeds • No surface active behavior, contact, or long dives; stay near surface
Social/ Surface Active	• Possible variable direction of movement by individuals within the group • Individuals in close proximity/touching • Frequent surface active behaviors, including leaps, tail slaps, and body slaps

Table 2.2 - Summary of effort and the number of common dolphin groups used for analysis for all surveys, conducted from the Floating Instrument Platform (FLIP) and from small boat work conducted off San Clemente Island (SCI).

Survey	**Effort (days)**	**Total Number of Groups**
FLIP 2006	17	14
FLIP 2007	27	4
FLIP 2008	25	14
SCI 2006	9	13
SCI 2007a	4	1
SCI 2007b	5	4
SCI 2008	10	15
TOTAL	**97**	**61**

Table 2.3 - Correct classification rates of surface behavior using random forest decision trees based on call features, with group size and group spacing included as a predictor variable in all but the first column.

Behavior	**All 50 call features (excluding group size and spacing)**	**All 50 call features**	**Top 30 call features**	**Top 10 call features**
Fast travel	52.1%	69.4%	75.7%	80.6%
Moderate travel	73.0%	81.9%	83.5%	84.6%
Slow travel	24.1%	42.7%	47.6%	59.8%
Mixed travel	19.8%	24.7%	24.7%	41.2%
Forage	26.0%	46.0%	46.0%	58.0%
Mill	22.2%	39.7%	42.1%	52.1%

Table 2.4 - Correct prediction rates of surface behavior using random forest decision trees based on the five-fold cross validation technique, with group size and spacing data excluded.

Behavior	**Top 30 call features**	**Top 10 call features**
Fast travel	55.9%	60.1%
Moderate travel	32.0%	42.0%
Slow travel	19.2%	39.2%
Mixed travel	65.6%	64.6%
Forage	26.8%	30.5%
Mill	7.1%	11.8%

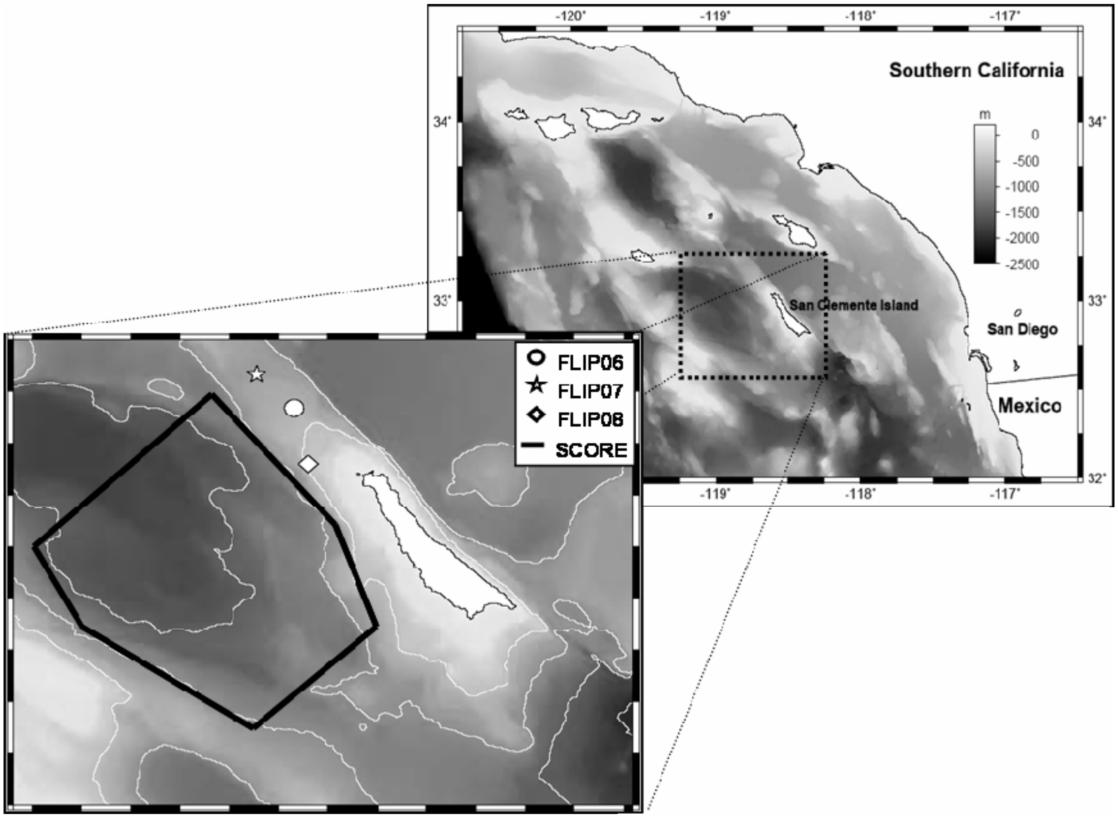

Figure 2.1 - Bathymetric map of the study area in Southern California Bight. The shapes indicate the locations of FLIP moorings in 2006, 2007 and 2008, northwest of San Clemente Island. The dark line indicates the border of the San Clemente Offshore Range (SCORE).

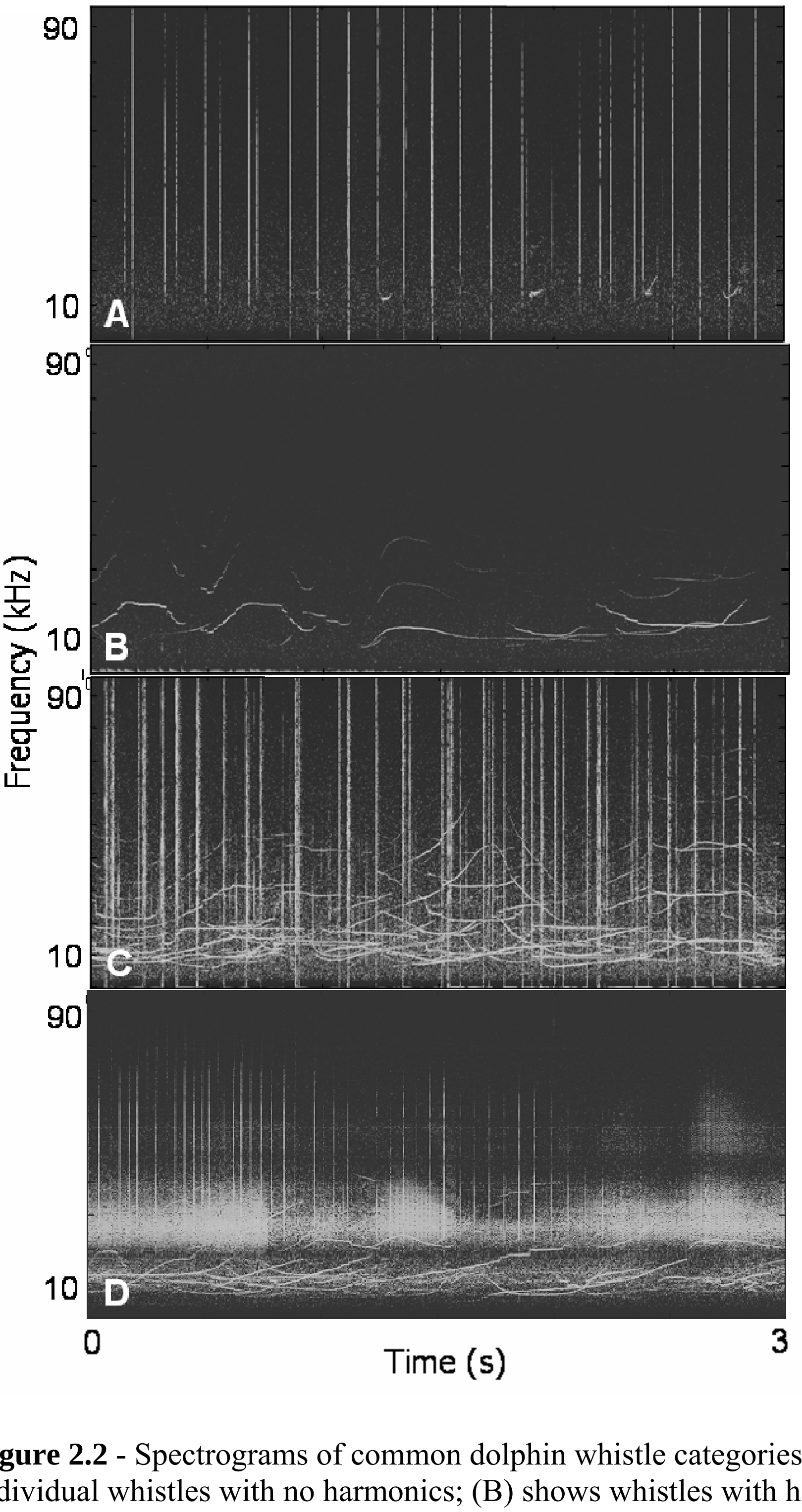

Figure 2.2 - Spectrograms of common dolphin whistle categories: (A) shows distinct individual whistles with no harmonics; (B) shows whistles with harmonics that are still individually distinct from each other; (C) and (D) show overlapped whistle bouts, with whistles that cannot to be uniquely identified. Clicks are also visible as vertical lines in (A), (C), and (D), and pulsed calls are shown in (D).

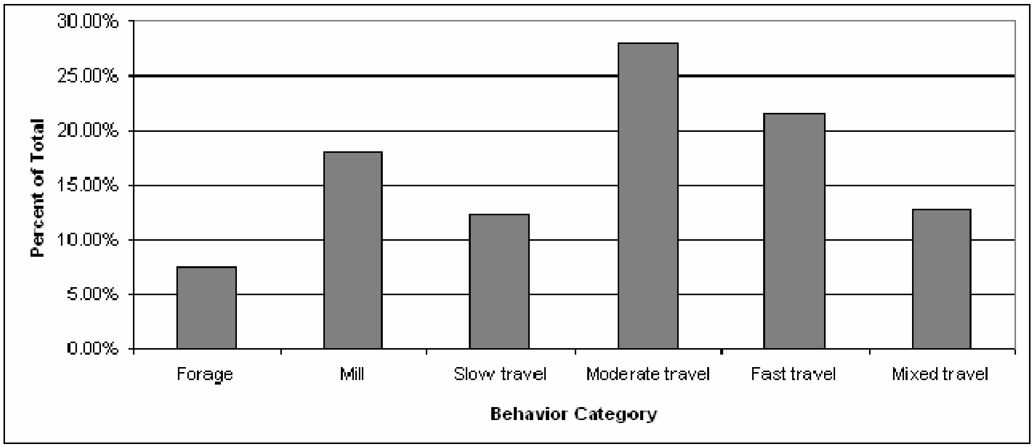

Figure 2.3 - Behavioral categories for common dolphins. The bars show the percent time animals were observed in each behavioral state.

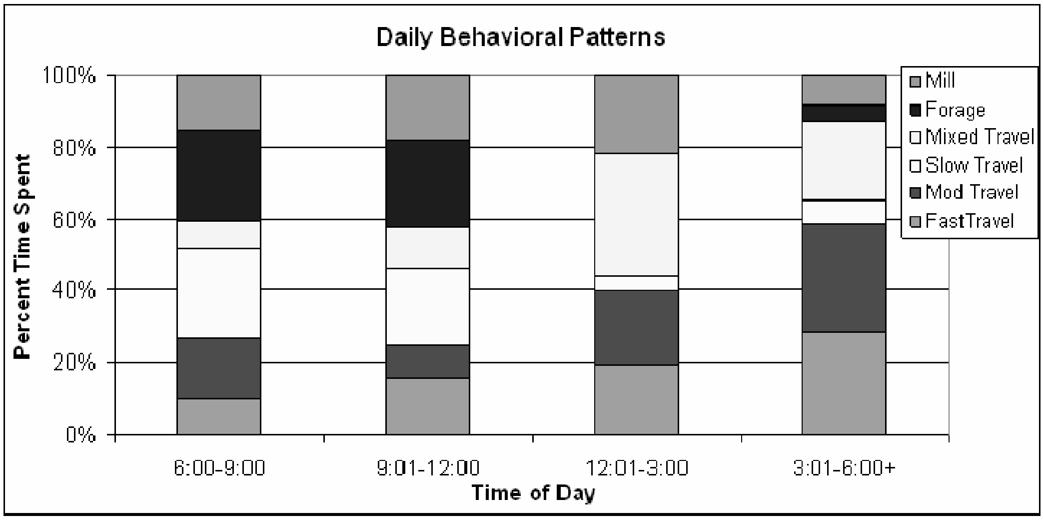

Figure 2.4 - Daily behavior patterns of common dolphins. Observed rates of all behaviors in each time period were significantly different from expected using Chi-Square analyses.

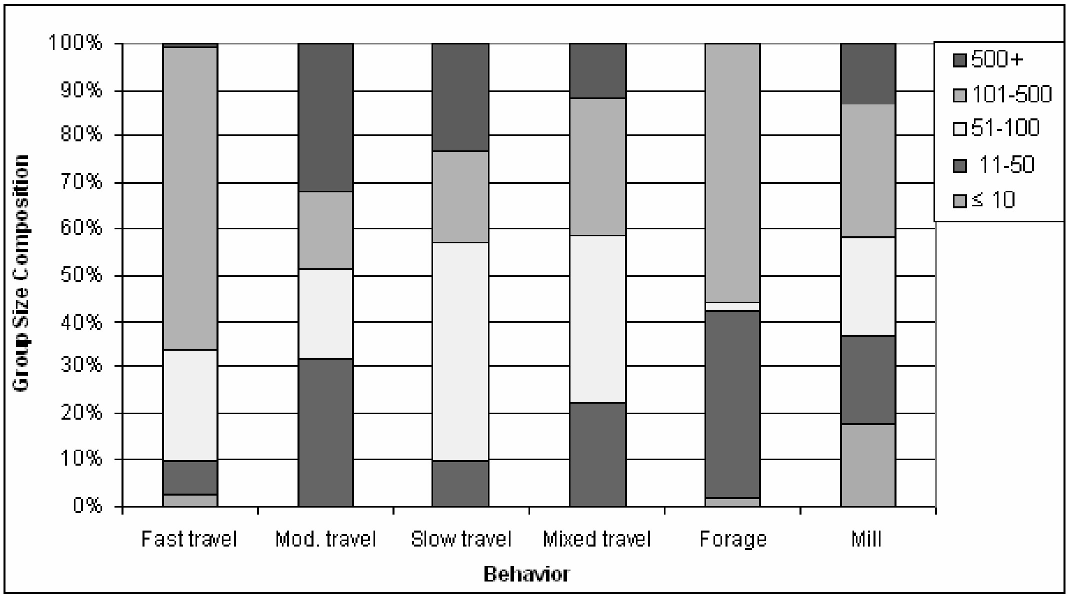

Figure 2.5 - Group size composition for each behavior category.

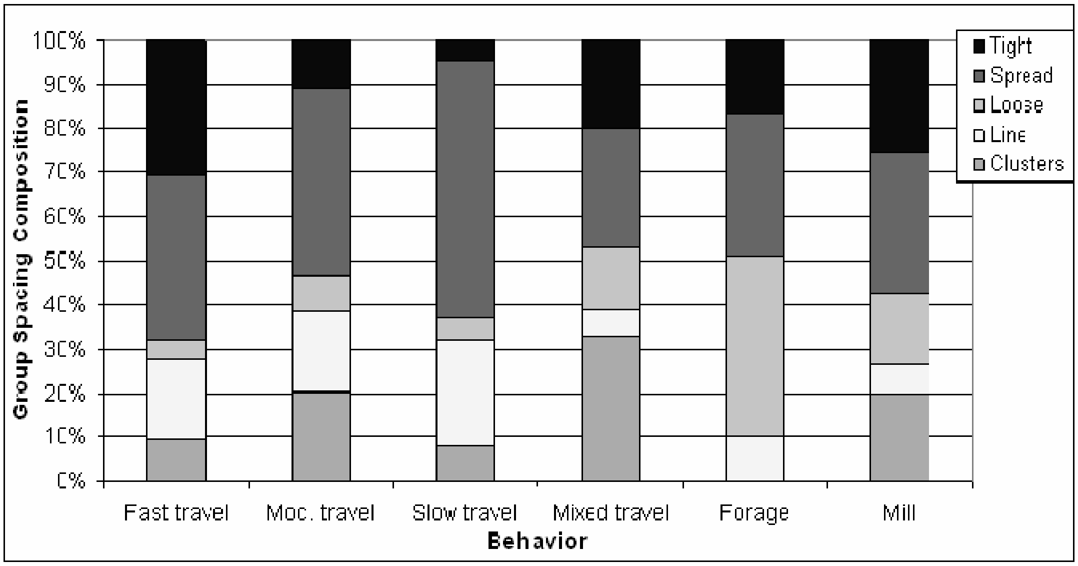

Figure 2.6 - Group spacing composition for each behavior category.

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CHAPTER 3

Classification of Behavior Using Vocalizations of Pacific White-Sided Dolphins (*Lagenorhynchus obliquidens*)

By E. Elizabeth Henderson, John A. Hildebrand, and Michael H. Smith

Abstract

Surface behavior and concurrent underwater vocalizations were recorded for Pacific white-sided dolphins in the Southern California Bight over multiple field seasons spanning three years. Clicks and pulsed calls were counted and classified based on acoustic measurements, leading to the identification of seventeen key call features used for analysis. These features included the number (per 30-second interval) and duration of clicks, pulsed calls, and call series. Kruskal-Wallis tests indicated that call features differ significantly across behavioral categories. Previous work had discovered two distinctive click types which may correspond to known subpopulations of Pacific white-side dolphins in the Southern California Bight; this study revealed that animals producing these different click types also differ in both their behavior and vocalization patterns. Behavioral differences may be characteristic of niche partitioning by overlapping populations; those coupled with differences in vocalization patterns may signify that these subpopulations are cryptic species. Finally, random forest decision trees were used to model the behavior and vocalization data and to predict behavior based on vocalizations alone. This study demonstrates the strong

potential for using vocalization patterns to predict behavior, allowing for a broader spatial and temporal understanding of behavior than ship-based surveys can provide, and creating a framework for "normal" acoustic behavior against which anthropogenic stresses can be evaluated. Finally, this work exhibits the use of acoustics as a tool for identifying cryptic species that cannot be visually distinguished.

Introduction

Cryptic species are closely related species that are genetically distinct but morphologically similar and often occur sympatrically (Mayr 1977). Phenotypic and genotypic divergence does not necessarily occur at the same rate (Harrison 1991), and behavioral traits may evolve even more rapidly due to sexual selection pressure (Jones 1997). Wyles et al. (1983) theorized that in higher vertebrates behavior may even be a driving force in evolution and speciation due to their capacity for innovation and cultural learning (e.g. Mesnick et al. 1999; Connor 2001; Rendell and Whitehead 2001), similar to the Baldwin effect (Baldwin 1896; Suzuki and Takaya 2007). Vocal behavior may evolve as an adaptation to differing habitats (Seddon 2005; Braune et al. 2008), or as a barrier to prevent gene exchange (Seddon 2005; Smith and Friesen 2007). Distinct vocal characteristics have been used to distinguish cryptic species or subspecies in a variety of taxa, including birds (Smith and Friesen 2007; Edelaar 2008; Foerschler and Kalko 2009), primates (Braune *et al.* 2008; Eschmann *et al.* 2008), amphibians (Gerhardt 1994), and bats (Jones 1997; Kingston *et al.* 2001).

There is both morphological and genetic evidence suggesting the existence of at least two distinct populations of Pacific white-sided dolphins (*Lagenorhynchus obliquidens*) in the eastern North Pacific (Walker et al. 1986; Lux et al. 1997). There appears to be a California/Oregon/Washington population found north of about 32°N, and a Baja California population distributed south of 34.5°N (Walker et al. 1986). Therefore both ranges extend into the Southern California Bight (SCB) where the two populations have overlapping distributions. Soldevilla *et al.* (2008) determined that there are two distinct click types made by Pacific white-sided dolphins in the SCB. Type A clicks, with a frequency peak at 27 kHz, were recorded throughout the SCB, while Type B clicks, with a frequency peak at 26 kHz, were only recorded near San Clemente and Santa Catalina Islands, which were the furthest inshore sites recorded in the SCB. Soldevilla (2008) hypothesized that the two click types may be representative of the two populations, with Type A clicks produced by the northern population and Type B clicks produced by the southern population. Soldevilla determined that Type A clicks were most common at night, with peak production at dawn and dusk, whereas Type B clicks were more common during the daytime. The predominance of Type A clicks at night could indicate night-time feeding, likely on mesopelagic fish and squid associated with the scattering layer (Norris et al. 1985; Benoit-Bird 2003), while the peak in Type B clicks during daylight hours could signify foraging on pelagic fishes. We hypothesize that this may represent resource partitioning, and furthermore could indicate possible evolutionary divergence into cryptic species by these partially sympatric populations of Pacific white-sided dolphins, which we will examine through behavioral and acoustic comparison.

The study of cetacean behavior can lead to insights to their social structure and habitat use (Herman 1979; Shane et al. 1986; Baird and Whitehead 2000; Craig and Herman 2000; Gowans et al. 2001). However, cetaceans spend limited amount of time at the surface, and long-term at-sea observations are limited by weather and budget considerations. Passive acoustic monitoring of cetaceans using autonomous instruments to record vocalizations can be conducted for long periods of time at relatively low cost (Wiggins 2003; Mellinger et al. 2007; Wiggins and Hildebrand 2007), but thus far has been largely limited to ascertaining presence or absence of animals and some species identification (Oswald et al. 2003; Soldevilla et al. 2008; Baumann-Pickering 2009). Some work has been conducted to combine visual and acoustic sampling in wild populations of a few delphinid species (Ford 1989; Weilgart and Whitehead 1990; Dawson 1991b; Herzing 1996; Van Parijs and Corkeron 2001b), but none of these studies have attempted to model the relationship between surface and acoustic behavior. If the types of calls produced and their rate of production can be associated with specific behavioral states, these vocalization patterns could then be used to predict behavior and generate a model of habitat use exclusively from acoustic monitoring. Highlighting regions of critical habitat will assist in parsing out whether these subpopulations are partitioning resources or otherwise utilizing the SCB differently.

Pacific white-sided dolphins are a cold temperate water species, distributed throughout the north Pacific, and are generally found between 38° and 47°N (Reeves *et al.* 2002), although their range extends further south along the west coast of North America as far as the southern tip of Baja California, Mexico. In coastal waters off north California, Pacific white-sided dolphins primarily consume epipelagic schooling fish and squid, including northern anchovy (*Engraulis mordax*), Pacific hake (*Merluccius productus*), Pacific saury (*Cololabis saira*), and market squid (*Loligo opalescens*) (Brownell *et al.* 1999). Stomach content analyses of pelagic animals show a preference for mesopelagic fish and squid (Walker and Jones 1993); and, off the coast of northern Japan, Pacific white-sided dolphins consume both epipelagic and mesopelagic fishes and cephalopods (Wilke *et al.* 1953). Group size ranges from the tens to hundreds along the coast into the thousands in the open ocean (Reeves *et al.* 2002).

Pacific white-sided dolphins produce echolocation clicks that range in frequency from 20 to over 100 kHz (Evans 1973; Richardson *et al.* 1995a; Soldevilla *et al.* 2008). Echolocation clicks are primarily used in foraging and navigation, although they may be used for communication as well (Dawson 1991b). In addition to clicks, Pacific white-sided dolphins produce burst pulses and buzzes, which are series of rapid click trains with very short inter-click intervals that are used for both foraging and communication (Lammers et al. 2003; Lammers et al. 2006). There is some debate over whether or not Pacific white-sided dolphins produce whistles (Caldwell and Caldwell 1971; Rankin *et al.* 2007); in either case whistles will not be considered in this analysis.

This study has four principle objectives in considering surface behavioral patterns of Pacific white-sided dolphins and concurrent vocalizations: (i) to investigate the correlation of surface and acoustic behavior of Pacific white-sided dolphins, (ii) to determine if those behavioral and acoustic patterns differ between Type A and Type B groups, (iii) to explore the capability of using vocalizations to classify and predict behavior, and (iv) to use the resulting acoustic-behavior relationships to examine the problem of cryptic species, shedding light on the general issue of cryptic species in odontocetes.

Methods

Study Area and Survey Platforms

This research was conducted in the SCB near San Clemente Island, about 60 miles offshore of San Diego (Figure 1). Data were obtained from August 2006 through November 2008 using two research methods. The primary method was surveys conducted on the Scripps Institution of Oceanography R/P Floating Instrument Platform (FLIP, http://www-mpl.ucsd.edu/resources/flip.intro.html), a live-aboard stationary moored platform from which visual and acoustic observations were simultaneously conducted (Fisher and Spiess 1963). FLIP was deployed during the fall of three sequential years northeast of San Clemente Island, (Figure 1, inset): from October 2 – November 3 in 2006 in 637 m water depth, from October 30 – November 29 in 2007 in 840 m water depth, and from October 17 – November 14 in 2008 in 347 m water depth.

The secondary research method was small boat surveys conducted within the Southern California Offshore Range (SCORE). This work was done in conjunction with the Naval Undersea Warfare Center's Marine Mammal Monitoring on Navy Ranges (M3R) program (Jarvis et al. 2003; Moretti et al. 2004; Falcone et al. 2009). The M3R system was developed to detect and localize marine mammal sounds. Experienced observers in small boats located the animals and verified species for M3R acoustic detections. Three rigid hulled inflatable boats (5.3 m to 5.9 m in length) were used for these surveys, conducted within the SCORE range August 14-20 in 2006, April 13-22 and October 22-26 in 2007, and August 2-10 in 2008.

Visual Observations and Behavioral Sampling

Trained marine mammal visual observers worked from three locations on FLIP to monitor and record marine mammal sightings. Initial detections were made from the crow's nest, located 26.5 m above the water line. From this position two observers watched 360° around FLIP using both 7x50 Fujinon binoculars, containing a reticle scale used to estimate distance, and the naked eye, and recorded all marine mammal and vessel sightings throughout daylight hours in Beaufort sea state 5 or less. On a few occasions observations were suspended when visibility became less than one nautical mile due to fog. These observers recorded species, group size, direction of travel, and general behavioral state for every marine mammal group sighted, and additionally recorded environmental data including Beaufort sea state, swell height, visibility, and overall sighting quality conditions every hour or when conditions changed. One observer assisted in species identification using 25 x 150 big-eye binoculars from the top deck level 15.24 m above the water line. This observer also acted as liaison between the crow's nest observers and acousticians by providing sighting information to the acoustics teams, thereby allowing the observers to remain blind to any acoustic cues of the presence of animals.

Focal follow observations were conducted from the top deck level on dolphin groups sighted by the crow's nest observers on the face side of FLIP. Focal follows were performed only on groups within 1 km to ensure that the focal observer could consistently determine the behavioral state of the majority of the group. Additionally, 1 km is the distance the acoustics team was able to reliably detect all vocalizations produced. Focal follows were conducted using instantaneous sampling methods (Altmann 1974; Mann 1999), whereby behavioral states and pertinent activities were recorded along with bearing, reticle, group size, orientation towards FLIP, and direction of travel every 1 to 3 minutes. Every effort was made to record behavior with a consistent interval period (e.g. 1 minute) within each group focal follow; however that interval varied slightly between groups depending on the surfacing period of the animals, the size of the group, or due to inter-observer differences.

Groups were defined as animals in apparent association, moving in the same direction and generally carrying out the same activity, following Shane (1990). There were 5 behavioral states used: slow, moderate or fast travel, mill, and forage (see Table 1 for behavior descriptions) (Shane 1990; Hanson and Defran 1993; Henderson and Würsig 2007). Observers monitored the entire group to assess behavior; behavior was classified as what the majority of the group was doing, and could be combined if the group as a whole was performing multiple behaviors (e.g. milling while generally traveling in one direction), or if different portions of the group were performing different behaviors (e.g. half of the group began foraging while the remainder continued to mill). Behavioral sampling continued for the duration of the time the group was on the face side of FLIP and within 1 km.

Focal follows were also conducted on delphinid groups from the small boats on the SCORE range. When groups were sighted, the vessel would attempt to approach the group without disrupting their behavior. Once the initial sighting information, including species, group size, and group envelope (the overall spread of the group) was gathered, instantaneous sampling protocol was implemented every 1 to 3 minutes using methods comparable to those used on FLIP. The only difference between methods was that small boat focal follow observations were made with the naked eye only, and so no bearing or reticle information was recorded. After the group appeared acclimated to the presence of the vessel, the boat would maneuver ahead of the group and deploy a drop hydrophone. Behavioral sampling would continue as the group passed the boat; once the dolphins had passed, the hydrophone was retrieved and the process repeated until several recordings had been obtained or until the group was out of sight. Finally, environmental data (Beaufort sea state, swell height, cloud cover, and visibility) were collected hourly, or when conditions changed.

Acoustic Sampling and Call Selection

FLIP hydrophones were deployed at depths ranging from 30 to 50 m and recorded continuously day and night. Small boat hydrophones were deployed at depths ranging from 20 to 30 m and were recovered after each group encounter. Both AQ-1 (Teledyne Benthos, North Falmouth, MA) and HS150 (Sonar Research and Development Ltd, Beverly, UK) hydrophones were used, connected to custom built preamplifiers and bandpass-filtered electronic circuit boards designed to flatten ambient noise over all frequencies (Wiggins and Hildebrand 2007). Analog signals from all hydrophones were filtered with a 2 kHz highpass filter and were digitally sampled at 192 kHz and 24-bits. Analog data received on FLIP hydrophones were digitally converted using a MOTU 896HD firewire audio interface with an internal anti-alias filter (Mark of the Unicorn, Cambridge, MA). While potential differences in gain between recordings could bias results, in all cases only data with a high signal-to-noise ratio (at least 7 dB re 1 μPa) were used to minimize that bias. In the 2006 and 2007 FLIP deployments, the sound analysis and recording software Ishmael (Mellinger 2001) was used to directly record the signal to computer hard-drive, while in 2008 the data was recorded to computer hard-drive using a program written in

MATLAB® (Mathworks, Natick, MA). The analog-to-digital converter used on board the small boats was the two-channel Fostex FR2 field memory recorder (Fostex America, Foster Electric, USA, Inc., Gardena, CA).

All acoustic data were segmented into 30-second intervals based on focal follow observation times. All segments were tagged with a behavior category, identified by click group type based on peak frequencies, and associated with supplemental sighting data, including group size, group orientation relative to the hydrophone, sighting distance and Beaufort. Each 30-second file was then examined using spectrograms created in a customized MATLAB® program (Wiggins 2003). A 1024-point Fast Fourier Transform (FFT) with a 50% overlapping Hann window was used to transform time series of the data into the frequency domain for analysis.

Clicks were detected automatically (Roch *et al.* 2007), using bandwidth filters and conservative threshold levels appropriate for each recording session such that the majority of clicks were detected while false positives were minimized. In most cases this method was sufficient to count all high-quality clicks (e.g. above a 7-8 dB signal-to-noise threshold). However, in some cases there were high numbers of clicks present which could not all be counted due to click envelope length constraints; as the minimum peak-to-peak value was set at 50 μs, clicks that occurred within that interval were not counted separately. An attempt was also made to remove from analysis any clicks resulting from echoes from the water's surface to avoid over-estimating the number of clicks and bias the inter-click interval (ICI) calculation. Therefore, the total number of clicks detected is a minimum estimate rather than an absolute count. The total number of clicks divided by group size was also calculated to get an estimate of clicks/individual per 30-second interval. Finally, ICI, click duration and number of bouts per 30-second interval (defined as groups of clicks spaced less than 0.4 s apart) were also calculated from automatic detections.

All files were also manually examined for burst pulses and buzz calls. Burst pulses are rapid series of broadband clicks with short inter-click intervals, thought to be used for communication (Lammers *et al.* 2003). Buzzes, often referred to as "terminal buzzes", are typically produced at the end of a click train as a dolphin is approaching its target (Johnson *et al.* 2006; Benoit-Bird and Au 2009; Verfuss *et al.* 2009). Some distant burst pulses may have been misclassified as buzzes, and some buzzes co-occurred with dense clicks, making it difficult to determine if they fell at the end of a click train. Therefore the burst pulse and buzz categories were lumped together as pulsed calls for analysis. In addition, a number of complex stereotyped call series were discovered in the data which were categorized separately from individual pulsed calls (Figure 2). The number of pulsed calls/individual and call series/individual were also calculated for each 30-second interval. Finally, the minimum and maximum frequencies, bandwidth and duration of each of these call types were measured.

Ultimately there were 17 call features selected for this analysis, all calculated in 30-second intervals: (i) ICI, (ii) click duration, (iii) number of clicks, (iv) number of clicks/individual, (v) number of click bouts, (vi) number of pulsed calls, (vii) number of pulsed calls/individual, (viii) pulsed call duration, (ix) minimum pulsed call frequency, (x) maximum pulsed call frequency, (xi) pulsed call bandwidth, (xii) number of call series, (xiii) number of call series/individual, (xiv) call series duration, (xv) minimum call series frequency, (xvi) maximum call series frequency, and (xvii) call series bandwidth.

Analysis

Data from Pacific white-sided dolphin focal follow groups were selected for analysis based on several criteria. First, only a single group could be present both acoustically and visually, so that all vocalizations could be confidently attributed to that group. Second, the group needed to be within a 1 km range so that behavioral categorization would be reliable and vocalizations would not be missed due to distance. Third, the group needed to be approaching, or at least moving parallel to, the hydrophone arrays for most of the focal follow encounter. Dolphin calls, particularly clicks, are highly directional and attenuate rapidly (Au 1993). Thus if the dolphins are pointed away from the hydrophone or at too great a distance, calls produced could be missed. The exceptions to this were foraging and milling groups, since they are inherently multi-directional by definition.

Detection results, including median call counts, minimum and maximum frequencies, bandwidth and durations per 30-second interval, were first randomly sampled with replacement 1000 times to increase the sample size. Kruskal-Wallis nonparametric tests, followed by Tukey-Kramer multiple comparison tests, were used to examine whether any of the 17 call features were significantly different for each behavioral category (Kruskal and Wallis 1952; Jaccard et al. 1984). To examine the ability to predict behavior based on vocalizations, random forest decision trees were created using call features and associated behavioral data (Brieman 2001; Siroky 2008). Random forest models are a series of unpruned classification trees, where 5000 bootstrap samples are taken from the original dataset, then 3 of the predictor variables are randomly selected at each node and the best split is chosen among those. The behaviors are then classified based on a majority vote from the 5000 trees. An estimate of the error rate is obtained using the data not used in each bootstrap iteration, termed the "out-of-bag" (OOB) data, as a test dataset. Classifications based on the OOB data are then aggregated and used to calculate an error rate, called the OOB error estimate (Brieman 2001; Liaw and Wiener 2002). Random forest models were first created using the entire dataset to look at rates of correct classification for each behavior for all groups combined as well as for click type A and B groups separately. Then a four-fold pseudo-jackknife procedure was conducted, with the dataset randomly divided without replacement such that 75% of the data were used for training and 25% were used for testing four times. Since individual 30-second segments were not independent of each other when they came from the same group, the division of data was done based on number of groups rather than segments. Thus 30-second files from one group were always included together in either the training or testing datasets. Group size information and the number of clicks and calls per individual were excluded from this procedure as that would not be known from acoustic data alone.

Results

There were a total of 28 different groups selected for analysis from 97 days of effort (Table 2), with 527 thirty-second intervals evaluated. All data were collected in Beaufort sea state 3 or less, with a median sea state of 1 (X ± SE = 1.37 ± 0.03, N = 527). Group size varied from 3 to 200, with a median size of 25 (X ± SE = 35.91 ± 1.93, N = 527). Focal follow duration ranged from 4 – 54 min, with a mean of 19.9 minutes.

Observers recorded the dolphins foraging while simultaneously milling or traveling in nine groups, therefore a “mixed forage” category was created. In addition, fast and moderate travel behavior categories were combined into “moderate/fast travel” due to smaller sample sizes. Ultimately, there were five behavioral categories used for analysis: moderate/fast travel, slow travel, mill, forage, and mixed forage. A summary of behavioral data is shown in Figure 3; slow travel was the predominant behavior (30.0%), followed by moderate/fast travel (21.5%), and then forage (15.4%) and mixed forage (18.8%). Behavior was also stratified by click type and compared using a chi-square analysis, which indicated that differences between click type groups were highly statistically significant ($X^2_4 = 2.02E\text{-}09$, $P < 0.0001$). Click type B groups had high rates of slow travel (25.0%) and moderate/fast travel (25.0%), followed closely by foraging (20.4%), with minimal milling (9.8%). In contrast, click type A groups were primarily observed to slow travel (39.9%) and mill (23.0%), with a very low rate of forage (5.6%).

Kruskal-Wallis nonparametric tests and Tukey-Kramer multiple comparison tests showed that differences across each behavioral category for the 17 call features were also significant (e.g. Figure 4); for every call parameter there was at least one behavior that ranked outside the confidence intervals of the other behaviors (X^2_6 ranges from 346.58 – 1665.01, $P < 0.0001$). Median click rates were lowest for forage (M = 112), moderate/fast travel (M = 107) and slow travel (M = 216.5), and were highest during mixed forage (M = 788, Figure 4a). Meanwhile, the median bout rates were highest for moderate/fast travel (M = 12) slow travel (M = 10), and forage (M = 10). The median ICI was also highest for moderate/fast travel (M = 0.09 s), forage (M = 0.09 s), and slow travel (M = 0.07 s). There were few pulsed calls during forage behavior (X ± SE = 2.19 ± 0.33, M = 1, N = 527) and no call series; in contrast, there were high numbers of both individual pulsed calls (X ± SE = 6.09 ± 0.54, M = 5, N = 527) and call series (X ± SE = 3.62 ± 0.49, M = 2, N = 527) during mixed forage behavior.

There was a strong positive relationship between group size and click rates ($R^2 = 0.66$), and a weaker positive relationship between group size and pulsed call rates ($R^2 = 0.35$). There was also a very weak relationship between group size and call series rates ($R^2 = 0.01$), indicating no increase in call complexity with larger group sizes. These non-significant results indicate that group size alone is not a good predictor of click or call rates, nor do calls become more complex with increased group size, and that therefore behavior plays an important role in determining call rate and call complexity.

Group size statistics were skewed for forage behavior; the inclusion of a single 200-animal group gave a median group size of 30 and a mean of 74.82 ± 0.95. However, this group was observed foraging in small subgroups and then coming together to travel, thus the inclusion as a single large group during forage behavior is misleading. Excluding this group led to a median group size of 10 with a mean group size of 18.09 ± 1.31, falling closer to the expected since foraging groups tend to be smaller. The next smallest group size was observed during milling (X ± SE = 21.31 ± 1.55, M = 25, N = 527), while larger group sizes occurred during mixed forage (X ± SE = 36.21 ± 3.16, M= 20, N= 527). Overall group sizes were also significantly smaller for click type A groups than for click type B groups during all behaviors except mill (X^2_4 = 1.99E-06, p << 0.0001) (Figure 5).

Random forest models were created first using all 17 call features as well as group size, then the Gini variable importance measure was implemented to estimate the importance of each variable. This metric is based on a weighted mean of the improvement of individual trees based on the inclusion of each variable as a predictor. Additional models were then created using only the top ranked call features (Gini > 10) until the OOB error estimate could no longer be reduced. Ultimately all click variables and combined pulsed call and call series data were used (Figure 6). In addition, rates of correct classification of behavioral state by random forest models changed notably with the inclusion of group size, therefore results are presented both with (Table 3) and without (Table 4) group size included. When group size and clicks/calls per individual were excluded, the OOB error rates were higher for all three group categories; the OOB error estimate for all groups was 42.67%, for click type A groups it was 50.28%, and for click type B groups it was 41.38%. When group size and clicks/calls per individual were included the overall OOB error estimate decreased to 34.86%, 43.50%, and 28.16% respectively for all groups, click type A groups and click type B groups. However, the inclusion of group size had a greater impact on some behaviors more than others. For example, for click type A groups there is little change in the rate of correct classification of slow travel or forage when group size is included, but a large increase from 33.3% to 60% was observed for the mixed forage category. Behaviors from Type B groups were most accurately classified, with only a 28.16% OOB error estimate. The behaviors with the best classification rates for all groups were slow travel and forage, while for Type A groups they were slow travel and mixed forage, and for Type B groups they were forage, mill, slow travel, and moderate/fast travel.

When the data were quasi-jackknifed using a four-fold method, the predictive capability of the acoustic data demonstrated promising behavioral classification results (Table 5). When using all groups, forage, slow travel, travel, and mixed forage were all classified correctly better than 50% of the time; all behaviors were classified correctly more than 20% of the time, which is better than chance. When using only click type A groups, slow travel was again the top predicted behavior at 78.3% correct;

and all behaviors other than forage and moderate/fast travel were classified correctly better than chance. The lower overall rates of correct classification for click type A groups is likely due to small sample size, which is split even smaller when using portions for training and testing. Finally, when using only click type B groups, mixed forage and forage were the top predicted behaviors at 67.6% and 67.0% correct respectively, with all other behaviors except mill over 50% correct as well. The average OOB error estimates for the predictive models were 43.7%, 47.9%, and 39.9% for all groups, click type A groups and click type B groups respectively.

Discussion

Pacific white-sided dolphin vocalizations differ both between click type A and click type B groups and between behavioral states within the groups. In addition, the high correct classification rates for most behaviors indicates clear potential to predict behavior based on vocalizations without the need for concurrent visual observations. This ability would help create an understanding of dolphin behavior across greater time and spatial scales than ship-based visual observations allow. There were characteristic differences between vocalizations for most behavioral states; forage, slow travel and mixed forage seem to have the most distinct call patterns; however there seems to be no clear vocal pattern for mill behavior. This may be due to unequal sample sizes of each behavioral category, inter-group differences, or possibly observer error in categorizing behaviors such that “mill” ended up as a default category.

Regardless of the reason, call parameters for mill were generally too similar to those from other categories to be distinctive and therefore were not readily classifiable. Finally, click type B groups had higher correct classification rates than click type A groups, which is likely due to a larger sample size. In particular, foraging behavior was highly classifiable for the click type B groups and was the second most frequently observed behavior, while very little foraging was recorded for click type A groups and so was difficult to characterize and thereby predict.

In addition to being vocally distinct, the two click groups also differed with respect to their behavioral time budgets. Click type B groups were observed foraging throughout daylight hours, while click type A groups were generally observed slow traveling and/or milling. This seems to indicate resource partitioning, or at least niche separation, between the two populations and supports Soldevilla's hypothesis that click type A dolphins may be foraging at night on squid and myctophids rising in the scattering layer, while click type B dolphins are foraging during the day on epipelagic schooling fish (2008). The strong behavioral and vocal distinctions between the two groups may in fact demonstrate that these groups are in the process of speciation, if not fully genetically distinct. Vocal differences have been used to distinguish cryptic species that are genetically different but morphologically similar (Smith and Friesen 2007; Braune et al. 2008; Foerschler and Kalko 2009), and may develop as a precursor to genotypic divergence. To fully verify this hypothesis, concurrent acoustic and genetic sampling needs to be conducted on these animals to determine if the click types represent the genetically distinct populations that have already been shown to overlap in the SCB (Lux *et al.* 1997). Additionally, genetic sampling and stomach content analysis of stranded animals could be conducted to determine if populations are consuming different prey as predicted. Finally, night-time feeding behavior by click type A dolphins needs to be substantiated, perhaps through the use of acoustic tags or active high-frequency sonar (e.g. Benoit-Bird and Au 2001) in addition to comparing daytime and nighttime acoustic recordings.

When correlating vocal and surface behavior, the fewest number of both clicks and pulsed calls were recorded during moderate/fast travel and forage behavior. This is consistent with some of the literature with respect to travel behavior and call rates, although there is wide variation. Van Parijs and Corkeron (2001) also found the fewest vocalizations during travel in Pacific humpback dolphins (*Sousa chinensis*); and Simon *et al.* (2007) found fewer clicks and calls in killer whales (*Orcinus orca*) during travel than during other activity. However, increased clicking and whistling were recorded for Hawaiian spinner dolphins (*Stenella longirostris*) during travel (Brownlee 1983), while the total number of whistles, as well as whistle complexity, increased as swim speeds increased in pilot whales (*Globicephala melas*). Atlantic spotted dolphins (*Stenella frontalis*) demonstrated more click trains but fewer whistles or chirps than expected during travel behavior (Dudzinski 1996).

In contrast, most studies have detected the highest number of clicks during presumed feeding activity (Weilgart and Whitehead 1990; Van Parijs and Corkeron 2001b; Simon *et al.* 2007a), and some have distinguished specific feeding-related vocalizations, such as the “bray” call (Janik 2000b) or “razor buzz” (Herzing 1996) in bottlenose dolphins (*Tursiops truncatus*). However, Dudzinski (1996) also found the fewest of all call types, including clicks, in foraging than in any other behavior for spotted dolphins. Forage behavior in the present study also had a high number of discrete click bouts, likely indicating search or scan behavior. In addition, an inherent feature of foraging behavior is variability in the direction of animal movement, and as clicks are highly directional and attenuate rapidly, there may have been low detection rates during foraging. Benoit-Bird and Au (2009) found the rate of detected clicks in spinner dolphins (*Stenella longirostris*) not related to the depth of the hydrophone, but rather to the depth of the hydrophone relative to the depth of the prey. These findings support the idea that directionality is highly important to receiving calls, and that clicks are only detected when the hydrophone is within the beam of the clicking animal. On the other hand, dolphins may be relying on visual cues or eavesdropping on coordinating conspecifics during forage behavior and therefore may not need to produce a high level of clicks to detect their targets (Gannon *et al.* 2005; Götz *et al.* 2006; Benoit-Bird and Au 2009). Click production could also vary depending on the prey being hunted. While most fish-produced sounds are below 3 kHz (Hawkins 1993), this is within the auditory range of most delphinids (Richardson *et al.* 1995a) and therefore the dolphins could be eavesdropping on their prey. Additionally, some fish species have been shown to be sensitive to sound (Schellart and Popper 1992), and so a “quiet” foraging strategy could be preferable for some prey species. However, Benoit-Bird et al. (2006) were not able to detect behavior changes in fish exposed to simulated odontocete clicks, and Pacific white-sided dolphin clicks may be too high in frequency to be detected by any prey species; in addition, none of the dominant prey species are known sound producers so prey eavesdropping in this case is unlikely.

In contrast, the highest click and pulsed call rates occurred during mixed foraging behavior. While mixed foraging groups had a higher median group size than foraging groups, they were smaller than slow or moderate/fast traveling groups. Therefore the increase in click and pulsed call rates may only be partially explained by group size. This behavior may represent search behavior and/or transitions between behaviors, when dolphins are looking for prey, coordinating movement, or beginning or ending a foraging bout and high rates of communication might be expected. Benoit-Bird and Au (2009) also recorded higher click rates for spinner dolphins during periods of transition between foraging stages. Further work is being done to explore these possibilities, including a spatial and temporal examination of behavior and call data with multiple widely space hydrophones.

Series of pulsed calls were recorded for many of the groups, and again had the highest rates during mixed forage behavior. It may be that these calls communicate specific information during the transitions between behaviors. Alternatively, these complex call series could be representative of social behavior. Pilot whale calls, including whistles and pulsed sounds, increased in complexity with surface active behavior (Weilgart and Whitehead 1990), and Hector's dolphin (*Cephalorhynchus hectori*) increased their "cry" calls during surface active and aggressive behavior (Dawson 1991b).

While there was a positive trend of increasing call rates with larger group sizes, behavior was a better indicator of call rates. In fact, rather than absolute group size, the spread of the group may be more strongly correlated to call rate as has been noted for common dolphins (*Delphinus* sp.) (Henderson et al. 2009). For example, the single group of Pacific white-sided dolphins with 200 animals was very spread out in foraging subgroups, with subgroups coming together at the end of the sighting. More clicks and pulsed calls were detected at the beginning of the sighting when the animals were spread out than at the end when they were closely spaced. This may indicate that over longer observation periods there could be changes in group composition or size related to behavior, similar to the fission-fusion effect as groups transition between behaviors as has been observed for spinner and dusky (*Lagenorhynchus obscurus*) dolphins (Norris and Dohl 1980; Würsig and Würsig 1980). While the inclusion of group size increased the correct classification rates in the random forest models, this improvement seemed to be behaviorally specific. As such, improvement may be an artifact of sample size, and an increased number of observations may help to reduce a possibly spurious effect. Alternately, call rates for some behaviors may be influenced by group size while in other cases the behavior alone may determine call rates. Ultimately these data demonstrate that group size estimates may be difficult to obtain from acoustic data alone, and that an understanding of the behavior will make those estimates more accurate.

These results will be used to begin to build a model of habitat use for Pacific white-sided dolphins in the SCB region, where a number of autonomous recording packages have been deployed since 2000 (Wiggins 2003; Oleson *et al.* 2007b). Recordings with Pacific white-sided dolphin acoustic data will be analyzed to examine behavior patterns over time and space. For example, foraging behavior can be identified, hotspots localized, and with additional oceanographic data, examined to detect patterns in sea surface temperature, salinity, chlorophyll or other parameters that may also correlate with feeding. Travel behavior could also be tracked to examine seasonal migrations, or illuminate frequent routes to feeding hotspots. There already appear to be some reliable differences in diel behavior, and with further work seasonal behavior patterns could be identified and compared between click type A and B groups. Finally, and perhaps most importantly, a baseline of “normal” acoustic behavior could be established to gauge against anthropogenic stressors such as heavy shipping traffic, sonar, and other acoustic signals that change the ambient noise level.

Conclusions

Pacific white-sided dolphin vocalizations differed across behavioral states, with strong correlations between surface and acoustic behavior for forage, moderate/fast travel, slow travel, and mixed forage behaviors. These correlations were used to predict behavior based solely on acoustic data, and will it possible to examine diel and seasonal behavior patterns across a wider spatial and temporal range than visual surveys allow. These behavioral patterns can provide insight into feeding hotspots and other areas of important habitat use, and can potentially be used as a framework against which anthropogenic impacts could be assessed. Finally, strong differences in calls and behavior provide further support for the hypotheses that click type A and click type B groups represent unique populations that overlap in the SCB, have developed distinct click types, possibly indicating that these populations are cryptic species or subspecies, and potentially have partitioned their prey resources to reduce overlap.

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Chapter 3, in full, is currently in preparation for submission. Henderson, E E., Hildebrand, J.A., and Smith, M.H. Classification of Behavior Using Vocalizations of Pacific White-Sided Dolphins (*Lagenorhynchus obliquidens*). The dissertation author was the primary investigator and author of this material.

Table 3.1 - Descriptions of the behavioral categories used for analysis.

Behavior	Description
Travel	■ Categorized by speed: slow, moderate or fast ■ Move in same direction ■ Move steadily/rapidly ■ Typically synchronous and frequent surfacings
Forage	■ Variable direction of movement ■ Generally remain in same area ■ Individuals spread out or in small clusters ■ Often repeated high arching dives/leaps ■ Possible fish chasing/tossing, or sudden bursts of increased swim speed
Mill	■ Variable direction of movement ■ Remain in one area, individuals in close proximity ■ Slow swimming speeds ■ No surface active behavior, contact, or long dives; stay near surface

Table 3.2 - Summary of effort and number of Pacific white-sided dolphin groups sighted for all surveys.

Survey	**Effort (days)**	**Total Number of Groups**	**Number of Click Type A Groups**	**Number of Click Type B Groups**
FLIP 2006	17	14	2	12
FLIP 2007	27	4	3	1
FLIP 2008	25	5	1	4
SCI 2006	9	1	1	--
SCI 2007a	4	1	1	--
SCI 2007b	5	1	1	--
SCI2008	10	2	2	--
TOTAL	**97**	**28**	**11**	**17**

Table 3.3 - Percent correct classification of surface behavior based on call features for random forest models with group size and clicks/calls per individual included as predictor variables.

Behavior	**All Groups**	**Click Type A Groups**	**Click Type B Groups**
Forage	77.8%	0.0%	87.3%
Mixed Forage	32.4%	60.0%	17.6%
Mill	67.7%	50.0%	78.3%
Slow Travel	74.7%	78.9%	70.1%
Mod/Fast Travel	61.9%	23.1%	77.0%

Table 3.4 - Percent correct classification of surface behavior based on call features for random forest models with group size and clicks/calls per individual excluded as predictor variables.

Behavior	**All Groups**	**Click Type A Groups**	**Click Type B Groups**
Forage	53.1 %	0.0 %	63.4 %
Mixed Forage	71.7 %	33.3 %	76.8 %
Mill	14.9 %	45.0 %	5.9 %
Slow Travel	72.2 %	81.7 %	59.8 %
Mod/Fast Travel	54.9 %	7.7 %	59.8 %

Table 3.5 - Percent correct rates of predicted surface behavior using call feature data for 4-fold pseudo-jackknifed random forest models. Group size and clicks/calls per individual were excluded as predictor variables.

.

Behavior	**All Groups**	**Click Type A Groups**	**Click Type B Groups**
Forage	51.6%	2.5%	67.0 %
Mixed Forage	62.3%	37.6%	67.6 %
Mill	21.2%	43.2%	7.1 %
Slow Travel	70.5%	78.3%	55.9 %
Mod/Fast Travel	45.6%	15.4%	59.2 %

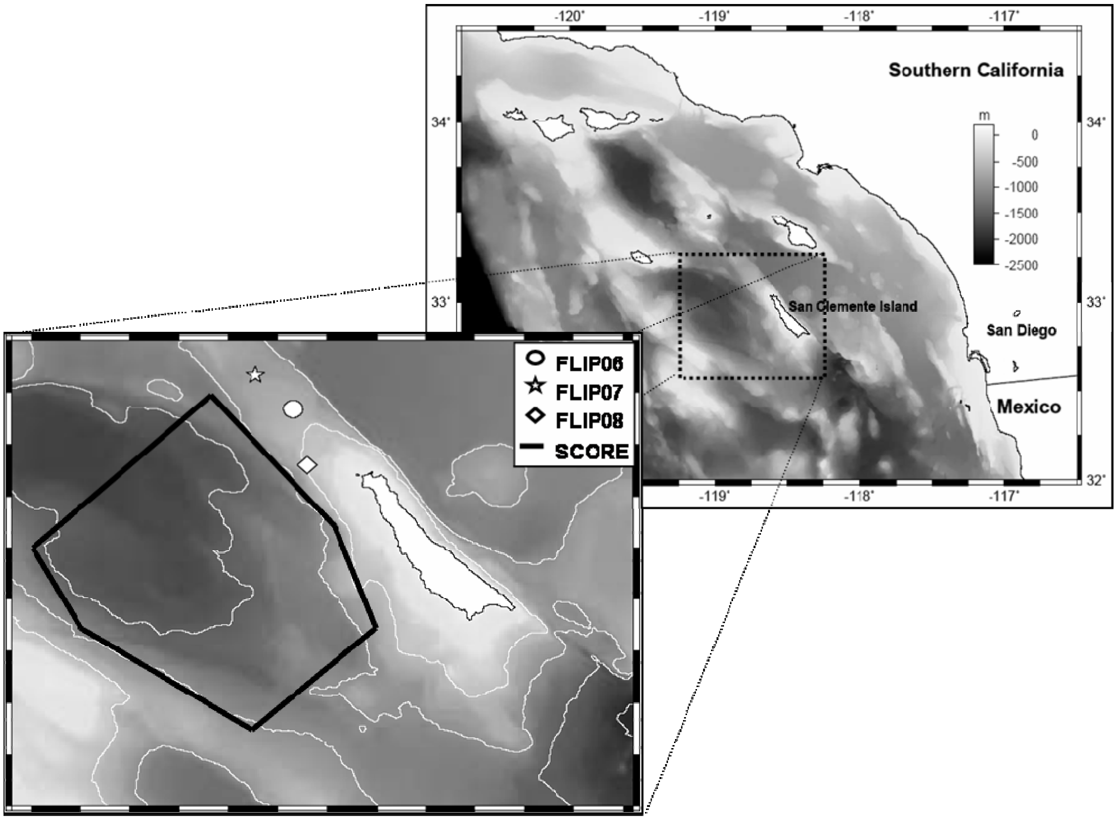

Figure 3.1 - Bathymetric map of Southern California Bight, with an inset of San Clemente Island. The shapes indicate the locations of FLIP moorings in 2006, 2007 and 2008. The dark line outlines the boundary of the SCORE range.

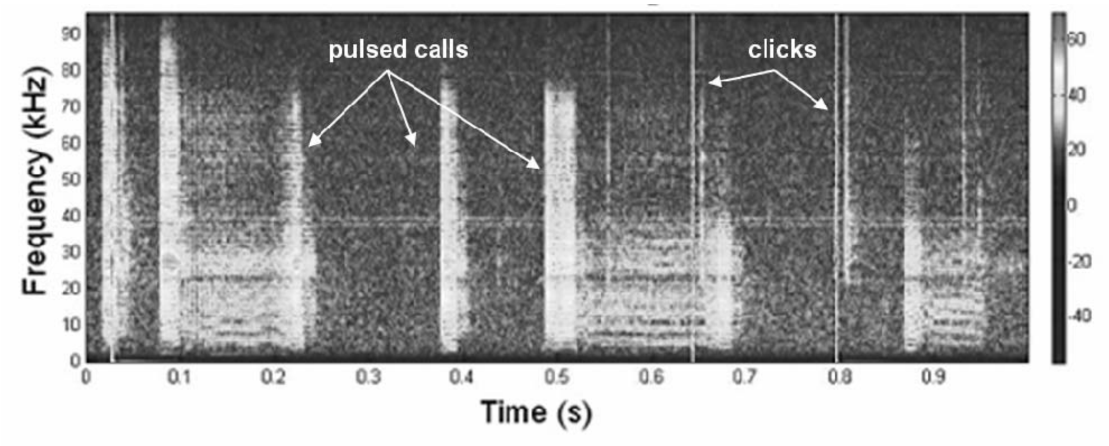

Figure 3.2 - Spectrogram of pulsed call series. Time in seconds is on the x-axis, frequency in kHz is on the y-axis, and intensity of the signal is indicated by color. Clicks are also visible in the spectrogram.

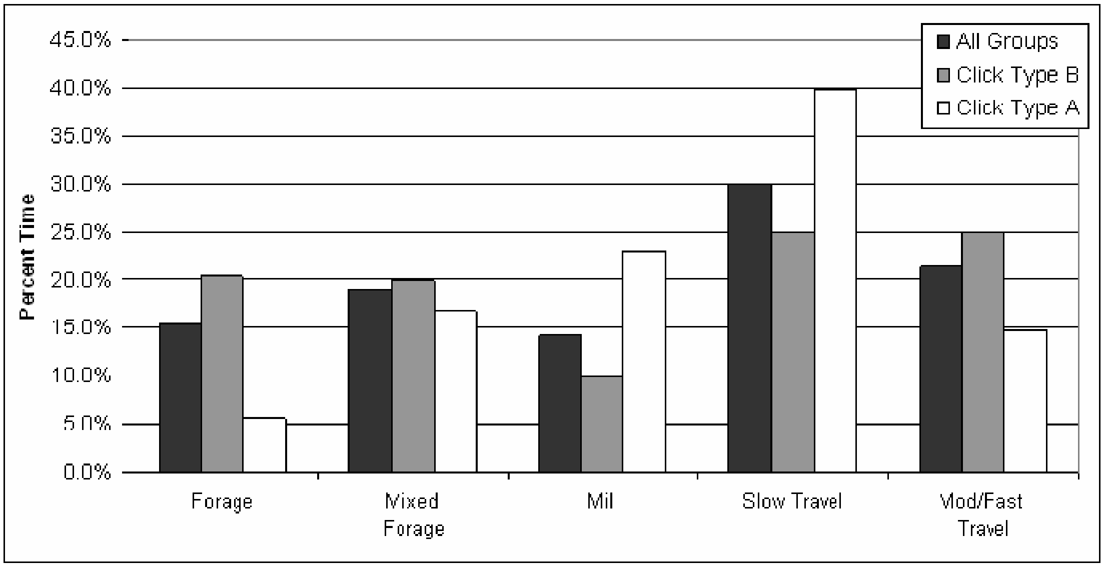

Figure 3.3 - Summary of behavioral data. Bars show the percent of time animals were observed at each behavior, with black indicating all groups, grey indicating click Type B groups and white indicating click Type A groups.

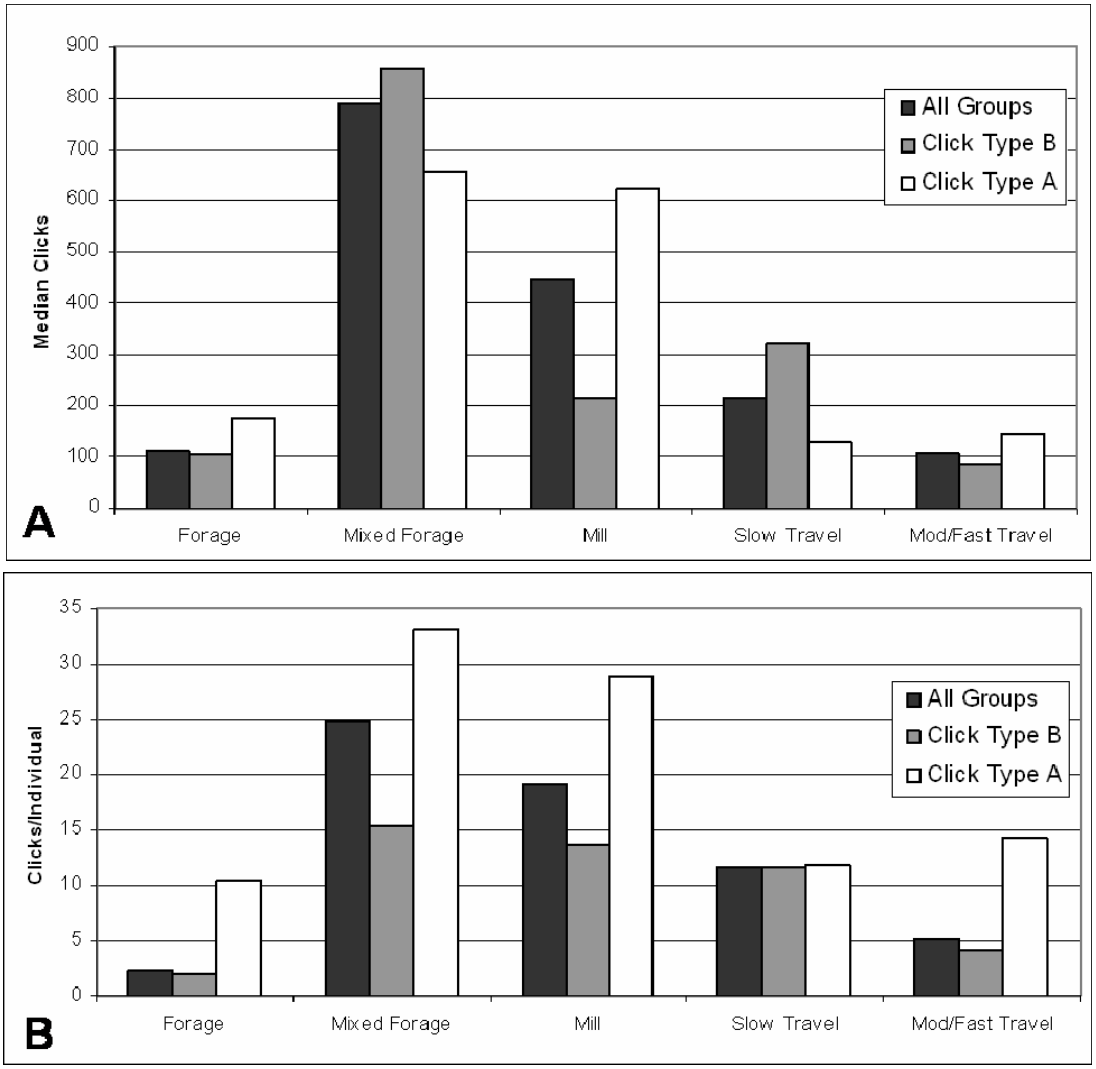

Figure 3.4 - Median click and clicks/individual rates for each behavior. 4A shows overall click rates for all groups in black, Click type B groups in grey and Click type A groups in white. 4B shows the total number of clicks divided by group size, with click rate per individual for each behavior.

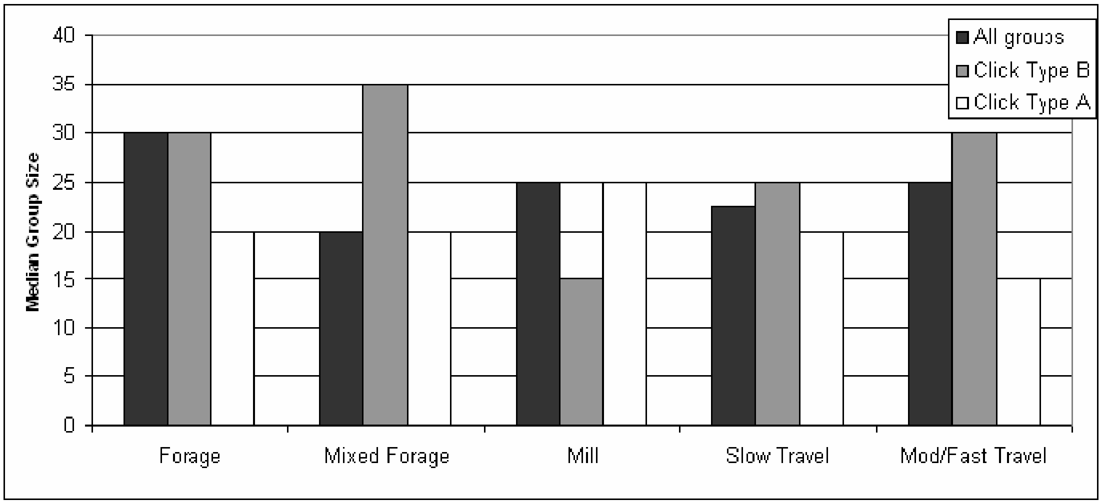

Figure 3.5 - Median group size for each behavior. Group size data for forage behavior is skewed by the inclusion of a 200 animal group. With that group excluded, the median for all groups is 10; the click Type B group median is 10; and the click Type A group median remains 20.

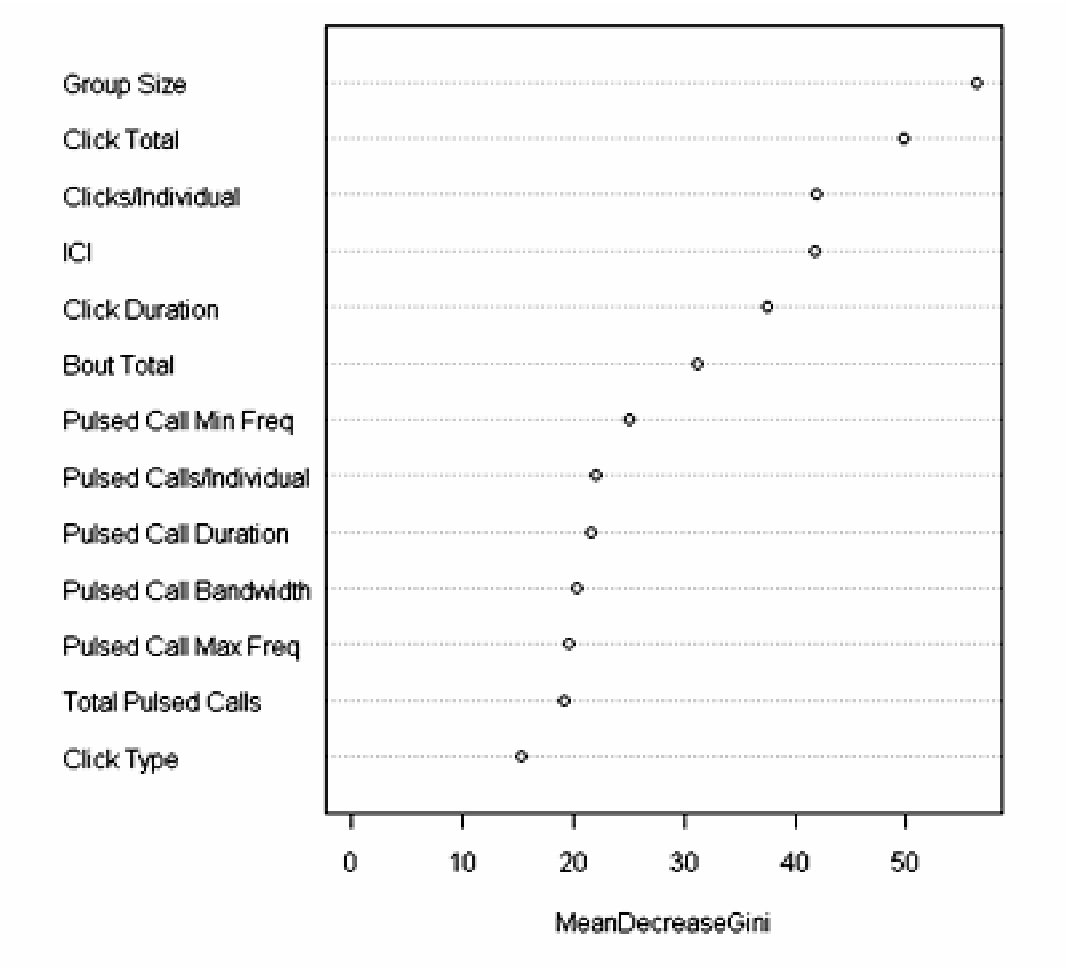

Figure 3.6 - Gini variable importance measures for the final top ranked call features, with group size and calls/clicks per individual included.

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CHAPTER 4

The Role of Marine Mammals as Top Predators: An Analysis of Marine Mammal Occurrence and Oceanographic Patterns in the Southern California Bight

E. Elizabeth Henderson, John A. Hildebrand, and David Demer

Abstract

Oceanographic parameters and all marine mammal sightings were recorded across three years off San Clemente Island in the Southern California Bight from the R/P Floating Instrument Platform (FLIP). We contrast warm, less stratified years (2006 and 2008), with a deep thermocline and deep chlorophyll maximum depth, with a cooler and more stratified year (2007), with a shallow and higher chlorophyll maximum. Encounter rates varied between years, with 2006 the most species-rich year, with a high number of encounters of a variety of species, including five delphinids, four balaenids, two toothed whales, and one pinniped. In 2007, there were few dolphin groups observed but hundreds of fin whales, and several northern elephant seals. In 2008 we had the fewest encounters with any species except California sea lions. In 2008, zooplankton abundances were measured using vertical net tows; non-eucalanid copepods and siphonophores were the dominant taxa, and three patterns of zooplankton abundance were observed. Fish biomass was estimated using a Simrad sonar system with a dual 38/200 kHz transducer; anchovy and jack mackerel were assumed to dominate the aggregations around FLIP, with an estimated

mean biomass of 10.60, SE = 1.7 kg m^{-2}. Fin whales were the most frequent baleen whale species observed, and their abundance correlated with the shallow thermocline and chlorophyll max depths in 2007, and with non-eucalanid copepods in 2008. Common dolphins and Pacific white-sided dolphins were the dominant delphinid species identified. Common dolphin abundance was correlated with the thermocline and chlorophyll max depth in 2007 and zooplankton abundances in 2008, and Pacific white-sided dolphin abundance was correlated with thermocline depth in 2006 and egg and bryozoan larvae abundance in 2008. Finally, California sea lion abundances were correlated with the depths of the thermocline and cholorphyll max, the chlorophyll max value, and with euphausiid abundance in 2008.

Introduction

In the marine realm, marine mammals are top predators whose distributions and abundances have been shown to correlate with that of their prey (Croll *et al.* 1998; Croll *et al.* 2005; Baumgartner and Fratantoni 2008), which in turn fluctuate in abundance following changes in primary and secondary productivity, sea surface temperature, and other oceanographic parameters including currents and mesoscale eddies (Tibby 1937; Muck 1989; Logerwell and Smith 2001; Nishimoto and Washburn 2002). There have been several studies showing close correlations between baleen whale distributions and their zooplankton prey, particularly euphausiids and copepods (Croll *et al.* 2005; Baumgartner and Fratantoni 2008; Santora *et al.* 2010); as top predators of a relatively short food chain, this link is often direct and potentially predictable (Fiedler *et al.* 1998; Friedlaender *et al.* 2006). The correlation is less clear between delphinids and pinnipeds and their fish prey; as top predators in multi-step food webs, there is often a temporal or spatial lag in their distributions relative to oceanographic parameters known to affect fish distribution, such as sea surface temperature (SST), chlorophyll concentrations, or bathymetric features (Au and Perryman 1985; Reilly 1990; Soldevilla 2008). Interannual variability can also strongly influence distribution patterns (Reilly and Fiedler 1994; Defran *et al.* 1999; Benson *et al.* 2002; Heath 2002; Stafford *et al.* 2009).

The dominant epipelagic fish in the SCB are northern anchovy (*Engraulis mordax*), Pacific sardine (*Sardinops sagax*), jack mackerel (*Trachurus symetricus*), Pacific mackerel (*Scomber japnoicus*), ocean sunfish (*Mola mola*), and Pacific saury (*Cololabis saira*), while Pacific hake (*Merluccius productus*) is an important mid-water species, and mesopelagic species include myctophids (e.g. *Diaphus theta*) (Cross and Allen 1993). Anchovy, sardine, hake and saury are planktivorous species, consuming euphausiids and copepods by filter feeding (Bailey *et al.* 1982; Cross and Allen 1993; Rykaczewski and Checkley 2008). Pacific and jack mackerel are opportunistic feeders, consuming both zooplankton and fish eggs and larvae (Cross and Allen 1993; Bertrand *et al.* 2004), and ocean sunfish eat gelatinous zooplankton (Cartamil and Lowe 2004). Sardine, hake and anchovy primarily spawn in the winter and spring in the southern extent of their ranges, including the SCB, although there is some year-round spawning by anchovy (Bailey *et al.* 1982; Cross and Allen 1993; Agostini *et al.* 2006; Checkley Jr. and Barth 2009). In the summer and fall, adult

Pacific hake and Pacific sardine are predominantly distributed further north in the California Current system, while juveniles remain off California (Agostini *et al.* 2008; Checkley Jr. and Barth 2009). The northern anchovy population is largely centered in the SCB, and in fall is generally located inshore (Smith and Eppley 1982). There are also market squid (*Loligo opalescens*) present in the region, although they are most abundant in the spring (Cross and Allen 1993).

This study examines both marine mammal sighting data and oceanographic data across three years to look for correlations between biotic and abiotic factors and marine mammal occurrence patterns. Unlike most studies that model marine mammal distribution or estimate abundance using ship-board observations, where sampling occurs across both spatial and temporal ranges (e.g. Gerrodette and Forcada 2002; Soldevilla *et al.* 2006; Barlow and Forney 2007), we take advantage of a unique point-sampling method, with repeated measures taken in a similar location and season across three highly varied years. We monitor species from three marine mammal groups: mysticetes (baleen whales); odontocetes (toothed whales); and pinnipeds (seals and sea lions), while concurrently assaying oceanographic features using a variety of tools. The objectives of this study were to sample oceanographic parameters and estimate the abundance of organisms representing multiple trophic levels, to examine the relationships between those parameters, and to correlate them with marine mammal sightings.

Methods

Study Area

This research was conducted in the Southern California Bight (SCB) near San Clemente Island, about 60 miles offshore of San Diego (Figure 1). The SCB is dominated by the southward flowing California Current, a cool, low saline, subarctic water current (Hickey 1993; Hickey *et al.* 2003; Caldeira *et al.* 2005). In addition, there are two poleward flowing currents, the California Countercurrent and the California Undercurrent, both of which bring warm, saline Equatorial waters north (Reid *et al.* 1958; Hickey 1993). The California Current is strongest and closest to shore in spring, when there is predominantly equatorward flow in the SCB and sea surface temperatures are cooler. In contrast, in summer and fall the California Countercurrent dominates, bringing warmer water further north and west into the SCB and pushing the California Current further offshore. There is also much interannual variability in the timing and strength of these currents. Finally, the region is bounded on the west by the North Pacific gyre, consisting of warm, saline North Pacific Central Water (Norton *et al.* 1985). The oceanographic diversity of this region supports populations of a variety of marine mammals, including at least ten species of delphinid, seven mysticete species, and four pinniped species.

Data Collection and Analysis

Data were obtained in three field seasons in the fall of 2006 through 2008 using the Scripps Institution of Oceanography R/P FLIP (Floating Instrument Platform, Fisher and Spiess 1963), a live-aboard stationary moored platform from which visual observations were conducted and oceanographic and biological parameters were measured. FLIP was deployed northwest of San Clemente Island from October 2 – November 3 in 2006 in 637 m water depth; October 30 – November 29 in 2007 in 840 m water depth; and October 17 – November 14 in 2008 in 347 m water depth (Figure 1). Although these sites are in close proximity, differences in water depth and distance to San Clemente Island could lead to differences in marine mammal encounter rates.

Oceanographic sampling - In 2006, a Sea-bird SBE39 CTD measuring temperature and pressure was deployed once or twice a day to a depth of approximately 180 m. In 2007 and 2008, a Sea-bird 29 CTD with temperature, pressure and fluorescence sensors was deployed daily to a depth of approximately 150 m. In all years, data were downloaded after each deployment using SBE Data Processing software (Sea-Bird Electronics, Bellevue, WA) and were binned in 2 m depth bins. Downcast data were used for temperature, density and salinity, while upcast data were used to estimate fluorescence. The daily thermocline and pycnocline depths were calculated as the depth with the maximum change in temperature or density, respectively. Satellite-derived SST data for each cruise were taken from NOAA Advanced Very High Resolution Radiometer (AVHRR) Pathfinder satellite data, with a spatial resolution of about 4.1 km (http://podaac.jpl.nasa.gov/DATA_CATALOG/sst.html). Weekly averaged SSTs were calculated using Windows Image Manager (WIM, M. Kahru, SIO).

Zooplankton abundance - In 2008, daily vertical net tows were added, using a custom-built 1 m double bongo net with a 333 μm mesh size. An 11.4 kg weight was attached to the spreader bar below the cod-end pieces to ensure a vertical deployment. No flow-meter was used, so resulting zooplankton counts were considered relative rather than absolute abundances. In addition, nets were deployed to a depth of either 40 or 80 m, depending on the strength of the current, but zooplankton abundances were standardized to abundance m^{-2} by dividing by the tow depth. While there may be some differences in taxa sampled at 40 m versus 80 m, diel vertical migrators are typically located at depths greater than 200-400 m during the day (Frost and McCrone 1979; Thomson and Allen 2000), therefore in the top 100 m zooplankton taxa should be relatively similar. Samples were preserved using a 5% solution of Formalin and supersaturated sodium borate decahydrate in pint-size glass jars topped with sea water (Annie Townsend, Scripps Institution of Oceanography, personal communication). Zooplankton samples were fractionated using a 2.5 mm mesh and scanned using ZooScan (Gorsky *et al.* 2010), a digital-imaging system. Individual images were sorted using a learning dataset developed with Plankton Identifier (Gorsky *et al.* 2010) by the Ohman lab (Scripps Institution of Oceanography), and then all image classifications were manually verified. Finally, feret dimension and cross-sectional area measurements were made using the ZooScan images.

Acoustic estimation of fish biomass and behavior – A dual-frequency (38 and 200 kHz) echosounder system (ES60, Simrad, Kongsberg Maritime, Horten, Norway) was used in 2008 to measure fish abundance and observe their behavior around FLIP. The echosounder was configured with a dual-frequency transducer (Combi-B, Simrad), which was attached 6.1 m below the water line on the hull of FLIP. The transducer was oriented to project horizontally. At 38 kHz, the beamwidths were 13° vertically and 21° horizontally, and the transmitted pulse durations were 0.256 ms. At 200 kHz, the beamwidths were 7° both vertically and horizontally, and the transmitted pulse durations were 1.024 ms. The measurements of volume backscattering strength (S_v; dB re 1 m^{-1}) at both frequencies were thresholded below -70 dB. The sonar system was calibrated before the cruise using standard sphere methods (Johannesson and Mitson 1993). Because it was unknown whether the sonar would have any effect on the behavior of marine mammals, it was only operated for 10-20 minutes every two hours between 5:00 to 22:00 (local time), every other day. Additionally, the sonar transmissions were stopped when marine mammals were observed visually within 5 km of FLIP.

The echosounder software (Simrad ES60) adds a time-varying systematic error to the S_v data. Consequently, another program (Ryan and Kloser 2004; Keith et al. 2005), was used to remove this bias before analyzing the data in a sonar analysis program (Echoview, Myriax Software Ltd, Tasmania, Australia).

Target strength (*TS*, dB re m^2) values were estimated at 38 and 200 kHz for fish and zooplankton observed at dorsal aspect, following Furusawa (1991), Trevorrow (2005), Barange and Hampton (1996; 1997), and Demer (2010) (Figure 2). However, the sonar measurements were made of animals at lateral aspect. Maximum S_v values may be higher and the mean S_v values may be lower for lateral versus dorsal incidence angles (Cutter and Demer 2007). Consequently, biomass estimates resulting from sonar measurements of S_v and dorsal-aspect TS are likely to be inflated. The TS estimates were converted to scattering volume (S_v, dB re 1 m^2/m^3) estimates using:

$$S_v = TS - 20\log r - 10\log(c\tau\psi/2) + C,$$

where r is the range from the transducer, c is sound speed (m/s), τ is the transmitted pulse duration (s), ψ is the two-way beam angle, and C is the calibration constant. The ψ values are $10^{(-13.3/10)}$ and $10^{(-20.7/10)}$ for the 38 and 200 kHz transducers, respectively. The difference in S_v at 200 kHz and 38 kHz (ΔS_v) was calculated and used to identify echoes from fish ($-30 < \Delta S_v < 3$ dB) and echoes from zooplankton ($3 < \Delta S_v < 35$ dB) in the original 38 and 200 kHz echograms (Figure 2). The S_v data apportioned to these taxa were then integrated in 1 m by 1 min cells, and in 53 m by 60 min cells, resulting in estimates of the area backscatter coefficients (S_a; m^2/m^2):

$$S_a = 10\ S_v /10 * T,$$

where T is the height of the integration cell. Finally, S_a for the i-th taxa (S_{ai}) was used to estimate its biomass density (ρ_i; kg/m^2):

$$\rho_i = S_{ai} / 10^{(TS_i/10)},$$

The actual proportions of each candidate species in the study area were not known. To explore possible ranges in total fish biomass, hypothetical proportions were estimated as 0, 25, 50, 75 and 100%. While no quantitative sampling regime was implemented to identify fish species, qualitative observations of species presence were made in all years, particularly in 2008 when an experienced fisherman was able to catch and identify several species.

Marine mammal monitoring - Observers in the crow's nest of FLIP, located 26.5 m above the waterline, monitored the ocean 360° around FLIP, recording all marine mammal and vessel sightings throughout daylight hours in Beaufort sea state 5 or less. Observers used both the naked eye and 7x50 Fujinon binoculars, containing a reticle scale to estimate distance and a magnetic compass to estimate bearing. In addition to distance and bearing, observers recorded the species, group size, general behavioral state, and an estimate of the number of calves present. All groups were monitored for the duration of their occurrence near FLIP, with sighting locations updated every 5-10 minutes. Each group was counted only once for this analysis regardless of their encounter duration, and the best group size estimate was used. Finally, environmental data (Beaufort sea state, swell height, cloud cover, and visibility) were collected hourly, or as conditions changed. California sea lions were frequently observed around FLIP, presumably drawn by the fish aggregations as they were frequently observed foraging on the aggregated fishes, and several would often return on multiple days. Since no photo-identification effort was conducted, California sea lion sighting numbers may be slightly inflated if individuals remained close to FLIP for multi-day periods.

Correlation coefficients were calculated for each year using the non-parametric Spearman's rank test (r_s) between the number of individuals encountered per day of each species of marine mammal (number of sightings multiplied times mean group size), daily mean Beaufort sea state, daily thermocline depth, daily deep chlorophyll maximum (DCM) values and DCM depth, and daily abundance estimates for each of the most abundant zooplankton taxa. Correlation coefficients were also calculated between each of the above parameters for each applicable year, to look for relationships between zooplankton and fish abundances and oceanographic processes such as mixing, advection, or fronts. A Bonferroni correction was applied to the resulting correlation data to correct for multiple comparison testing, and results are compared between the original results and the corrected results.

Results

Marine mammal composition - There were a total of 97 days of visual effort across three years. Five species of delphinids were identified, including long-beaked common dolphins (*Delphinus capensis*), short-beaked common dolphins (*D. delphis*), Pacific white-sided dolphins (*Lagenorhynchus obliquidens*), bottlenose dolphins (*Tursiops truncatus*), and Risso's dolphins (*Grampus griseus*), although bottlenose and Risso's dolphins were both only observed in 2006. Five species of large whale were observed, including the only species of odontocete whale, sperm whales (*Physeter macrocephalus*), as well as the baleen whale species blue whale (*Balaenoptera musculus*), fin whale (*Balaenoptera physalus*), minke whale

(*Balaenoptera acutorostrata*), and humpback whale (*Megoptera novaeangliae*). One beaked whale species, Cuvier's beaked whale (*Ziphius cavirostris*) was observed. Two species of pinniped were documented, California sea lions (*Zalophus californianus*) and northern elephant seals (*Mirounga angustirostris*). Table 1 summarizes the number of groups sighted for each species across all three years. The most species-rich year was 2006, with five species of dolphin and four species of baleen whale observed, plus the only sightings of a sperm whale and Cuvier's beaked whales, and the highest total number of observations as well. Fewer, smaller dolphin groups were observed in 2007, but there were a very high number of whales, fin whales in particular, as well as a high number of California sea lion and northern elephant seals. Finally, 2008 had the fewest number of species and the fewest observations overall for dolphins and whales but was the most abundant year both in number of sightings and group size for California sea lions. Time series of these observations are shown in Figure 3 (A-C).

Oceanographic parameters - The daily mean Beaufort sea state, mean swell height in meters, and temperature and fluorescence profiles are shown in Figure 3 (D-F), while T-S diagrams for 2007 and 2008 are depicted in Figure 4. 2007 was the coolest year, with more stratification in the water column, a weaker pycnocline and a shallow thermocline. The mean thermocline depth was 34.3 m, the mean pycnocline depth was 35.0 m, and the deep chlorophyll maximum (DCM) occurred at 17.0 m depth, with an average DCM value of 6.67 μg/l (median = 6.17 μg/l). In contrast, 2008 was the warmest year with a deeper pycnocline and windier conditions, leading to greater mixing. Mean thermocline depth was 32.2 m, mean pycnocline depth was 40.7 m, and mean DCM depth was 35.6 m, with a mean DCM of 6.47 μg/l (median = 4.82 μg/l). 2008 also had the strongest storm fronts, particularly during the last week of observations, which led to an increase in mixing and a shoaling of the thermocline towards the end of the cruise. 2006 appears to fall between these years, with warmer temperatures than 2007 but also a deeper pycocline, as in 2008. In fact, the mean thermocline depth was the deepest in 2006, at 37.4 m. Satellite SST images, averaged over each of four weeks for each cruise, are shown in Figure 5. The uniformity of cool SST's are evident in 2007, while the warm, poleward flowing California Countercurrent can be seen in 2006 and 2008. In 2006, the warmest waters remain inshore of the Channel Islands, while in 2008 they extend further offshore. This may be why our sensors measured warmer ocean temperatures in 2008, while satellite images indicate that 2006 was warmer.

Zooplankton abundance - Zooplankton abundances m^{-2} for each daily net tow are shown in Figure 6, while length distributions are shown in Figure 7. Non-eucalanid copepods, including species from the orders Poecilostomatoida, Harpacticoida and Calanoida (e.g. *Calanus pacificus*), were the most abundant zooplankton taxa, with a mean of 11.61 m^{-2}. While this group was dominated by small calanoids, all three orders were lumped to distinguish them from the larger eucalanid copepods (e.g. *Eucalanus californicus*; Figure 7) which had a much lower abundance of 1.23 m^{-2}.

Siphonophores, including calycophorans, hydrozoan medusas, and ctenophores, were the second most abundant group at 6.14 m^{-2}. The other top zooplankton taxa were appendicularians (larvaceans), such as *Oikopleura* sp., with a mean abundance of 2.38 m^{-2}, and bryozoan larvae at 2.35 m^{-2}. Fish eggs had a mean abundance of 3.32 m^{-2}. Euphausiids (e.g. *Euphausia pacifica* and *Thysanoessa spinifera*) were present, but in low numbers (mean abundance of 1.25 m^{-2}) and mostly in calyptopis, furcilia and juvenile phases rather than as adults. *E. pacifica* is a diel vertical migrant (Brinton 1967; Ohman 1990), and the adult phase was likely well below the mean 60 m depth we sampled during the day. Other zooplankton recorded included chaetognaths, ostracods, other crustaceans such as hyperiid amphipods and decapods, polychaetes, doliolids, salps and pteropods (e.g. *Limacina* sp. and *Cavolinia* sp.).

Local abundance varied substantially for each group, with three apparent patterns (Figure 6). The first group included siphonophores, euphausiids, eucalanid copepods, polychaetes and chaetognaths. This group had an early peak in abundance and then a decrease, and finally another peak in the last week, during and after the two major storms. The second pattern, exemplified by fish eggs and bryozoan larvae, was a presence in low levels, with some fluctuation in the first few weeks, but then a peak in abundance in the last, stormy week. The third pattern, demonstrated by the non-eucalanid copepod taxa, ostracods and appendicularians, was a lower abundance in the first week, then an increase, remaining at relatively high levels for the duration of the cruise. This increase in abundance occurred just after the peak in chlorophyll (Figure 2F).

Parameter correlations - Correlation coefficients were calculated for oceanographic parameters and encounter rates of common dolphins (lumped together as *Delphinus* sp. since long-beaked common dolphins were only sighted in 2006), Pacific white-sided dolphins, Risso's dolphins (2006 only), bottlenose dolphins (2006 only), fin whales, blue whales, minke whales (2006 and 2007 only), humpback whales, California sea lions and northern elephant seals (2007 and 2008 only). These were calculated between the number of individuals encountered per day, the mean daily Beaufort, daily thermocline depth, daily DCM and DCM depth (2007 and 2008), and daily abundance estimates for appendicularians, bryozoan larvae, fish eggs, eucalanid and non-eucalanid copepods, siphonophores and euphasiids (2008 only). This led to a matrix of r_s-values and a matrix of p-values for each year, with an initial significance level of $p = 0.05$ (Appendix I). Subsequent Bonferroni corrections reduced the number of significant results, such that for the 3 correlations per species in 2006 the new p-value was 0.017, for the 10 correlations per species in 2007 the new p-value was 0.005, and for the 66 correlations per species in 2008 the new p-value was 0.00075. P-values reported below are only considered significant under the Bonferroni correction if they fall below those values, and are italicized.

Beaufort sea state correlated negatively with several species in both 2006 and 2008, but not in 2007. In 2006, minke whale sightings were negatively correlated with Beaufort sea state (r_s = *-0.46*, p = *0.014*), as were Pacific white-sided dolphin sightings (r_s = *-0.48*, p = *0.01*). Only California sea lion sightings negatively correlated with

Beaufort in 2008 ($r_s = -0.56$, $p = 0.004$). This result is not surprising for 2006 or 2007; the winds and sea state fluctuated throughout 2006, and smaller or more elusive cetaceans such as dolphins and minke whales become more difficult to see in rougher conditions, while 2007 was relatively calm most of the time. However, 2008 also had some strong storm fronts move through, and so it is interesting that dolphin sightings did not correlate with sea state. It may be that the correlation occurred in 2006 due to the high number of dolphins in the area, so daily fluctuations in sighting numbers were more noticeable, whereas in 2008 there were an overall lower number of dolphin sightings per day, and so the correlation with sea state was not significant.

Thermocline depth was also correlated with marine mammal sightings in all three years. In 2006, the number of of blue whales negatively correlated with the thermocline depth ($r_s = -0.35$ and p approached significance at 0.067), while the number of Pacific white sided dolphins were positively correlated ($r_s = 0.45$, $p = 0.017$). In 2007, fin whale sightings were correlated with the thermocline depth ($r_s = 0.46$, $p = 0.021$). In 2008, California sea lion sightings correlated with thermocline depth ($r_s = 0.63$, $p = 0.001$), DCM depth ($r_s = 0.57$, $p = 0.004$) and the DCM value ($r_s = 0.58$, $p = 0.003$). In 2007 and 2008, the thermocline depth correlated with the DCM ($r_s = 0.44$, $p = 0.029$; $r_s = 0.71$, $p < 0.001$) and the depth of the DCM ($r_s = 0.56$, $p = 0.004$; $r_s = 0.65$, $p < 0.001$), and the DCM was correlated with its depth ($r_s = 0.39$, p approached significance at 0.054; $r_s = 0.65$, $p < 0.001$).

In 2008, fin whale sightings were correlated with non-eucalanid copepod abundance ($r_s = 0.46$ and $p = 0.023$). Common dolphin sightings were positively correlated with all seven zooplankton taxa (r_s ranges from 0.37 to 0.55, p ranges from 0.074 to 0.005). Pacific white-sided dolphin sightings were correlated with egg abundance ($r_s = 0.41$, $p = 0.044$) and bryozoan larvae abundance ($r_s = 0.38$, p approaches significance at 0.067). The zooplankton taxa were all correlated with each other as well (r_s ranges from 0.51 to 0.96, p ranes from 0.012 to <<0.001).

There were also correlations between zooplankton groups and oceanographic parameters. The thermocline depth was correlated with siphonophore ($r_s = 0.4$, $p = 0.053$) and euphausiid ($r_s = 0.52$, $p = 0.009$) abundances, while the DCM value correlated with euphausiids as well ($r_s = 0.4$, $p = 0.052$). These correlations suggest a relationship between the abundances of these species and either advection or deep mixing concurrent with storm fronts.

Echosounder data and fish biomass - Results from the analyses of echosounder data are shown in Figure 8. The S_v data for each day were plotted versus range from 1 to 53 m and in one minute by one meter bins (Figure 8, top row). At larger ranges, the 38 kHz beam intersects the sea surface and the reflections confound the data. This assumption is supported by strong correlations between the Beaufort sea state and the daily mean S_v from 53-100 m range at 38 and 200 kHz ($r = 0.69$, $p = 0.38$; $r = 0.69$, $p = 0.039$). However, as evidenced by changes in the mean daily S_v in the 3 to 53 m ranges (Figure 8, middle row), the reflections off the sea-surface were occurring at ranges closer than 53 m on days with stronger winds, at both 38 and 200 kHz, although the correlations were not significant.

There does not appear to be a diel pattern in S_v for zooplankton. However, there is a slight decrease in the S_v attributed to fish during the day (Figure 8, bottom row). Apparently, fish are attracted to FLIP during the day and gather in large fish balls, as evidenced by the strong backscatter at close range in Figure 8 (top row). These schools then disperse at night.

The fish biomass was estimated using the S_v data, and assumptions were made regarding the proportions of the four most common fish in the Southern California Bights (SCB): northern anchovy, Pacific sardine, Pacific mackerel and jack mackerel (Kramer and Smith 1971; Smith and Eppley 1982; Cross and Allen 1993; Cartamil and Lowe 2004; Emmett et al. 2005). Pacific hake, although an important fish species in this region, has a midwater distribution and is less likely to aggregate around FLIP during the day; additionally this fish migrates offshore and north during the fall to feed and is therefore less abundant at this time (Bailey et al. 1982). A total length (TL) range of 15-22 cm was assumed for anchovy, 10 – 30 cm for sardine, 25 – 60 cm for jack mackerel, and 30 – 55 cm for Pacific mackerel (Cross and Allen 1993; Barange *et al.* 1996; Bertrand *et al.* 2004; Demer *et al.* 2010). These length ranges assume that the fish of all species present, except sardine, were mostly adults; sardine would more likely be juveniles in this area at this time (Lynn 2003; Checkley Jr. and Barth 2009). The hypothetical proportions used for each species were 0, 25, 50, 75 and 100%, and were integrated across the closest 53 m of range and for the duration of each scan. The average sound speed (c) in 2008 was calculated to be 1507.8 m/s. The estimated density of each species ranged from 0.002 to 769.4 kg/m^2. Table 2 summarizes the results for each species. Density estimates were generally largest for mackerel, but were variable across days for all species. For example, on 10/29, anchovy: mean = 22.17 kg/m^2, sd = 32.64; sardine: mean = 28.89 kg/m^2, sd = 40.20; and Pacific and jack mackerel: mean = 185.04 kg/m^2, sd = 250.09; and on 10/25, anchovy: mean = 0.44 kg/m^2, sd = 0.40; sardine: mean = 0.53 kg/m^2, sd = 0.48; and Pacific and jack mackerel: mean = 3.39 kg/m^2, sd = 3.05. Histograms of fish densities at each estimated proportion are shown in Figure 9.

Discussion

Marine mammal occurrence patterns fluctuate with changes in oceanographic regimes that impact primary and secondary production, as well as fish abundance and species' assemblages (Pyle and Gilbert 1996; Tynan *et al.* 2005). While the sampling location or time of year was held relatively constant across the three years examined here, the oceanography of the area did change from year to year, and a response was observed in the species and numbers of marine mammals present. Over a larger spatial scale these sampling locations are fairly similar, however on a micro-habitat level they vary in depth and proximity to the island, therefore some site differences may also exist in these results that cannot be teased apart from the inter-annual variability.

Oceanographic synthesis – The warmest of the three years was 2006, with a deep pycnocline and deep thermocline, with moderate storms occurring every 4-6 days, consistent with the 2-6 day weather fluctuations observed in the northern California Current system (Bane *et al.* 2007). As shown in the satellite SST data, the water inshore and south of San Clemente and Santa Catalina Islands was much warmer than the water just offshore of the islands, indicating the strength of the poleward flowing California Countercurrent and possibly indicating the presence of a front very near the location of FLIP. This year had the highest number of dolphin and whale species represented as well as the most dolphin sightings. Risso's dolphins, bottlenose dolphins, sperm whales and beaked whales were only observed in this year, although both dolphin species are common in the SCB, and Cuvier's beaked whales have been frequently observed in the deep water off San Clemente Island (Falcone *et al.* 2009). In addition, this was the only year without northern elephant seals.

In stark contrast, 2007 was a much colder year, with a stratified water column, shallow but high chlorophyll concentrations, and the fewest storms and calmest wind patterns of all three years. This year also had an incredibly high number of fin whale sightings, while dolphin sightings were few and dolphins were observed in smaller groups. In addition, a distinct pattern in both the oceanography and corresponding marine mammal sightings was observed, with cooler temperatures and higher chlorophyll concentrations in the first half of the cruise, along with high fin whale sightings each day. In the second half of the cruise, the sea surface temperature was warmer, the chlorophyll concentration decreased and the DCM shoaled. At the same time, fin whale sightings decreased significantly and northern elephant seals were observed almost daily, although they had not been observed in the first half of the cruise. Fin whale sightings and group size were strongly correlated with the DCM and thermocline depth; the cool SST's and shallow pycnocline may have entrained phytoplankton and zooplankton near the surface, leading to an increase in grazing behavior by fin whales.

In 2008 we were able to sample more levels of the pelagic food chain, and to make some additional links between the measured oceanography and the observed marine mammal distributions. This was the warmest year as measured on FLIP, however as shown in the satellite SST data, it appears as though the warm tongue of the California Undercurrent had moved further offshore than in 2006 and could be measured by our sensors. The DCM was also twice as deep as it was in 2007, and while there was a strong peak in chlorophyll in the first week, there was very little measured for the duration of the cruise. The pycnocline was also deep, but this year had more storms and stronger winds, particularly in the last week, which caused the surface layer to mix and then shoal. The fewest number of whales was observed in 2008, and while dolphin sightings were moderate, they occurred in large groups that grew larger towards the end of the cruise. California sea lions were quite abundant this year as well, particularly in the first half of the cruise, and were correlated with the depth of the thermocline and DCM.

There were also some significant correlations between marine mammal and zooplankton abundances. The correlation between fin whales and non-eucalanid copepod abundance is somewhat surprising, as these whales predominantly forage on larger krill or fish (Simard *et al.* 2002; Santora *et al.* 2010), and the size class of the non-eucalanid copepods was small. However, fin whales have been shown to be opportunistic feeders, and can include copepods or cephalopods in their diet (Flinn *et al.* 2002). Also surprising were the correlations between common dolphins, Pacific white-sided dolphins, and California sea lions and the zooplankton. However, these correlations may be indicative of an unsampled trophic link; the fish prey of the dolphins and sea lions could be responding to zooplankton, and a corresponding response was observed in the marine mammals. Common dolphin and Pacific white-sided dolphin group size were also correlated with egg abundance; this could also be indicative of the link between fish prey and dolphin distributions.

Zooplankton abundance - The three observed patterns in zooplankton abundances were likely related to the peak in chlorophyll in the first half of the cruise, the high winds that would have led to increased mixing, and advection into and out of the sampling region. For example, the pattern demonstrated by the siphonophores showed high abundances at the beginning of the cruise, overlapping with the peak in chlorophyll. Once that patch of phytoplankton was grazed down, advected from the area or pushed out by a storm front, siphonophore abundance decreased. However, the strong mixing following the storms in the final week may have brought some of the deeper species to surface (e.g. eucalanid copepods, euphausiids, and some siphonophores), leading to a second peak in abundances. The increased storm activity is also a likely explanation for the pattern demonstrated by non-eucalanid copepods (e.g. Mullin *et al.* 1985), which contrasted with the first group in that their abundances did not peak until after the chlorophyll concentrations decreased, but then remained relatively high for the duration of the cruise.

Fish biomass - Fish biomass estimates were made for northern anchovy, Pacific sardine, and jack mackerel and Pacific mackerel. However, it is most likely that the aggregations around FLIP were predominantly northern anchovy and jack mackerel because these species, along with ocean sunfish, were frequently observed from FLIP (Joe Verissimo, personal communication), and these three species are also associated in the northern California Current (Brodeur *et al.* 2005) along with high temperature and salinity. Nothern anchovy and jack mackerel are also present in the diet of common and Pacific white-sided dolphins (Fitch and Brownell 1968; Walker et al. 1986; Osnes-Erie 1999), the two dominant delphinid species observed in this study and throughout the SCB. Therefore, the best estimates of fish proportions and biomasses are 50% anchovy and 50% jack mackerel, with a range of 0.005 to 88.83 kg/m^2, a mean of 10.60 ± 1.67 kg/m^2, and a median of 4.56 kg/m^2. These estimates are reasonable, even taking into account the potential positive bias due to horizontal versus vertical angles of incidence. Correlations between daily mean fish biomass and visually-estimated abundances of common dolphin, Pacific white-sided dolphin, and California sea lions were not significant; mean fish biomass did negatively correlate with the DCM value ($r_s = -0.68$, $p = 0.05$) but this value was no longer significant after the Bonferroni correction was applied.

Diel vertical migration and other vertical movement patterns were not examined, as S_v varies both with range and vertical movement, and those were difficult to tease apart with a horizontally mounted echo sounder. A diel decrease in S_v was observed for fish due to the aggregations that occurred at close range during the day, and appeared to disperse at night. The horizontal aspect and close proximity to the surface also led to daily S_v differences due to increased sea surface backscatter noise on windy days, which also made an assessment of diel patterns challenging, particularly for zooplankton.

Marine mammal occurrence patterns - While fin whales were the predominant species in 2007, they have been recorded in the SCB year-round (Munger *et al.* 2009), and were observed in all three years of this study. Blue and humpback whales were also recorded in all three years, but in much lower numbers. Oleson (2005) found a fall peak in fin whale call production, while Stafford *et al.* (2009) found a peak in calling from December through March, with a 4-month SST lag. Stafford *et al.* (2009) also recorded fin whales throughout the North Pacific, with similar call rates in the north central, northeast and southeast regions but with slightly different peak calling periods. Fin whale sightings peaked in July and August in the coastal region off British Columbia, and were strongly associated with areas of high productivity and possible zooplankton entrainment (Gregr and Trites 2001). Fin whales are likely migrating throughout the North Pacific and are seasonally found in areas of high productivity. Blue and humpback whales also utilize the SCB as a feeding ground

(Calambokidis *et al.* 2000; Oleson *et al.* 2007a), although blue whale foraging occurs in summer and fall, while humpback foraging peaks in summer (Munger *et al.* 2009). Blue whales forage exclusively on euphausiids (Fiedler *et al.* 1998), and their feeding grounds in the SCB are focused around the northern Channel Islands and Santa Barbara Channel (Oleson *et al.* 2007a), while the humpback whale diet is similar to fin whales, including both zooplankton and fish (Clapham *et al.* 1997). Sightings in the SCB for all three species have been correlated with cool SST's and high zooplankton displacement volumes (Munger *et al.* 2009), which is consistent with our findings.

Northern elephant seal sightings also peaked in 2007. The Channel Islands are a major haul-out site for northern elephant seals, where they breed in winter, and molt in the summer. The rest of the year they are distributed as far west as the Hawaiian and Aleutian Islands, and as far north as the Gulf of Alaska, foraging for mesopelagic fish and squid (Hindell 2002; Reeves *et al.* 2002). It is interesting that their presence showed the opposite pattern than the fin whales; this may indicate a lagged response by the northern elephant seals to the increased productivity in the region. On the other hand, if the fin whales are responding to euphausiids or copepods, it might be expected that they would respond before the northern elephant seals that occupy a higher trophic level.

California sea lions are ubiquitous in the SCB, also hauling out on the Channel Islands year-round. They exhibit a breeding peak in the summer, then males migrate north while females and juveniles remain near the islands, feeding on epipelagic schooling fish, such as northern anchovy or jack mackerel, in upwelled waters near the coast or along the shelf (Lowry *et al.* 1986; Heath 2002; Reeves *et al.* 2002). They were one of the most abundant marine mammals in all three years, although their sightings peaked in 2008, likely due to the close proximity to San Clemente Island haul-out sites. This peak in sightings may be due to the closer proximity of FLIP to San Clemente Island and therefore to California sea lion haul-out sites. In all years they were observed daily around FLIP, opportunistically foraging on the aggregated fishes. As their constant presence made them difficult to count and individuals were certainly resighted, their encounter rate was likely overestimated. However, they did occur in larger groups in 2008 than in other years.

Common dolphins are considered a warm temperate and tropical species, while Pacific white-sided dolphins are considered a cool temperate species. However their distributions overlap in the SCB and both species were sighted all three years (Dohl *et al.* 1986; Walker *et al.* 1986; Forney and Barlow 1998). Common dolphins are found in the SCB year-round, but have a seasonal inshore-offshore migration, while Pacific white-sided dolphins are typically sighted in the SCB from October through April, when SST's are cooler (Forney and Barlow 1998). Both species forage opportunistically on similar prey, including both epipelagic schooling fish and myctophids and squid (Brownell *et al.* 1999; Osnes-Erie 1999). The correlations with zooplankton and egg abundances but not fish biomass are surprising. However, these fishes aggregate around objects in the ocean, and FLIP acts as a large aggregating device. Therefore, the estimated biomass of fish around FLIP is likely related to that aggregating behavior and may not be representative of the general biomass in the area.

On the other hand, copepods and euphausiids are a primary prey of anchovy, sardine and other epipelagic fish species (e.g. Rykaczewski and Checkley 2008), and so the correlation between zooplankton and delphinids may be indicative of a higher trophic response that we were unable to capture.

It is interesting that both Risso's and bottlenose dolphins were only observed in 2006, as both species are associated with San Clemente and Santa Catalina Islands, and are frequently observed in small boat studies of the region (Elizabeth Henderson, unpublished data). However, they are both strongly associated with islands and coasts, and occur in small, less visible groups than common dolphins. It may be that sightings away from the islands only occur occasionally, and that the higher Beaufort sea state and winds in 2008 interfered with our ability to see those species.

Summary and Limitations – Marine mammal occurrence patterns were examined relative to both biotic and abiotic oceanographic parameters, including temperature, chlorophyll concentrations, zooplankton abundance, and fish density. Correlations were found between these parameters and marine mammal abundances, including fin whales, common dolphins, Pacific white-sided dolphins and California sea lions. Oceanographic parameters varied strongly across all three years, and the response by marine mammals was equally strong. Fin whales and northern elephant seals were most abundant in 2007, when cooler SST's, a shallower thermocline and higher, shoaled chlorophyll concentrations occurred. 2006 and 2008 were both relatively warm years, with deeper thermoclines and less stratification, yet they varied significantly in both the species diversity and the numbers and group sizes of each species, with high diversity and high counts of all species in 2006, and low diversity but large delphinid groups in 2008.

Time lags of trophic level response were not explored for our one-month sampling period, because the lagged response time of marine mammals can often be greater than a month (e.g. Stafford *et al.* 2009). A longer duration deployment would be necessary to tease out some of the patterns, as dynamics of the ecosystem we sampled was set in motion before we arrived and continued to change after we left. In addition, a limitation to point-sampling is that we cannot be sure whether patches of phytoplankton bloomed and were grazed, or advected into and out of our sampling area, or were mixed to the surface from deeper waters. Therefore, additional data from gliders, moorings, or cruises would be beneficial to incorporate with visual observation data. In addition, a deeper and more quantitative zooplankton sampling method should be implemented in the future so that the entire assemblage, including diel vertical migrants, can be examined. Finally, a vertically oriented, downward sampling echosounder should be utilized so that sea surface backscatter noise is reduced and vertical movement patterns, such as diel vertical migration, can be accurately captured without the confounding effect of range on S_v.

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Chapter 4, in full, is currently in preparation for submission. E. E. Henderson, J. A. Hildebrand, and D. Demer. The Role of Marine Mammals as Top Predators: An Analysis of Marine Mammal Occurrence and Oceanographic Patterns in the Southern California Bight.. The dissertation author was the primary investigator and author of this material.

Table 4.1 - Number of sightings for each year of FLIP deployment.

Species	2006	2007	2008
Minke whale	11	5	0
Blue whale	5	2	1
Fin whale	25	231	2
Humpback whale	3	4	6
Sperm whale	1	0	0
Unidentified whale	27	164	10
Short-beaked common dolphin	36	9	19
Long-beaked common dolphin	2	0	0
Common dolphin sp.	148	28	36
Pacific white-sided dolphin	98	8	11
Risso's dolphin	12	0	0
Bottlenose dolphin	14	0	0
Unidentified dolphin	93	14	29
California sea lion	39	64	74
Northern elephant seal	0	12	1
Cuvier's beaked whale	2	0	0

Table 4.2 - Biomass estimates (kg/m^2) for each fish species in 2008, estimated from scattering volume and averaged across all echosounder measurments.

Species	**Minimum Biomass**	**Maximum Biomass**	**Median Biomass**	**Mean Biomass**	**Standard Deviation**
Northern anchovy	0.002	256.47	3.25	10.34	20.46
Pacific sardine	0.002	256.47	3.31	11.00	21.49
Pacific or jack mackerel	0.002	769.40	4.21	21.55	57.83

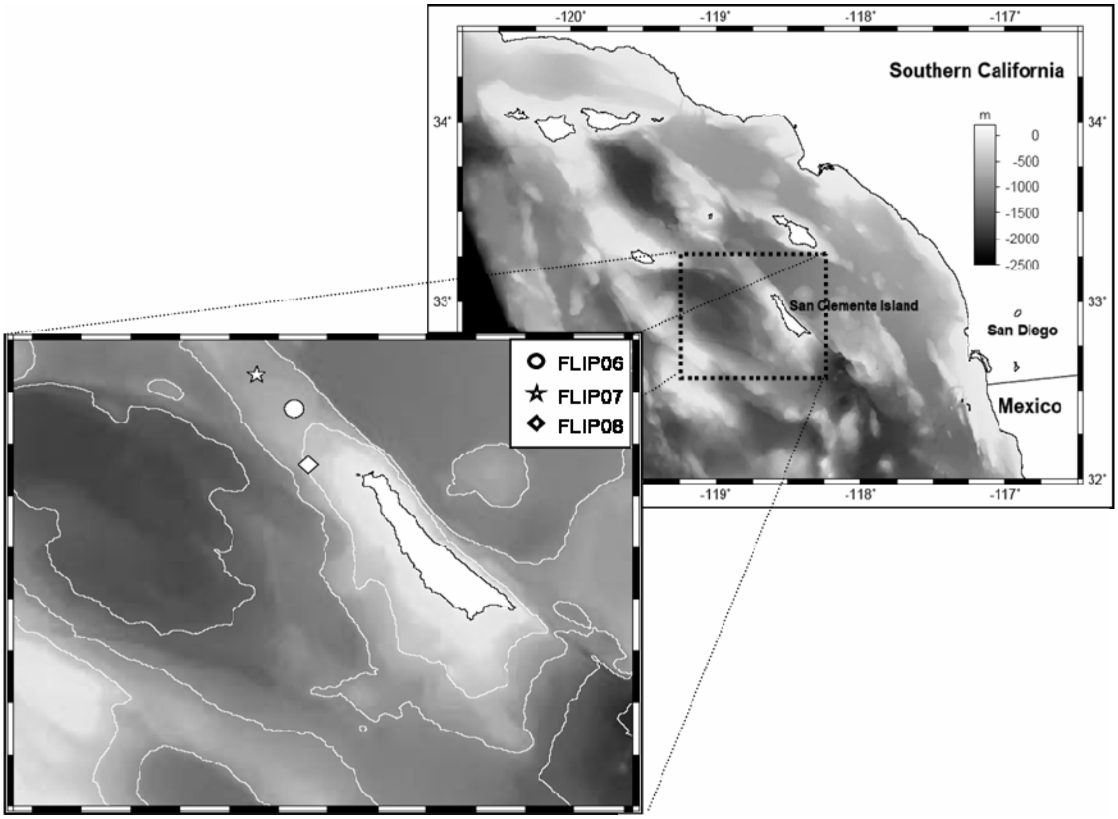
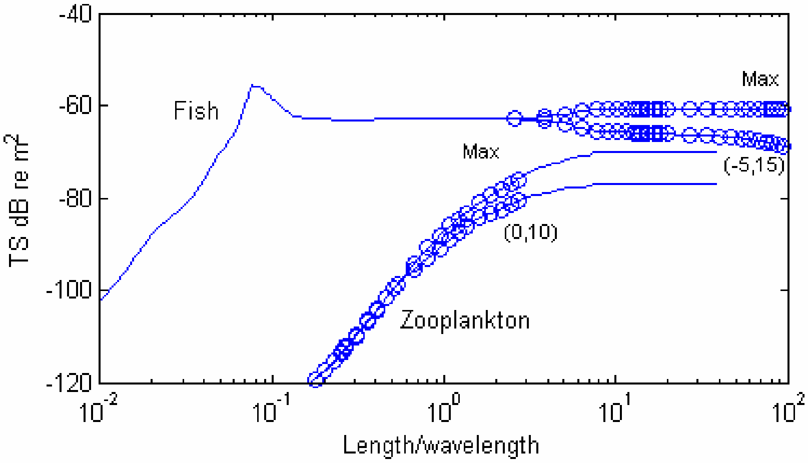
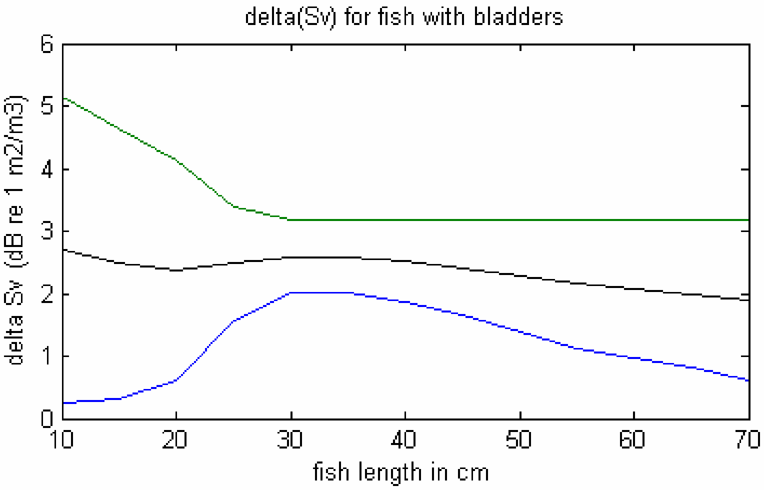


Figure 4.1 – The Southern California Bight, with an inset of San Clemente Island and the location of each FLIP deployment.

Figure 4.2 – Following Furusawa (1991), normalized *TS* of fish and zooplankton were plotted as a function of L/λ (top) for both maximum tilt angles and standard deviation pairs, with estimated lengths added as circles (top). ΔSv were then calculated as Sv_{200} – Sv_{38} for fish (middle) and zooplankton (bottom) at those estimated lengths, with ΔSv of maximum tilt angle in green, ΔSv of the off-axis tilt angle in blue, and mean ΔSv in black.




delta(Sv) for fish with bladders

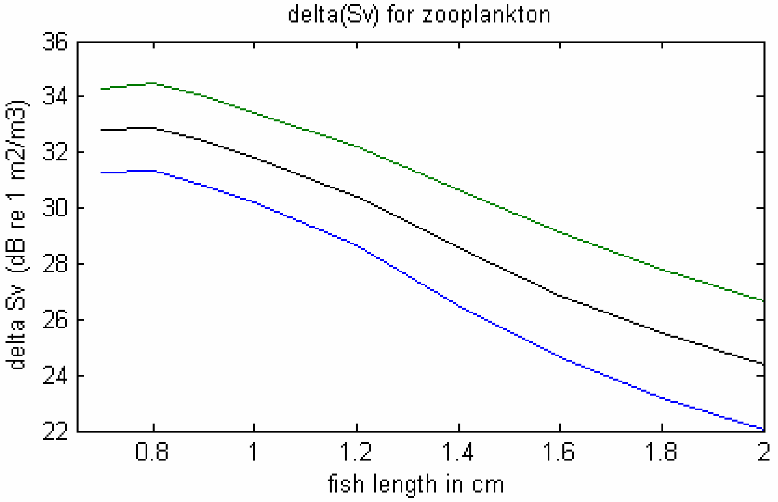
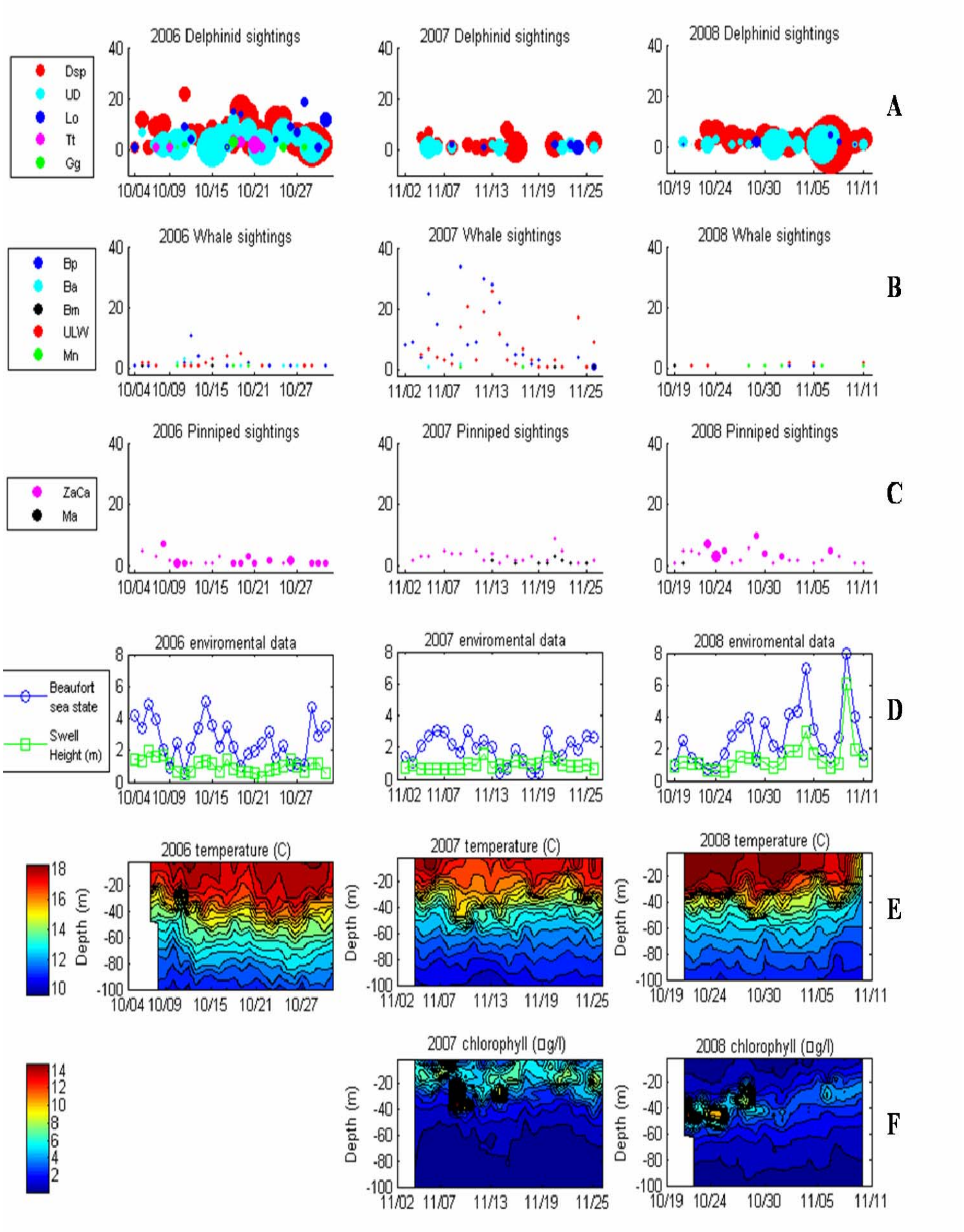

delta(Sv) for zooplankton

Figure 4.3 – Time series of (A) delphinid, (B) whale, and (C) pinniped sightings. Y-axes are number of sightings, size of bubble indicates average daily group size. Also plotted are: (D) environmental data, including Beaufort sea state (scale 0-12) and swell height in meters; (E) temperature contours in °C; and (F) fluorescence contours in μg/l. There are no fluorescence data for 2006.


2006 Delphinid sightings
2007 Delphinid sightings
2008 Delphinid sightings
Dsp
UD
Lo
Tt
Gg
A
2006 Whale sightings
2007 Whale sightings
2008 Whale sightings
Bp
Ba
Bm
ULW
Mn
B
2006 Pinniped sightings
2007 Pinniped sightings
2008 Pinniped sightings
ZaCa
Ma
C
2006 enviromental data
2007 enviromental data
2008 enviromental data
Beaufort sea state
Swell Height (m)
D
2006 temperature (C)
2007 temperature (C)
2008 temperature (C)
Depth (m)
E
2007 chlorophyll (□g/l)
2008 chlorophyll (□g/l)
Depth (m)
F
10/04 10/09 10/15 10/21 10/27
11/02 11/07 11/13 11/19 11/25
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10 12 14 16 18
2 4 6 8 10 12 14

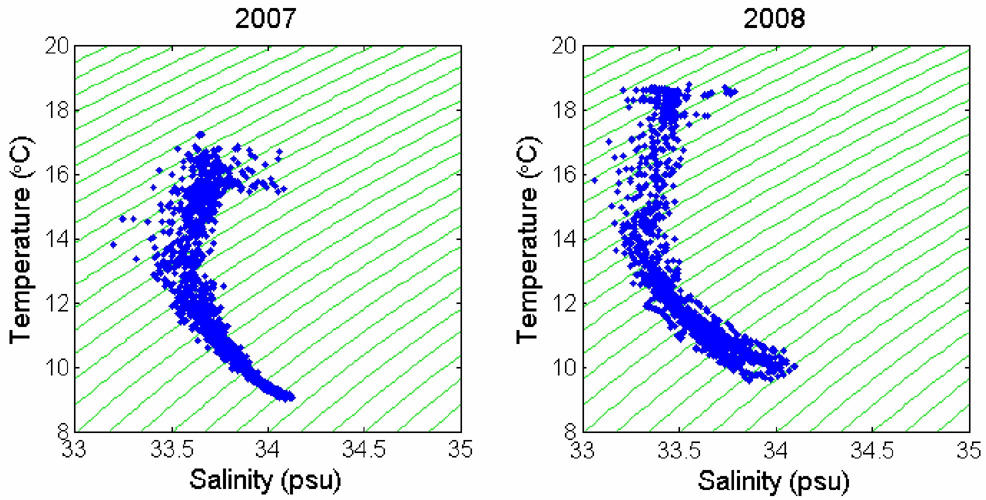

Figure 4.4 – T-S plots for 2007 and 2008 with isopycnals.

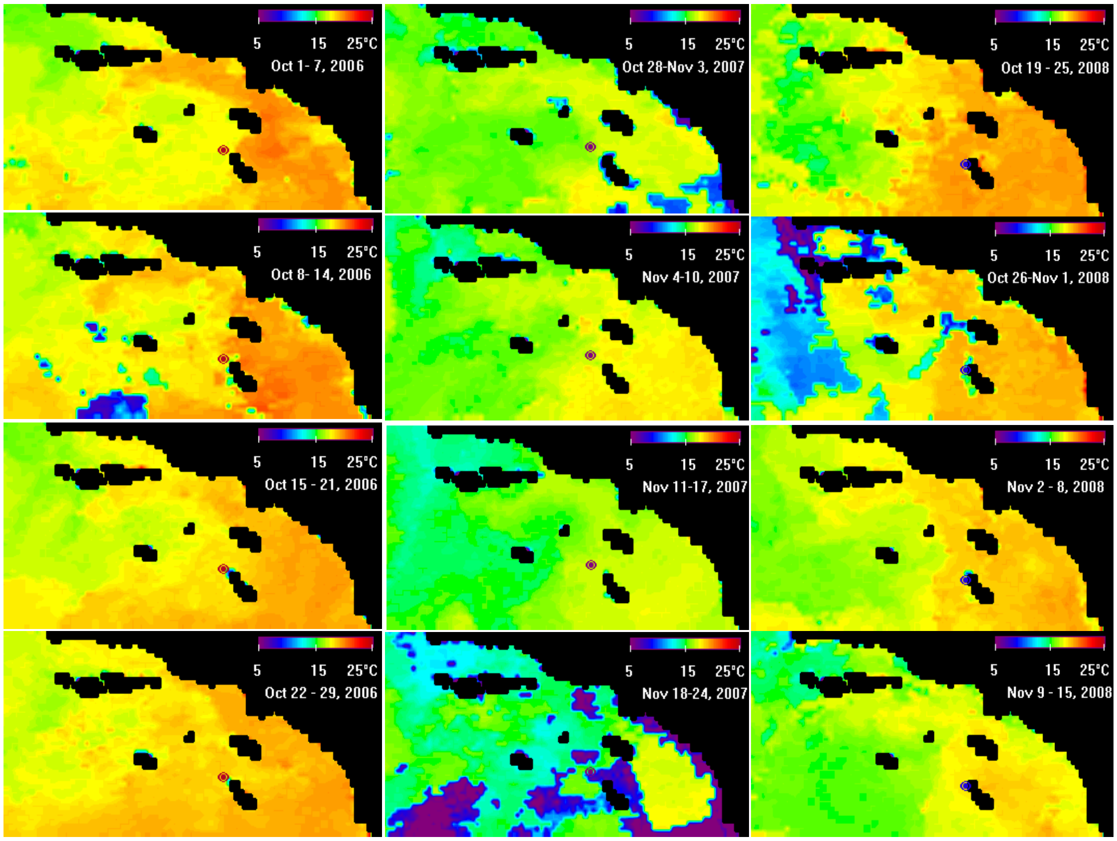

Figure 4.5 – Satellite-derived SST's, averaged over each of four weeks for each cruise. Blue and purple areas indicate cloud cover, not sea surface temperature data. FLIP locations are also plotted for each year.

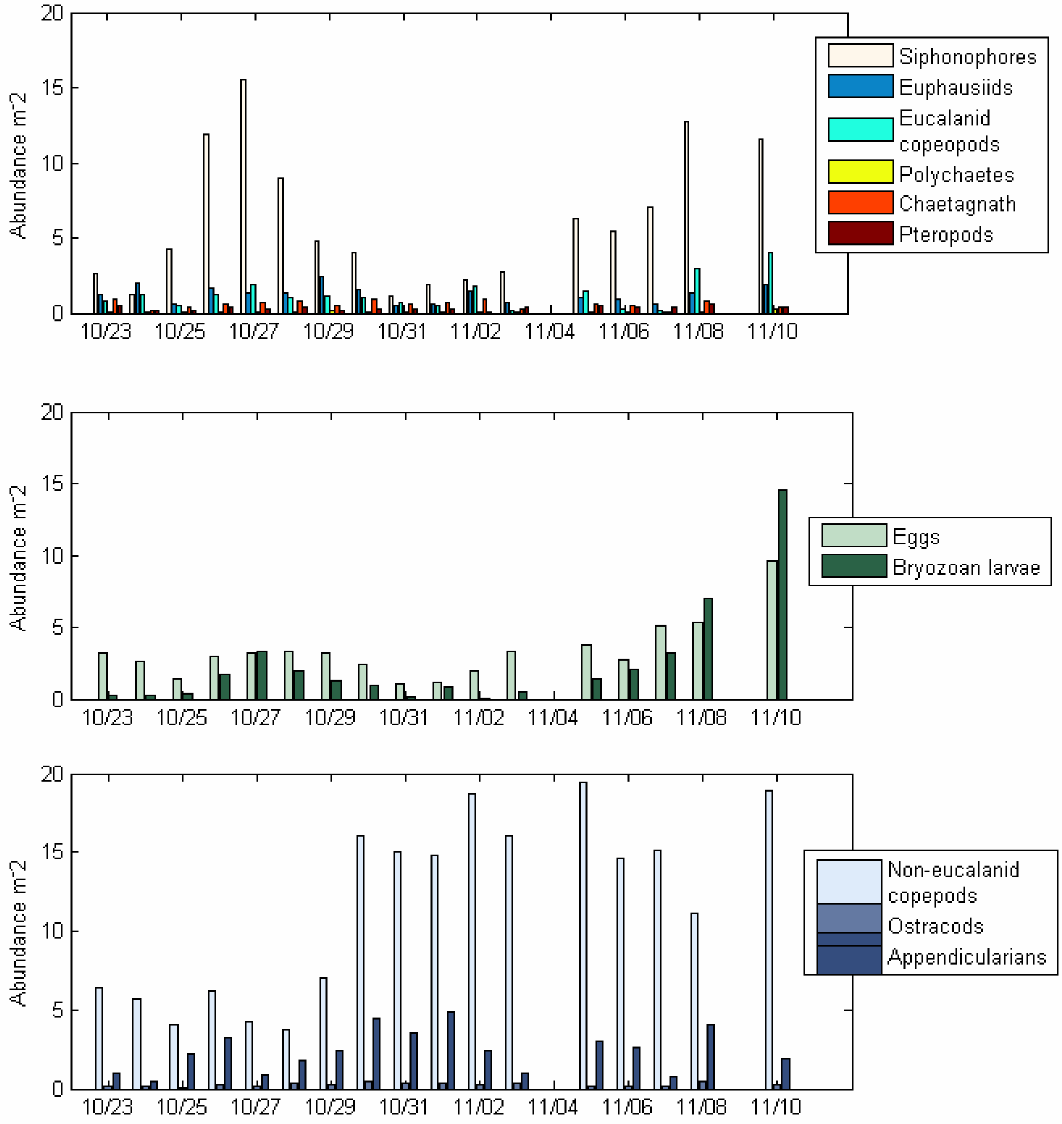

Figure 4.6 – Zooplankton abundances (averaged in m^{-2}) from bongo net tows in 2008.

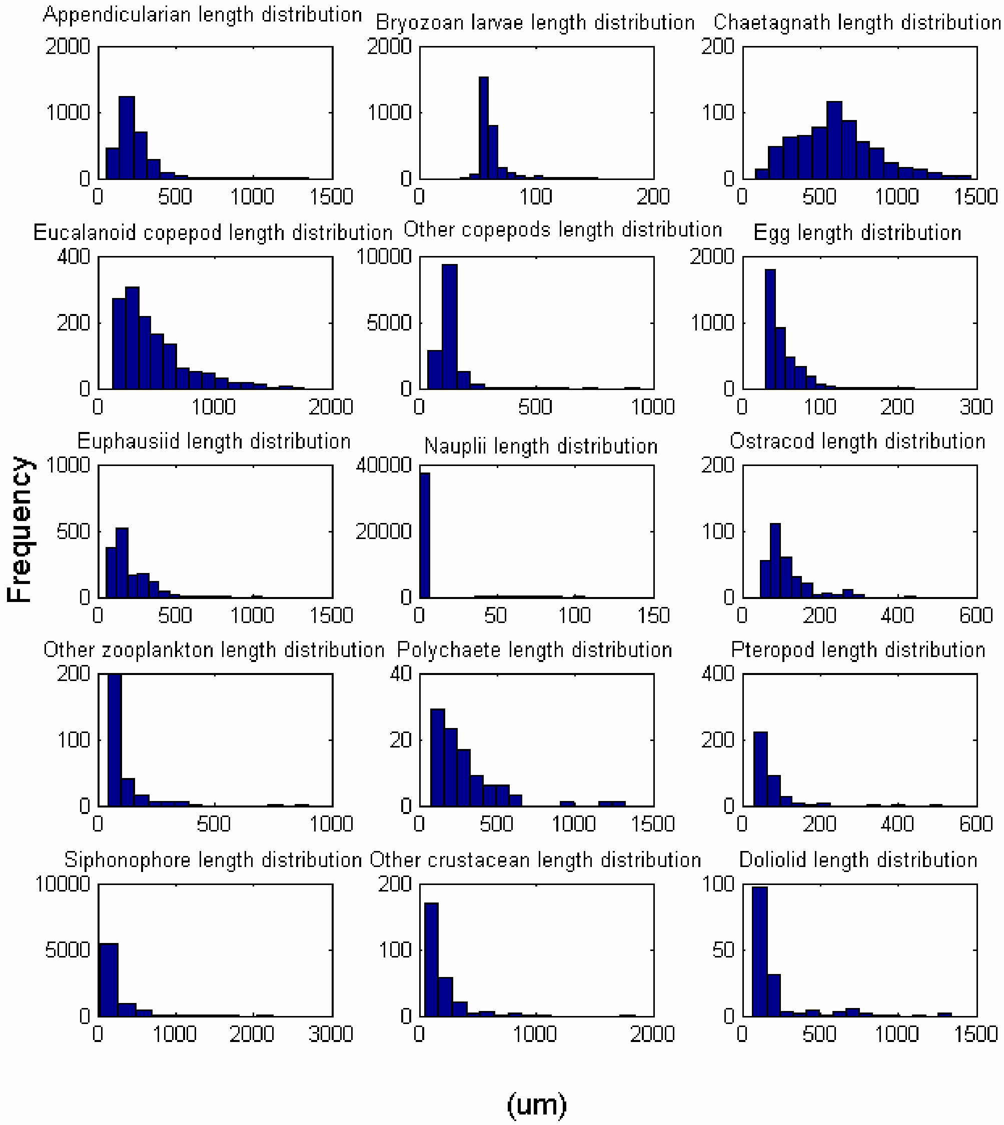

Figure 4.7 – Length (in feret diameters) distributions for all zooplankton. Note differing axis scales.

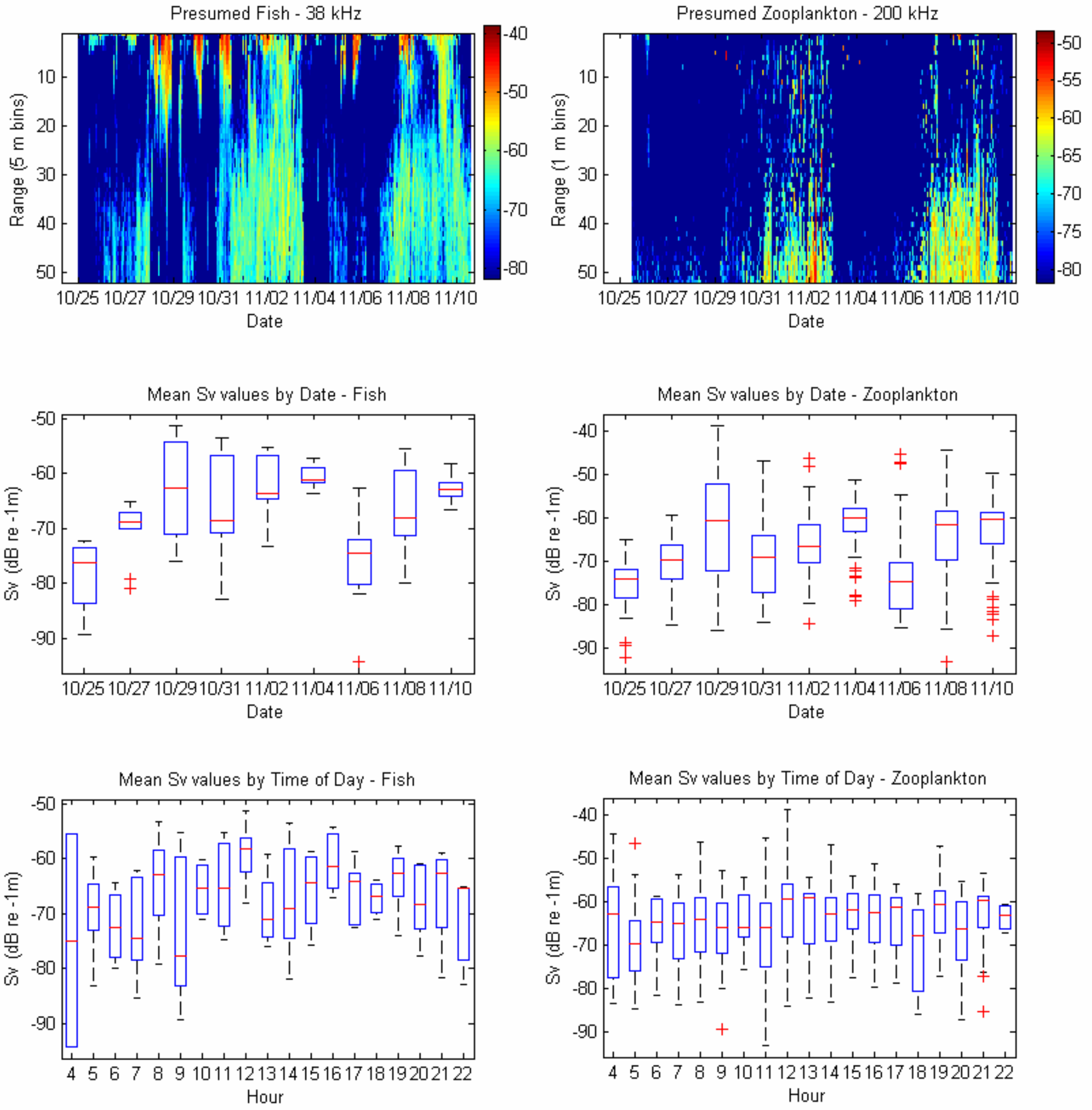

Figure 4.8 – Time series of volume backscattering strength (Sv) for fish (left column) and zooplankton (right column). Echograms show Sv versus range and date (top row); and box plots show the mean Sv for each day (middle row) and for each hour (bottom row).

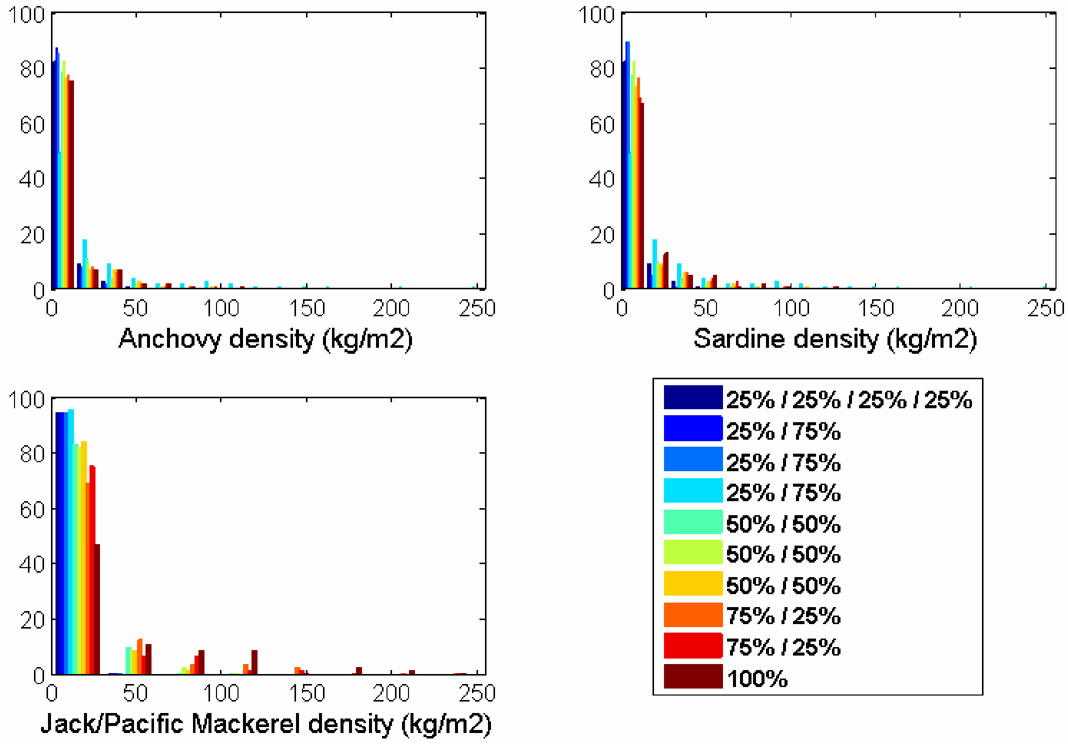

Figure 4.9 – Fish biomass density (kg/m^2), estimated using the different proportions of four fish species. For example, in the three cases of 25% anchovy, the remaining proportions are 75% sardine, 75% Pacific mackerel, and 75% jack mackerel. Since *TS* estimates were the same for jack and Pacific mackerel the results are identical, and so are shown on the same graph.

Appendix I – Spearman rank correlation test results for 2006, 2007 and 2008

R_s values for Spearman rank correlation tests for 2006 data.

Species	Number of individuals	Beaufort sea state	Thermocline depth
Minke whales	NA	-0.46	0.04
Blue whales	NA	0.10	-0.35
Fin whales	NA	0.03	-0.06
Humpback whales	NA	-0.11	0.12
Common dolphins	NA	-0.29	-0.07
Risso's dolphins	NA	-0.32	0.04
Bottlenose dolphins	NA	-0.26	0.06
Pacific white-sided dolphins	NA	-0.48	0.45
California sea lions	NA	-0.21	-0.06
Beaufort sea state	-0.46	NA	-0.34
Thermocline depth	0.04	-0.34	NA

P-values for Spearman rank correlation tests for 2006 data. The Bonferroni corrected alpha value for 2006 was 0.017. P-values that were still significant after the correction are italicized.

Species	Number of individuals	Beaufort sea state	Thermocline depth
Minke whales	NA	*0.01*	0.83
Blue whales	NA	0.63	0.07
Fin whales	NA	0.88	0.76
Humpback whales	NA	0.59	0.54
Common dolphins	NA	0.13	0.74
Risso's dolphins	NA	0.09	0.83
Bottlenose dolphins	NA	0.19	0.77
Pacific white-sided dolphins	NA	*0.01*	*0.02*
California sea lions	*0.00*	0.28	0.77
Beaufort sea state	NA	NA	0.07
Thermocline depth	0.83	0.07	NA

R_s values for Spearmank rank correlation tests for 2007 data.

Species	Number of individuals	Beaufort sea state	Thermocline depth	Fluoresence max depth	Fluor. value at max depth
Minke whales	NA	0.10	-0.04	-0.08	0.14
Blue whales	NA	-0.01	-0.06	0.10	0.09
Fin whales	NA	0.00	0.46	0.34	0.07
Humpback whales	NA	-0.09	0.01	-0.13	0.20
Common dolphins	NA	0.19	0.30	0.30	0.23
Pacific white-sided dolphins	NA	0.04	0.02	0.22	-0.04
Northern elephant seals	NA	-0.04	-0.15	0.01	0.20
California sea lions	NA	-0.08	0.12	-0.05	0.31
Beaufort sea state	0.10	NA	0.08	0.20	0.24
Thermocline depth	-0.04	0.08	NA	0.56	0.44
Fluoresence max depth	-0.08	0.20	0.56	NA	0.39
Fluoresence value at max depth	0.14	0.24	0.44	0.39	NA

P-values for Spearman rank correlation tests for 2007 data. The Bonferroni corrected alpha value for 2007 was 0.005. P-values that were still significant after the correction are italicized.

Species	Number of individuals	Beaufort sea state	Thermocline depth	Fluoresence max depth	Fluor. value at max depth
Minke whales	NA	0.63	0.87	0.70	0.49
Blue whales	NA	0.96	0.76	0.65	0.68
Fin whales	NA	0.99	0.02	0.10	0.74
Humpback whales	NA	0.66	0.97	0.55	0.33
Common dolphins	NA	0.37	0.15	0.14	0.27
Pacific white-sided dolphins	NA	0.86	0.94	0.29	0.84
Northern elephant seals	NA	0.84	0.48	0.97	0.33
California sea lions	NA	0.71	0.58	0.80	0.13
Beaufort sea state	0.63	NA	0.71	0.34	0.26
Thermocline depth	0.87	0.71	NA	*0.00*	0.03
Fluoresence max depth	0.70	0.34	0.00	NA	0.05
Fluoresence value at max depth	0.49	0.26	0.03	0.05	NA

R_S values for Spearman rank correlation tests for 2008 data

Species	Number of individuals	Beaufort sea state	Thermocline depth	Fluoresence max depth	Fluor. value at max depth	Appendic.	Bryozoan larvae	Eucalanid copepods	Non-eucalanid copepods	Eggs	Siphon	Euphausiids
Blue whales	NA	-0.29	-0.30	-0.30	-0.30	-0.26	-0.26	-0.26	-0.26	-0.26	-0.26	-0.26
Fin whales	NA	0.26	-0.07	-0.08	-0.20	0.23	0.00	0.35	0.46	0.15	0.09	0.18
Humpback whales	NA	0.04	0.04	0.06	-0.02	0.28	0.13	-0.10	0.06	-0.08	0.02	0.03
Common dolphins	NA	-0.16	0.27	0.17	0.13	0.43	0.48	0.37	0.55	0.49	0.41	0.48
Pacific white-sided dolphins	NA	-0.10	0.13	-0.30	-0.09	0.06	0.38	0.19	0.18	0.41	0.31	0.20
Northern elephant seals	NA	0.02	-0.30	-0.30	-0.30	-0.26	-0.26	-0.26	-0.26	-0.26	-0.26	-0.26
California sea lion	NA	-0.56	0.63	0.57	0.58	0.15	0.19	0.10	0.13	0.24	0.16	0.32
Beaufort sea state	-0.29	NA	-0.22	-0.27	-0.36	0.16	0.19	0.20	0.26	0.18	0.22	0.10
Thermocline depth	-0.30	-0.22	NA	0.65	0.71	0.29	0.35	0.34	0.19	0.29	0.40	0.52
Fluoresence max depth	-0.30	-0.27	0.65	NA	0.65	0.36	0.01	0.25	0.14	-0.03	0.02	0.35
Fluoresence value at max depth	-0.30	-0.36	0.71	0.65	NA	0.09	0.30	0.29	-0.07	0.22	0.33	0.40
Appendicularians	-0.26	0.16	0.29	0.36	0.09	NA	0.63	0.67	0.74	0.51	0.61	0.60
Bryozoan larvae	-0.26	0.19	0.35	0.01	0.30	0.63	NA	0.74	0.63	0.91	0.96	0.69
Eucalanid copepods	-0.26	0.20	0.34	0.25	0.29	0.67	0.74	NA	0.66	0.75	0.78	0.88
Non-eucalanid copepods	-0.26	0.26	0.19	0.14	-0.07	0.74	0.63	0.66	NA	0.70	0.57	0.59
Eggs	-0.26	0.18	0.29	-0.03	0.22	0.51	0.91	0.75	0.70	NA	0.90	0.71
Siphonophores	-0.26	0.22	0.40	0.02	0.33	0.61	0.96	0.78	0.57	0.90	NA	0.72
Euphausiids	-0.26	0.10	0.52	0.35	0.40	0.60	0.69	0.88	0.59	0.71	0.72	NA

P-values for Spearman rank correlation tests for 2008 data. The Bonferroni corrected alpha value for 2008 was 0.00076. P-values that were still significant after the correction are italicized

Species	Number of individuals	Beaufort sea state	Thermocline depth	Fluoresence max depth	Fluor. value at max depth	Appendic	Bryozoan larvae	Eucalanid copepods	Non-eucalanid copepods	Eggs	Siphon	Euphausiids
Blue whales	NA	0.18	0.15	0.15	0.15	0.22	0.22	0.22	0.22	0.22	0.22	0.22
Fin whales	NA	0.22	0.76	0.72	0.36	0.28	1.00	0.09	0.02	0.47	0.68	0.41
Humpback whales	NA	0.84	0.85	0.77	0.93	0.19	0.55	0.65	0.79	0.70	0.91	0.89
Common dolphins	NA	0.46	0.21	0.42	0.54	0.04	0.02	0.07	0.01	0.02	0.04	0.02
Pacific white-sided dolphins	NA	0.66	0.55	0.16	0.68	0.79	0.07	0.38	0.39	0.04	0.14	0.34
Northern elephant seals	NA	0.94	0.15	0.15	0.15	0.22	0.22	0.22	0.22	0.22	0.22	0.22
California sea lion	NA	0.00	0.00	0.00	0.00	0.50	0.38	0.63	0.56	0.26	0.46	0.13
Beaufort sea state	0.18	NA	0.31	0.19	0.08	0.45	0.38	0.34	0.23	0.41	0.30	0.65
Thermocline depth	0.15	0.31	NA	*0.00*	*0.00*	0.16	0.09	0.10	0.37	0.16	0.05	0.01
Fluoresence max depth	0.15	0.19	0.00	NA	*0.00*	0.09	0.96	0.24	0.50	0.89	0.92	0.09
Fluoresence value at max depth	0.15	0.08	0.00	0.00	NA	0.68	0.16	0.16	0.75	0.29	0.12	0.05
Appendicularians	0.22	0.45	0.16	0.09	0.68	NA	0.00	*0.00*	*0.00*	0.01	*0.00*	*0.00*
Bryozoan larvae	0.22	0.38	0.09	0.96	0.16	0.00	NA	*0.00*	0.00	*0.00*	*0.00*	*0.00*
Eucalanid copepods	0.22	0.34	0.10	0.24	0.16	0.00	0.00	NA	*0.00*	*0.00*	*0.00*	*0.00*
Non-eucalanid copepods	0.22	0.23	0.37	0.50	0.75	0.00	0.00	0.00	NA	*0.00*	0.00	0.00
Eggs	0.22	0.41	0.16	0.89	0.29	0.01	0.00	0.00	0.00	NA	*0.00*	*0.00*
Siphonophores	0.22	0.30	0.05	0.92	0.12	0.00	0.00	0.00	0.00	0.00	NA	*0.00*
Euphausiids	0.22	0.65	0.01	0.09	0.05	0.00	0.00	0.00	0.00	0.00	0.00	NA

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CHAPTER 5

Effects of Sea Surface Temperature Variation on the Distribution of Small Cetaceans in the Southern California Bight: Implications for Climate Change

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Abstract

This paper examines the link between ocean temperature and distribution patterns for eight species of small cetaceans in the Southern California Bight for the period 1979-2009. Sea surface temperature (SST) anomaly data are a proxy for sea surface temperature fluctuations on three temporal scales: seasonal temperature fluctuations on an annual scale, El Niño/Southern Oscillations (ENSO) on a 2-7 year time scale, and Pacific Decadal Oscillations (PDO) on a decadal time scale. Poisson-based generalized additive models of small cetacean distribution were created using SST anomaly and depth data, and a stepwise model fitting procedure was used to select the best model. Seasonal SST anomalies were included as a predictor for every species except striped dolphins (*Stenella coeruleoalba*) and bottlenose dolphins (*Tursiops truncatus*), while the ENSO index was an important predictor for striped dolphins, Risso's dolphins (*Grampus griseus*), northern right whale dolphins (*Lissodelphis borealis*), and Dall's porpoise (*Phocoenoides dalli*). The PDO index was included as a predictor for common dolphins (*Delphinus* sp.), northern right whale dolphins, bottlenose dolphins, and Dall's porpoise. Striped dolphins were the only species to show a distinctive far-

offshore distribution, while northern right whale dolphins were associated with the slope, and long-beaked common dolphins were located inshore. In addition, an interaction term between the SST indices and mean water depth was included for most species, indicating a change in spatial distribution associated with changes in ocean temperature. The distinctive spatial distributions for each species may represent niche or resource partitioning where multiple species have overlapping distributions. While the temporal changes in distribution are likely in response to changes in prey abundance or dispersion, these patterns associated with SST variation may be indicative of future, more permanent range shifts due to global climate change.

Introduction

Cetaceans are apex marine predators whose movement patterns and habitat preferences are typically related to the distribution of their prey. Unlike their whale counterparts, small cetaceans generally do not undertake large scale migrations to track prey or move between breeding and feeding grounds. Rather, delphinoid populations may display a high degree of habitat affinity, or may move seasonally inshore and offshore or along coastlines (Leatherwood *et al.* 1984; Dohl *et al.* 1986; Shane *et al.* 1986). While many species may overlap in any one region, they will often differ in their occurrence or habitat-use patterns, perhaps reflecting competitive exclusion or niche partitioning. This separation of habitat and resources often occurs along depth, slope, sea surface temperature (SST) and other oceanographic gradients (Reilly 1990; Forney 2000; Ballance *et al.* 2006; MacLeod *et al.* 2008). These preferences are likely reflections of differences in preferred prey, and dolphins track these habitats or water masses as they shift not only seasonally but through climate-driven changes such as the El Niño/Southern Oscillation (ENSO) (Shane 1995; Defran *et al.* 1999; Benson *et al.* 2002; Ballance *et al.* 2006).

Temperature fluctuation patterns such as ENSO, the Pacific Decadal Oscillation (PDO) and the North Atlantic Oscillation (NAO), impact current strength, coastal upwelling, and SST (Mantua and Hare 2002; Lluch-Belda *et al.* 2003; Hurrell and Van Loon 2004). Temperature variability has been documented to affect marine mammal prey, including the strong relationship between the copepod *Calanus finmarchicus* life cycle and recruitment of larval cod (*Gadus morhua*); changes in the cycle of the NAO impact *Calanus* life cycles which in turn increase or reduce the prey availability for the cod (Stenseth *et al.* 2002). Population fluctuations of small pelagic fish such as anchovy (*Engraulis* sp.) and sardine (*Sardinops sagax*) are strongly correlated with both ENSO and PDO regime shifts (Stenseth *et al.* 2002; Ñiquen and Bouchon 2004; Lehodey *et al.* 2006). Isolated occurrences have also been noted of dolphins changing their distribution patterns after strong temperature shifts, including the expansion of the northern extent of bottlenose dolphin range along the California coast, and the replacement of short-finned pilot whales (*Globicephala macrorhynchus*) by Risso's dolphins as the primary squid consumer near Catalina Island, both after the strong 1982/83 ENSO event (Shane 1994; 1995; Defran *et al.* 1999). This study will examine the distribution and movement of multiple species of dolphin across shifting temperature regimes.

Two long term ship-based surveys have been conducted in the Southern California Bight (SCB), making it an ideal region for this investigation. California Cooperative Oceanic Fisheries Investigations (CalCOFI) has been conducting quarterly cruises that sample a wide breadth of oceanographic and biological measurements since 1949, with marine bird and mammal observations added in 1987. Southwest Fisheries Science Center (SWFSC), a division of NOAA, has also regularly been carrying out marine mammal abundance surveys that incorporate this region since 1979. In addition, the SCB is a region of complex currents and bathymetry, marking the boundary between subarctic cold water from the North Pacific and warm equatorial water. It is therefore home to both cold- and warm-water endemic marine mammal species. This mix of species and the availability of two long term data sets make this the ideal location to examine the impact of temperature fluctuations on small cetacean distribution patterns at different temporal scales. SST's fluctuate with current patterns that shift seasonally, but are also controlled by climate-driven temperature fluctuations on decadal scales like ENSO and PDO (Reid *et al.* 1958; McGowan 1985; Mantua and Hare 2002). These changes in SST have been linked to changes in all levels of food web, from immediate phyto- and zoo-plankton responses to lagged alterations in numbers, diet and even reproductive success of organisms at higher levels (Tibby 1937; Hubbs 1948; McGowan 1985; McGowan *et al.* 2003). It follows that small cetacean populations are expected to respond to these temperature shifts, either as a response to the movements of their prey, or because of physiological restrictions related to temperature in smaller species. This paper aims to investigate that response by eight species of small cetaceans across 30 years, using SST anomaly indices on three time scales: seasonal (yearly), ENSO (two-seven years) and PDO (~30 years). The cetaceans' responses to these fluctuations in temperature may be indicative of their response to future ocean conditions as global ocean temperatures rise, and so the distribution patterns of these small cetaceans is discussed in light of a future, permanent regime shift.

Methods

Study Area

The SCB is the region between 116° W and 128°W longitude, and from 30° N to 35° N latitiude (Figure 1). The SCB is dominated by the southward flowing California Current, the strength of which is mediated by the PDO. This current generally contains cool, low saline, subarctic water. In addition, there are two poleward flowing currents, the California Countercurrent and the California Undercurrent, both of which bring warm, saline Equatorial waters north (Reid *et al.* 1958; Hickey 1993). The meeting of these currents forms strong mesoscale eddies, which have been shown to play an important role in fish larvae retention (Logerwell *et al.* 2001; Logerwell and Smith 2001), creating hotspots for predators. Furthermore, the region is bounded on the west by the North Pacific gyre, consisting of warm, saline North Pacific Central Water (Norton *et al.* 1985). Thus this region represents the convergence of both warm and cold water regimes, and supports populations of both warm and cold water small cetacean species.

The California Current is strongest and closest to shore in spring, when there is predominantly equatorward flow in the SCB. In contrast, in summer and fall the California Countercurrent dominates, bringing warmer water further north and west into the SCB and pushing the California Current further offshore (Hickey 1993; Hickey *et al.* 2003; Caldeira *et al.* 2005). Strong El Niño years bring increased downwelling and higher SST's to the SCB region as trade winds across the equator relax and Kelvin waves propagate eastward (Norton *et al.* 1985), bringing warm equatorial waters eastward and poleward into Eastern Tropical Pacific and California waters. This downwelling effect in the SCB has been linked to a depression of the thermocline, decreases in nutrients, a subsequent reduction in zooplankton abundance and an increase in nekton normally found further south (Sette and Isaacs 1960; McGowan 1985). The PDO is a similar but longer-lived pattern of climate variability to ENSO. The primary effects of ENSO occur in the tropics with secondary effects in the North Pacific, whereas the opposite occurs for the PDO (Mantua and Hare 2002). During the warm PDO phase, the California Current is weakened and the Countercurrent is strengthened, bringing warmer waters further north and west into and beyond the SCB and creating anomalously warm SST's along the California coast. In contrast, during the cool PDO phase the California Current is stronger, bringing cool water further south and east into the SCB (Mantua and Hare 2002). Sardine and anchovy, as well as other fish species, have been shown to respond to these changes (Tibby 1937; Hubbs 1948; Lluch-

Belda *et al.* 2003). A PDO regime shift from cool to warm occurred around 1977, and a shift back to a cool PDO occurred in the late 1990's (Zhang and McPhaden 2006; Wang *et al.* 2010).

Surveys

Marine mammal visual sighting data were used from 105 separate survey cruises from 1979-2009 conducted by both CalCOFI and SWFSC. Tracklines for all surveys are shown in Figure 2. CalCOFI surveys have been conducted quarterly in the SCB since 1949; marine mammal observations began in 1987. On surveys from May 1987 to April 2004, marine mammals were recorded as part of the standardized CalCOFI top predator surveys which were focused primarily on marine birds and used the methods of Tasker *et al.* (1984). Observations were made by a single observer stationed on the flying bridge, or outside the main bridge. Observations were made on the side of the ship with least glare while it traveled between CalCOFI stations, spaced 40 to 60 nm apart, at a speed of >5 nmi. Marine mammals were recorded if they occurred within the 300m strip transect used for birds, or up to 1000m of the vessel for large cetaceans; generally there was no attempt to estimate distances or angles to the marine mammals, so "encounter rates" rather than densities were reported. Marine bird and mammal data, while continuously obtained, were summarized into 3 km "bins", with the latitude and longitude determined for the centroid of each bin. Details of field methods can be found in Veit *et al*.(1996, 1997), Hyrenbach and Veit (2003) and Yen *et al*. (2006). The survey data are available from DataZoo (http://oceaninformatics.ucsd.edu/datazoo/) maintained by Karen S. Baker of SIO as part of the CCE LTER program.

In July 2004 two dedicated marine mammal visual observers were added to the CalCOFI cruises, using standard line-transect protocol (Burnham *et al.* 1980; Buckland *et al.* 1993). Each observer monitored a 90° field of view from bow to abeam, alternating between scanning with Fujinon 7x50 bionoculars and the naked eye. Sighting information included the distance and bearing from the ship, species, group size and composition, and behavior. In addition to sighting data, a periodic record was made of the ship's position, heading and speed, weather and sea state conditions, and observer identification (Soldevilla *et al.* 2006). Survey effort was calculated as the latitude and longitude at the start and end of each trackline. For all CalCOFI surveys, observations were made on daytime tracklines between stations, with no visual observation effort conducted at station, and all visual effort was conducted in sea state condition of Beaufort 5 or less, although only sightings made in Beaufort 3 or less were used in this analysis. These surveys were conducted on a variety of NOAA and SIO vessels that varied in length from approximately 50 m to 100 m, with observer height (height of the bridge above water plus the height of the observer) varying from 8.1 m to 12 m. Data for this analysis are generally from four surveys a year (winter, spring, summer and fall) from 1987 to 2009. In five years there were only three surveys conducted, and in 1998 surveys were carried out monthly to capture a time series of oceanographic measures in a strong El Niño year. A full summary of surveys can be found in Appendix I.

SWFSC has conducted a number of cruises that have encompassed the SCB; data for this analysis came from 10 different cruises (Appendix I). SWFSC cruises also utilized standard line-transect protocols. These cruises had at least three visual observers on the bridge, two of whom used 25 x 150 big-eye binoculars to scan 90° from bow to abeam on either side of the flying bridge, while the third observer monitored the entire forward 180° using 7x50 binoculars and the naked eye. Sighting and supplemental information was similar to that of CalCOFI cruises, however search effort was typically discontinued when animals were seen within 3 nm of the transect line, and the vessel was directed to approach the animals to more accurately estimate group sizes and determine species present (Kinzey *et al.* 2000; Barlow and Forney 2007). For the cruises conducted from 1979-1984, survey effort was calculated as latitude and longitude positions at the start and end of each trackline. For the cruises from 1991-2005, effort was recorded as a latitude and longitude position approximately every 10 minutes. In all cruises observations were conducted during all daylight hours, in sea state conditions of Beaufort 5 or less; for this analysis only sighting data collected in Beaufort 3 or less were used.

Eight species of small cetacean were examined in this analysis: short beaked common dolphins (*Delphinus delphis;* Dd), long beaked common dolphins (D. *capensis;* Dc), Risso's dolphins (Gg), Pacific white-sided dolphins (*Lagenorhynchus obliquidens;* Lo), northern right whale dolphins (Lb), striped dolphins (Sc), bottlenose dolphins (*Tursiops truncatus;* Tt) and Dall's porpoise (Pd). Dall's porpoise, Pacific white-sided and northern right whale dolphins are considered cold temperate water species, while long and short beaked common, striped and Risso's dolphins are considered warm temperate and tropical species, and bottlenose dolphins are cosmopolitan species located in both warm and cold temperate and tropical waters (Reeves *et al.* 2002). All bottlenose dolphin sightings in this study were presumed to be offshore/island associated animals, as most coastal animals remain within one km of the shore, and no surveys were conducted that close the coast. A *Delphinus* species (Dsp) category was also used that combined both short and long beaked species, as they were not distinguished to species on SWFSC cruises prior to 1991, nor in CalCOFI cruises prior to August 2004.

Model data

Monthly averaged SST data from 1985 through 2009 were taken from NOAA Advanced Very High Resolution Radiometer (AVHRR) Pathfinder satellite data, with a spatial resolution of ~4.1 km (http://podaac.jpl.nasa.gov/DATA_CATALOG/sst.html). For 1981 – 1984 NOAA AVHRR data were also used, using a Multi-Channel averaged SST with a 5.7 km resolution. There were no satellite data available prior to 1981. Seasonally averaged SSTs were calculated using Windows Image Manager (WIM, M. Kahru, SIO). Seasons were defined as 'warm' from May-October, and 'cold' from November – April. Using seasonally averaged SST's, a seasonal SST anomaly value was calculated for each warm and cold period from 1981-2009. NOAA ENSO SST anomaly data, derived from the Oceanic Niño Index (ONI) as a three month running mean of SST anomalies from 1950 through 2009 in the Niño 3.4

region around the equator (http://www.cpc.ncep.noaa.gov) was used as a proxy for ENSO for 1979-2009. The Niño 3.4 is centered on the equator, and so the index indicates the relative strength of the ENSO event rather than SST anomaly values for the SCB. PDO SST anomaly data averaged from 1900 through 2009 from the University of Washington (http://jisao.washington.edu/pdo) was used as a proxy for the PDO regime from 1979-2009. The PDO Index is derived from a monthly averaged SST for North Pacific waters poleward of 20° N.

A generalized additive model (GAM) of species sighting rates as a function of these SST anomalies was created using R (www.r-project.org), a readily available statistical software package. GAMs are a generalization of generalized linear models (GLM), where a response variable, y, is modeled as the sum of linear functions of the variables, x_n:

$$y = \sum \beta_i * x_i + \varepsilon_i$$

In the case of GAMs, y is modeled as the sum of non-linear functions of the variables:

$$y = \sum f_i(x_i) + \varepsilon_i$$

Both GLMs and GAMs may also utilize a link function, relating the predictor variables to the distribution of the response variable. GAMs are ideal for modeling distribution data since the constraint of linearity is lifted and a more flexible approach to the relationship between variables can be taken. In addition, nonparametric functions can be fit to the predictor variables using smoothing functions such as Loess or spline smoothers to predict the relationship between the predictor and the response variables (Hastie and Tibshirani 1986).

In this case, a Poisson distribution of the number of sightings of each species was used with a log link function, and the effort data (in km) was used as the offset to normalize the sighting data. In addition, the SCB region was divided into 52 one-degree latitude by one-degree longitude grid sections. These grid squares were then used as data units, with all effort, sighting, and seasonal SST data calculated for each square, thereby normalizing spatial and temporal differences in survey data. The potential predictive variables in the model included: seasonal SST anomalies of each grid sector (SeasAnom); ENSO Index (ENSO); PDO Index (PDO); combinations of all the above to look for interaction effects (e.g. SeasAnom*ENSO); the mean (DepthMean), minimum (DepthMin) and maximum (DepthMax) depth for each grid section; and the quarter (Quarter) to look for seasonal changes (quarter 1: February-April; quarter 2: May-July; quarter 3:August-October; quarter 4: November-January). Although sea state has been demonstrated to be an important predictor in other habitat models (Becker 2007), this was not recorded in early CalCOFI observations and so has not been included in this analysis; instead, only data recorded in Beaufort sea state 0-3 were used in order to standardize for differences in survey effort. A forward/backward stepwise model fitting procedure was then carried out for each species to determine which variables had the most explanatory power in predicting their distributions. Each predictor variable was tested in the model on its own as well as using a smoothing spline with 2 to 4 levels of degrees of freedom. The best model was selected using Akiake's Information Criterion (AIC):

$$AIC = -2*\log(L(\Theta \mid y) + 2*P$$

where $(L(\Theta \mid y)$ is the likelihood of the parameters given the data y, and P is the number of parameters. The best fit model minimizes AIC by maximizing the log-likelihood, with penalties for the number of parameters included (Akaike 1976). In addition to using AIC, the best model was also verified using an Analysis of Deviance, comparing the residual deviance of several models using a Chi Square method. The best fit model was one that minimized both AIC and residual deviance.

However, since GAM's can be easily overspecified due to their flexibility (Forney 2000; Ott and Longnecker 2001), a cross-validation procedure was applied using the predictive sum of squares (PRESS), calculated as:

$$PRESS = \sum (y_i - \hat{y}_t)^2$$

where y_i is the observed value and $\hat{y}_t$ is the predicted value. The data for all species except short- and long-beaked common dolphins were divided into five subsets, each of which consisted of five years of data, other than the 1979-1989 subset which was combined due to small sample size. The data for short- and long-beaked common dolphins was divided into three subsets of three or four years each. The stepwise model fitting procedure was repeated for each subset of data, and then the best model from each subset was applied to the remainder of the data. The model that minimized the predictive sum of squares value was selected as the best overall model for each species.

Results

The SST for the SCB over this period ranged from 12.0° - 22.05° C, with a mean of 16.69° C (Figure 3). Years with a strong positive PDO (Index > 1) were 1983, 1987, 1993, 1997 and 2003, while a strong negative PDO (Index < -1) occurred in 1999 and 2008 (Figure 4). Strong positive ENSO years were 1982-83, 1987-88, 1991-92, 1997-98 and 2002-03, while strong negative ENSO years were 1988-89 and 1999-2000 (Figure 4). No long-term trends in SST are apparent in our data given the levels of seasonal, ENSO, and PDO variation seen.

In the SCB, a mean depth of less than 1100 m, along with a very low minimum depth (<10 m) and a maximum depth less than 2000 m, indicates an inshore distribution, while a mean depth peak at around 900 m indicates a strong island association. A depth mean ranging from about 1000-3200 m, along with a depth minimum less than 500 m and a maximum ranging from about 3500 – 4000 m indicates an association with the slope region of the SCB, along the 2000 m isobath. Finally, a depth mean greater than 3500 m, with a minimum greater than about 1200 m and a maximum greater than 4000 m indicates an offshore or deep-water distribution.

The initial model results for all species are shown in Table 1, and the best overall models after the cross-validation procedure are shown in Table 2. Values for explained deviance range between 22.9% and 53% for the initial models and between 21.5% and 50% for the best overall models. Almost all the models included quarter and a seasonal SST variable, indicating seasonal variation in the numbers of sightings for each species that is likely associated with changes in SST.

All models also included either the PDO or ENSO index, or both, as either direct predictors or as interaction terms, demonstrating the importance of those regimes on small cetacean distribution. In addition, all the models included at least one depth metric, which has been shown to be an important predictor variable (Becker, 2007), as well as at least one interaction term between depth and an SST variable, indicating changes in distribution following differences in SST with seasonal, ENSO and/or PDO shifts. In addition, an illustration of the changes in distribution for six of the species across different regimes using mean SST data for the year derived from AVHRR satellite data is shown in Figure 14. Mean SST's from 1997 through 2000 are plotted, along with the CalCOFI sighting data for Dall's porpoise, and common, Pacific white-sided, northern right whale, Risso's, and bottlenose dolphins. A strong El Niño occurred in 1997-98, followed by a strong La Niña in 1998-99, while 1997 – 1999 marked the transition from a warm PDO phase to a cool PDO phase, with a high positive PDO index in 1997 and a low negative PDO index in 1999. 2000 sighting data are included to exemplify the sustained small cetacean response to this transition. A closer examination of the model results for each species follows.

Common dolphins

Three different models were used for common dolphins: short-beaked commons (Dd), long-beaked commons (Dc), and *Delphinus* sp. (Dsp), which included data from 1979-1984 (SWFSC) and CalCOFI cruises prior to 2004, when common dolphins were not identified to the species level, as well as combined long- and short-beaked sightings from the remainder of the dataset. The Dsp model (Figure 7), had one of the lowest explained deviance (23.1%) and the highest residual deviance. This is in part due to species-specific differences as observed in the respective Dd and Dc models (Figures 5 and 6). The Dc model had a much higher value of explained deviance, which at 50.0% was the highest value of all models. The Dd model on the other hand had the lowest value of all models at 21.5%, likely due to the broad distribution and behavioral plasticity of this species. Common dolphins were associated with SST's at or above the mean in all three models, and there was a peak in overall common dolphin sightings in the summer. PDO indices were included for Dsp, which showed a preference for a negative PDO index, and for Dc, whose sightings peak at a slightly positive PDO index. Depth was an important predictor of common dolphin distribution in all three models, with Dc found almost exclusively inshore while Dd/Dsp were found both inshore and offshore. The Dsp and Dd models included interactions between the different SST anomaly variables, and also included an interaction between one or more SST anomalies and the mean depth, indicating a change in spatial distribution with varying SST. Thiscould result from the known seasonal inshore/offshore pattern observed for short-beaked common dolphins (Dohl *et al.* 1986; Forney and Barlow 1998), but also could indicate a similar pattern may occur during ENSO or PDO shifts. The Dc model did not include any interaction terms; their year-round nearshore distribution did not appear to change with temperature shifts, however they did increase in abundance with warmer temperatures.

As warm temperate species, common dolphins were observed more frequently in the SCB during the summer and fall when SSTs are higher. It seems this effect may be compounded by long-term SST oscillations such as the PDO or ENSO; when there is a positive interaction between a seasonal temperature increase and those oscillations there is a corresponding increase in common dolphin sightings. This pattern can be seen in Figure 14; in 1997 and 1998 there are more common dolphin sightings than in 1999 and 2000, and in the warmest year, 1997, their distribution appears to be more offshore than inshore (likely short-beaked common dolphins), while in 1998 there is a strong inshore presence (likely short- and long-beaked common dolphins). The fact that the most sightings in this four-year period occurred in 1998 and the fewest occurred in 2000 may indicate a lagged response between the onset of a temperature fluctuation and a subsequent change in common dolphin distribution.

Risso's dolphins

The Risso's dolphin (Gg) model indicated an increase in sightings in the winter and in neutral/warm seasonal SST's (Figure 9). They were also associated with strong positive ENSO indices, and their model includes an ENSO and PDO interaction term as well. In fact, a peak in sightings occurred in the early 1980's, when there was a very strong El Niño and a well-documented shift from pilot whales to Risso's dolphins dominating the waters around Catalina Island (Shane 1994; 1995). Risso's dolphins displayed a fairly strong inshore distribution and island association, generally remaining inshore of the continental shelf, although they had an offshore presence as well. This inshore distribution and affiliation with positive PDO and ENSO phases is exemplified in Figure 14. In 1997 and 1998 Risso's dolphins were observed in abundance near the Channel Islands; however in 1999, when SST's are much cooler, the only Risso's dolphin sightings occurred far offshore, and there were no sightings in 2000.

Striped dolphins

Striped dolphins (Sc) are a tropical species associated with warm water masses, and were predominantly observed offshore of the 2000m depth contour (Figure 8). Both ENSO and PDO indices were included in the model, with sightings peaking in neutral to positive index values for both. In addition, interactions of multiple SST indices were included, along with an interaction between seasonal SST's and mean depth. The extent of their offshore distribution was affected by SST such that when warm water extended further inshore the range of striped dolphins followed, while when cool water from the California Current extended further into the SCB, striped dolphins were found further offshore. This model had a relatively low explained deviance (24.5%). This is in part due to the limitation of including only sightings made in Beaufort sea state 3 or less; as most striped dolphin sightings occurred offshore, many were made in higher sea states and were therefore not included.

Bottlenose dolphins

While bottlenose dolphins (Tt) are a cosmopolitan species distributed worldwide both inshore and offshore, in the SCB region they tended to display a strong inshore and island association, generally within the continental shelf, although they were occasionally observed offshore (Figure 10). This model indicated an association with negative PDO indices. Interaction terms were also included between depth mean and both seasonal SST's and the ENSO index, and between the PDO and ENSO indices, indicating a possible inshore/offshore movement associated with changing regimes. One such interaction was documented after the 1982/83 ENSO event, when coastal bottlenose dolphins shifted the northern extent of their range from the SCB to north-central California (Defran *et al.* 1999). In keeping with these results, bottlenose dolphins were sighted most abundantly near the Channel Islands in the more SST neutral years of 1998 and 2000 than during the strongly warm or cold years (Figure 14).

Northern right whale dolphins

Northern right whale dolphins (Lb) are one of three cold temperate species strongly associated with the California Current, whose extent into the SCB correlated with cold water intrusions. Sightings peaked in spring, when the California Current is the strongest and SST's are coolest (Figure 11). However, sightings were also associated with positive ENSO and PDO indices, which generally indicate warmer conditions. Northern right whale dolphins had a strong slope association, with a peak in sightings following the 2000-m depth contour.

Also included in the model were interactions between seasonal and ENSO indices, and between ENSO and PDO indices. There were also interaction terms included between seasonal SST's and mean depth, and between PDO indices and mean depth, indicating an inshore/offshore or north/south shift in distribution associated with temperature. There were only one or two sightings of northern right whale dolphins each year from 1997-2000 (Figure 14). In the warmer years of 1997-98, they were sighted once each year, south of Point Conception, just inshore of the slope. In 1999 there were two sightings, one in the same location and one further inshore. In 2000 their single sighting was much further north and offshore on the slope. In all cases, they appear to be tracking the cold water tongue of the California Current as it wraps into the SCB, and the extent of their distribution into the SCB may be mediated by the strength of the current.

Dall's porpoise

Dall's porpoise also seem to follow cold water intrusions into the SCB, with peak sightings during the spring in cool seasonal SST's (Figure 13). They were distributed both inshore and offshore, and also included interactions between mean depth and seasonal SST's. The PDO index appears to be an important predictor for this species; their sightings increased with a positive PDO index, and the model also included interactions between PDO and seasonal SST's, and the ENSO index, as well as between seasonal SST's and the ENSO index. They were also associated with a negative ENSO index. There were few sightings of Dall's porpoise in 1997-99, and they were observed both inshore and offshore in those years, while in 2000 there were several sightings, all further north and/or offshore than in the previous years (Figure 14).

Pacific white-sided dolphins

Pacific white-sided dolphins demonstrated a surprising negative response to cooler water, with fewer sightings associated with cooler seasonal SST's (Figure 12), although sightings also peaked during the spring quarter when the water temperature is cooler. Pacific white-sided dolphins also demonstrated an inshore and offshore distribution. Neither PDO nor ENSO indices were directly included in this model, however PDO and ENSO were included as interaction terms with seasonal SST's. An interaction term between seasonal SST's and depth was also included. These patterns are demonstrated in Figure 14; in 1997 and 2000 Pacific white-sided dolphins were observed both inshore and offshore, while in 1998 their range seemed to contract inshore and in 1999 only two groups were sighted, and both were located offshore. Pacific white-sided dolphins may contract their range to remain further north in strong PDO years and only extend their range into the SCB in warmer years, leading to the association with slightly warmer SST's.

Discussion

The models presented in this study demonstrate that oscillations in sea surface temperature regimes do influence the distribution of small cetaceans, although it is likely that this represents an effect on prey and a subsequent response by the dolphins. Dolphins have previously been shown to be sensitive to changes in

SST and to shift their distributions in response to regime oscillations like ENSO. However, this is the first study to model responses to multiple temperature shifts over a long time period for a variety of species. The resulting models were different for every species, indicating that each demonstrates a unique habitat occurrence pattern related to both prey and SST dynamics despite the overlap in their distributions in the SCB. Long-beaked common, bottlenose, and Risso's dolphins demonstrated a preference for coastal and island-associated waters; while short beaked common and Pacific white-sided dolphins and Dall's porpoise were observed both inshore and offshore; northern right whale dolphins were associated with the slope; and striped dolphins were observed only in deep offshore waters. Dall's porpoise, Pacific white-sided dolphins, and northern right whale dolphin sightings peaked in cool spring months, while common dolphin and striped dolphin sightings peaked in the warm summer and fall. Risso's dolphin sightings increased throughout the year, peaking in the late fall/winter.

The relationship of each species to the different temperature fluctuations, modeled using seasonal SST anomaly data, and PDO and ENSO indices, were also quite varied. As expected, Dall's porpoise and northern right whale dolphins demonstrated strong preferences for cooler temperatures, while common dolphins preferred warmer water (Forney 2000; Reeves *et al.* 2002; Becker 2007). The lack of association with cool water is unusual for Pacific white-sided dolphins, as they are considered a cool water species. However, two populations of Pacific white-sided dolphins have been shown to overlap in the SCB based on genetic and morphological evidence (Walker *et al.* 1986; Lux *et al.* 1997). One population, found along California, Oregon and Washington, may be associated with the cool water of the California Current, while the other population, found along the Baja Peninsula, may be associated with the warm California Countercurrent. Both populations were likely encountered in the SCB by SWFSC and CalCOFI cruises, and therefore the model results presented here likely represent both populations. Finally, the offshore distribution of striped dolphins may indicate an association with warm North Pacific gyre waters, located outside of the cool California Current. Striped dolphins are also found further offshore in deep water in the Eastern Tropical Pacific (Au and Perryman 1985), although they tend to overlap more with common dolphins in that region. These are similar depth and temperature relationships to those found by Becker (2007), who saw an increase in encounter rates in shallower water for Pacific white-sided dolphins and Dall's porpoise, and an increase in encounter rates in deeper water for striped dolphins. Becker (2007) also found higher encounter rates for Pacific white-sided dolphins, northern right whale dolphins and Dall's porpoise in cooler temperatures, while striped and common dolphins were encountered in warmer SST's. Forney (2000) also found Dall's porpoise to have an inshore distribution and a close link with cool SST's, while short-beaked common dolphins were associated with warmer SST's, with a variable depth distribution dependent on temperature.

Most models also included the PDO and ENSO indices. An increase in sightings occurred for Dall's porpoise, northern right whale dolphins, striped dolphins and long-beaked common dolphins during positive PDO phases, while common dolphins (Dsp) and bottlenose dolphins were associated with the negative

PDO phase. Likewise, Risso's dolphins, northern right whale dolphins, and striped dolphins were associated with positive ENSO indices, while Dall's porpoise were associated with negative ENSO indices. During positive PDO and ENSO phases, upwelling waters are reduced and productivity decreases throughout the California Current System, while water temperatures increase, particularly as warm equatorial waters are pushed poleward. This may drive the normally cool water associated species to extend their ranges into the SCB in search of prey, while warm water species extend their ranges poleward as temperatures rise and warm-water endemic prey expand their range. Finally, most species included interactions among the different SST indices, and between those indices and mean depth, indicating spatial changes in distribution occurred for all species across at least one SST shift. These results support the hypothesis that these small cetacean species alter their distributions in response to fluctuations in SST. While there is some overlap in responses between species, each has a unique pattern which may represent niche partitioning with the SCB.

The PDO regime was in a positive, warm phase for most of the study period, and there were more strong positive ENSO events than strong negative ones during this time. Therefore these results have strong implications on the impact of climate change upon these species; as ocean temperatures rise these models may assist in predicting how each dolphin species may shift their distribution. Species associated with sea-ice and those with highly limited ranges are the most obvious species to be affected by changing ocean temperatures and sea levels. However, even open water or coastally migrating species such as those presented here are likely to be affected, either indirectly by shifts in the distribution or abundance of their prey, or directly by a change in the conditions that a species can physiologically tolerate (Learmonth *et al.* 2006; Simmonds and Eliott 2009). MacLeod (2009) categorized cetacean species as either cold-water limited, whose ranges would contract poleward as water temperatures increased, cold- and warm-water limited, whose ranges would shift poleward, or warm-water limited whose ranges, centered around the equator, would expand. He then determined whether those range shifts would be favorable or unfavorable for a given species. Under these categorizations, bottlenose, striped, common and Risso's dolphins were warm-water limited species, with favorable range expansions predicted, while Pacific white-sided and northern right whale dolphins were cold- and warm-water limited, and Dall's porpoise was cold-water limited, all with unfavorable range contractions predicted. An example in support of this idea was demonstrated in Scotland, where as water temperatures off Scotland increased, the number of common dolphins expanded, while the number of white-beaked dolphins (*Lagenorhynchus albirostris*) decreased, possibly indicating a poleward shift in range for both species (MacLeod *et al.* 2005; Simmonds and Isaac 2007). In addition, an increase in strandings of warm-water species with a concurrent reduction in strandings of cold-water species was observed (MacLeod *et al.* 2005). Similar range shifts are likely to be observed in the SCB, with the southern range extent of Pacific white-sided and northern right whale dolphins and Dall's porpoise contracting poleward, while the northern extent of the ranges of common, striped, bottlenose and Risso's dolphins expands poleward. Most importantly, the range changes observed by MacLeod *et al.* (2005) occurred over a relatively short time span, about 15 years, unlike historic climate change events that occurred on slow enough time spans that marine mammals could adapt behaviorally and genetically. Niche conservatism is the tendency of species to retain their ancestral niche (Wiens and Graham 2005), and may be one explanation of historical allopatric speciation. On the time-scales of global climate change, cetaceans may not be able to shed their historical ecological niches rapidly enough to adapt as conditions change.

Temperature shifts related to both global climate changes and regime shift changes have also been linked to reproductive success in a number of marine mammals, including North Atlantic right whales, humpback whales, sperm whales and dusky dolphins (Learmonth *et al.* 2006). A mass stranding of bottlenose dolphins in the Gulf of Mexico was also linked to an anomalous cold-water event (IWC 1997). Indirect effects of increasing temperature include impacts on prey resources, leading not only to a reduction in prey availability, but further to the reliance on blubber resources, which could mobilize contaminants and lead to disruptions in immunization and reproductive systems (Learmonth *et al.* 2006). Finally, an increase in ocean temperature may also lead to increases in toxic algal blooms, which have been linked in the past to mass stranding events (Simmonds and Mayer 1997). In addition to the direct impact of climate change on ocean temperature, other effects include rising sea levels, changes in ocean circulation, increases in ocean acidification, and changes in salinity (Learmonth *et al.* 2006). Cephalopods are sensitive to fluctuations in both salinity and pH (Fiedler 2002; Simmonds and Isaac 2007); changes in these as rainfall and ocean acidification increase could deplete some squid species in the SCB, shifting the primary prey resource for Risso's dolphins and an important food resource for other dolphins as well. Rising sea levels could impact the small cetaceans with strong coastal and island distributions, such as bottlenose, long-beaked common and Risso's dolphins by increasing their ranges as shorelines shift. Finally, a change in ocean circulation would primarily impact small cetaceans associated with fronts and eddies, and secondarily those associated with the California Current, as its strength seems linked to the distribution of the cold-water associated species.

Conclusions

The distributions of eight small cetacean species have been demonstrated to be effected by both short- and long-term sea surface temperature fluctuations related to climate regime changes. Both north-south and inshore-offshore movements were linked to seasonal, yearly and decadal changes in SST, and some strong coastal and island associations were shown for several species. These results are most likely indicative of the small cetaceans' response to movements of prey in response to changing oceanographic conditions, and so an analysis of zooplankton and fish distribution and abundance against the same SST data should be conducted. In addition, a lagged response by the small cetaceans should be tested to determine the time-frame in which a response may occur. These data may be used to predict the distribution of these small cetacean species throughout the SCB, and might be applicable to other related habitats as well. These data may also be used as a tool to understand the possible responses of these small cetaceans to rising ocean temperatures as global climate change intensifies.

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Chapter 5, in full, is currently in preparation for submission. E. E. Henderson, J. Barlow, K. A. Forney, J. A. Hildebrand, J. Calambokidis and W. J. Sydeman. Effects of Sea Surface Temperature Variation on the Distribution of Small Cetaceans in the Southern California Bight: Implications for Climate Change. The dissertation author was the primary investigator and author of this material.

Table 5.1 - The intial best-fit model using the AIC and residual deviance for each species, along with the AIC score, residual deviance and degrees of freedom for each model.

Species	Best Initial Model	AIC	Explained Deviance	Residual Deviance	Residual DF
Dd	s(Quarter, 3) + s(SeasAnom, 4) + s(PDO,2) + s(DepthMax, 3) + s(DepthMean,3) + SeasAnom PDO + SeasAnom:ENSO + S + SeasAnom:DepthMean + PDO:DepthMean + ENSO:DepthMean	1453.3	22.9%	970.5	675
Dc	s(SeasAnom, 2) + s(PDO, 3) + s(ENSO, 3) + s(DepthMax, 3) + SeasAnom:ENSO	404.4	53.0%	281.5	683
Dsp	s(Quarter, 3) + s(SeasAnom, 4) + s(PDO, 3) + s(ENSO,3) + s(DepthMax,3) + s(DepthMin, 3) + s(DepthMean, 3) + SeasAnom:PDO + PDO:ENSO + SeasAnom:DepthMean + ENSO:DepthMean	5586.52	23.8%	3823.9	2514
Gg	s(Quarter, 2) + s(SeasAnom, 4) + s(PDO, 2) + s(ENSO, 3) + s(DepthMax,3) + s(DepthMean, 3) + SeasAnom:PDO + PDO:ENSO	1376.2	27.4%	1014.9	2521
Lb	s(Quarter,2) + s(SeasAnom,2) + s(ENSO,3) + s(DepthMean,3) + SeasAnom:ENSO + ENSO:PDO + SeasAnom:DepthMean	562.6	26.6%	419.1	2527
Lo	s(Quarter, 3) + s(SeasAnom, 4) + s(PDO,3) + s(DepthMean, 3) + SeasAnom:PDO + SeasAnom:ENSO + PDO:ENSO + SeasAnom:DepthMean	1369.1	24.7%	1026.6	2523
Pd	s(Quarter, 2) + s(SeasAnom, 4) + s(PDO, 3) + s(ENSO,2) + s(DepthMax, 3) + s(DepthMean, 3) + SeasAnom:PDO + SeasAnom:ENSO + SeasAnom:DepthMean	1357.6	32.8%	972.3	2520
Sc	s(PDO, 3) + s(ENSO, 3) + s(DepthMean, 3) + PDO:SeasAnom + PDO:ENSO + DepthMean:SeasAnom	274.3	25.7%	200.8	2528
Tt	s(SeasAnom, 3) + s(PDO, 3) + s(DepthMax, 3) + s(ENSO,3) + s(DepthMean, 3) + PDO:ENSO + DepthMean: SeasAnom + ENSO:DepthMean	796.9	38.3%	583.0	2522

Table 5.2 –The model with the lowest predictive sum of squares value was selected as the overall best fit model after the 5-fold (3-fold for Dd and Dc) cross-validation procedure was applied.

Species	Best Overall Model	PRESS	Explained Deviance
Dd	s(Quarter, 3) + s(SeasAnom, 4) + s(DepthMax, 3) + SeasAnom:PDO + SeasAnom:ENSO + SeasAnom:DepthMean + PDO:DepthMean + ENSO:DepthMean	360.07	21.5%
Dc	s(Quarter,2) + s(SeasAnom, 2) + s(PDO, 2) + s(DepthMean, 3)	262.02	50.0%
Dsp	s(Quarter, 3) + s(SeasAnom, 4) + s(PDO, 3) + s(DepthMax,3) + SeasAnom:PDO + PDO:ENSO + SeasAnom:DepthMean + PDO:DepthMean + ENSO:DepthMean	310.22	23.1%
Gg	s(Quarter, 3) + s(SeasAnom, 4) + s(ENSO, 2) + s(DepthMean,3) + PDO:ENSO	44.76	24.0%
Lb	s(Quarter,2) + s(SeasAnom, 2) + s(PDO, 3) + s(ENSO, 3) + s(DepthMean,3) + SeasAnom:ENSO + ENSO:PDO + SeasAnom:DepthMean + PDO:DepthMean	14.22	28.8%
Lo	s(Quarter, 3) + s(SeasAnom, 4) + s(DepthMax, 3) + s(DepthMean,3) + SeasAnom:PDO + SeasAnom:ENSO + SeasAnom:DepthMean	34.19	24.7%
Pd	s(Quarter,2) + s(SeasAnom, 4) + s(PDO, 3) + s(ENSO, 3) + s(DepthMean,3) + SeasAnom:PDO + SeasAnom:ENSO + PDO:ENSO + SeasAnom:DepthMean	40.85	32.3%
Sc	s(PDO,2) + s(ENSO, 3) + s(DepthMean,2) + PDO:SeasAnom + PDO:ENSO + DepthMean:SeasAnom	0.004	24.5%
Tt	s(PDO,2) + s(DepthMax, 3) + s(DepthMean, 3) + PDO:ENSO + DepthMean:SeasAnom + ENSO:DepthMean	9.01	36.2%

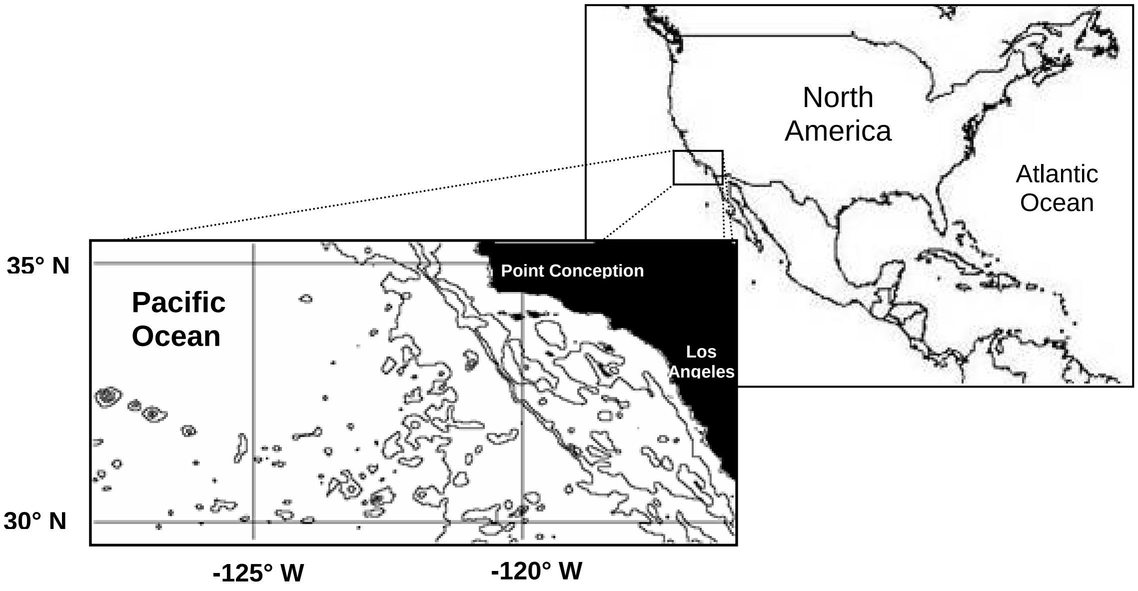


Figure 5.1 – The Southern California Bight study area, located in the Eastern North Pacific Ocean, south of Point Conception and incorporating the Channel Islands. 500-m depth contours are plotted.

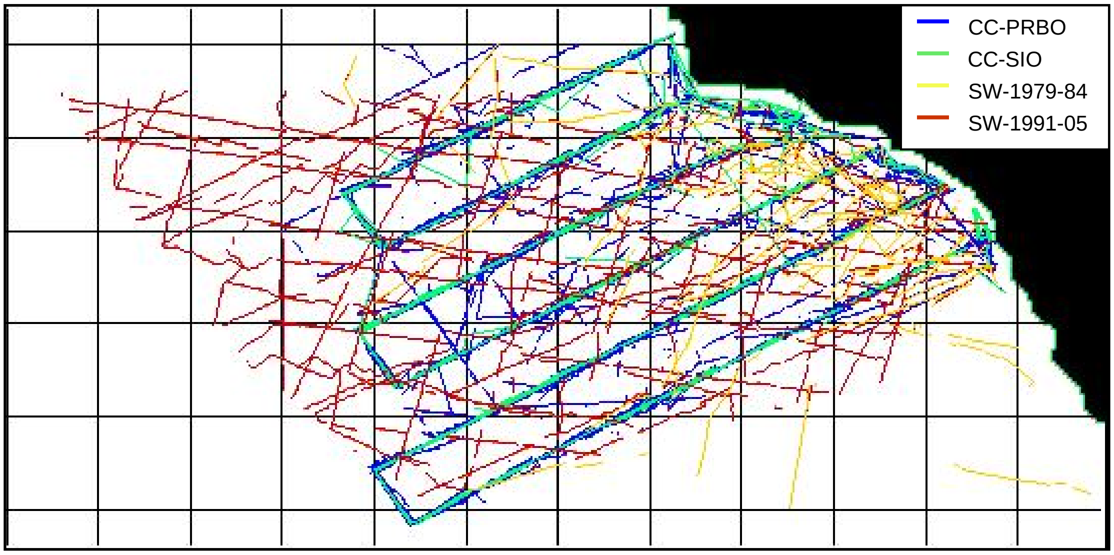


Figure 5.2 – Transect lines surveyed for all studies. CalCOFI - PRBO surveys are in purple, CalCOFI - SIO surveys are in blue, SWFSC surveys from 1979-1984 are in red and SWFSC surveys from 1991-2005 are in orange. Black lines indicate latitude and longitude in 1 degree increments, used to create the grid sections utilized in the GAM analysis.

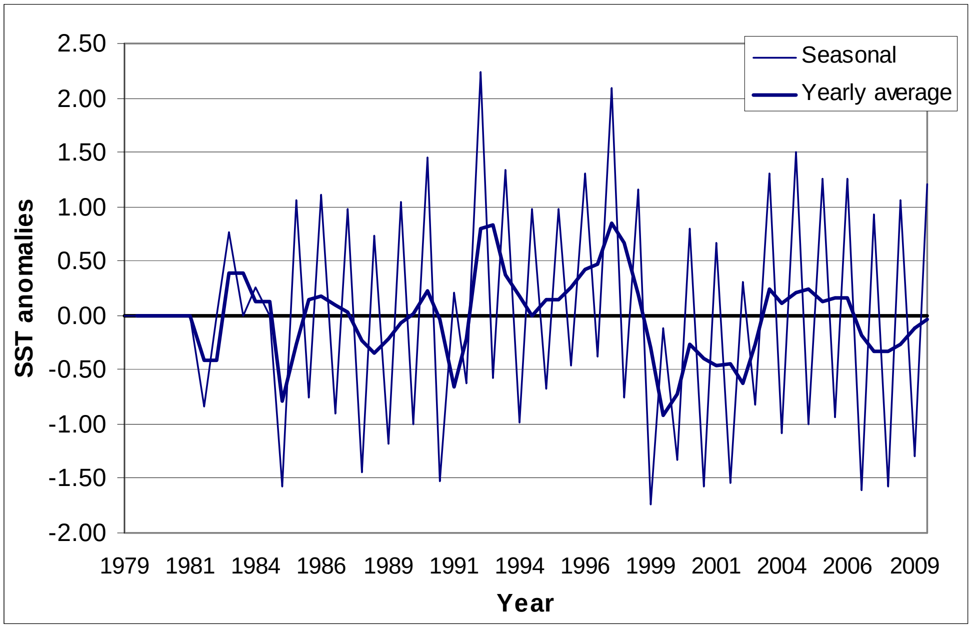


Figure 5.3 - Seasonal SST anomalies from the SCB from 1981 to 2009, and the yearly moving average SST anomalies.

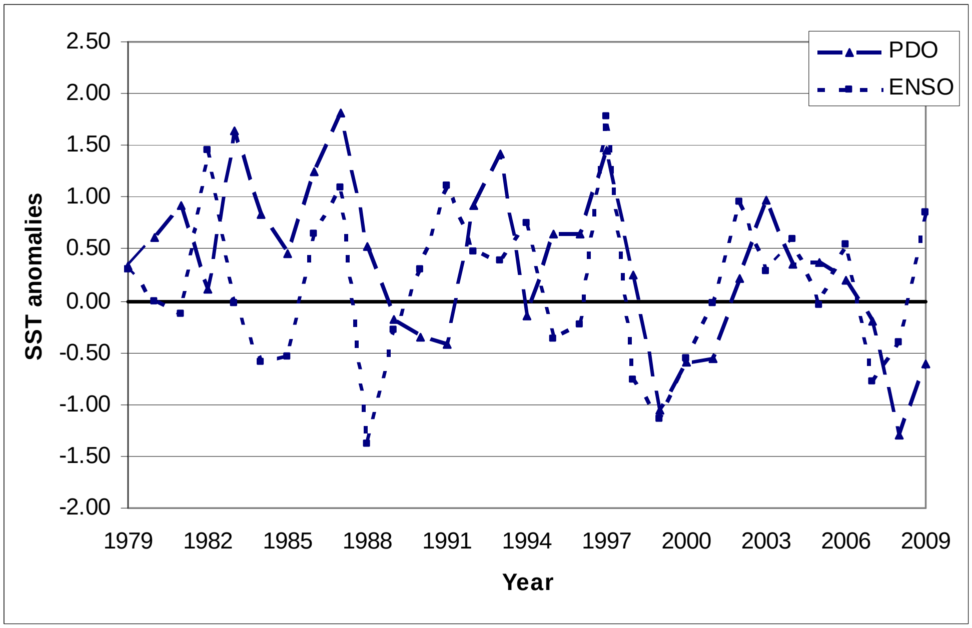


Figure5.4 - ENSO and PDO SST anomalies from 1979-2009. PDO SST anomalies were calculated using data from 1900-2009, while ENSO anomalies were calculated using a three month running mean from 1950-2009.

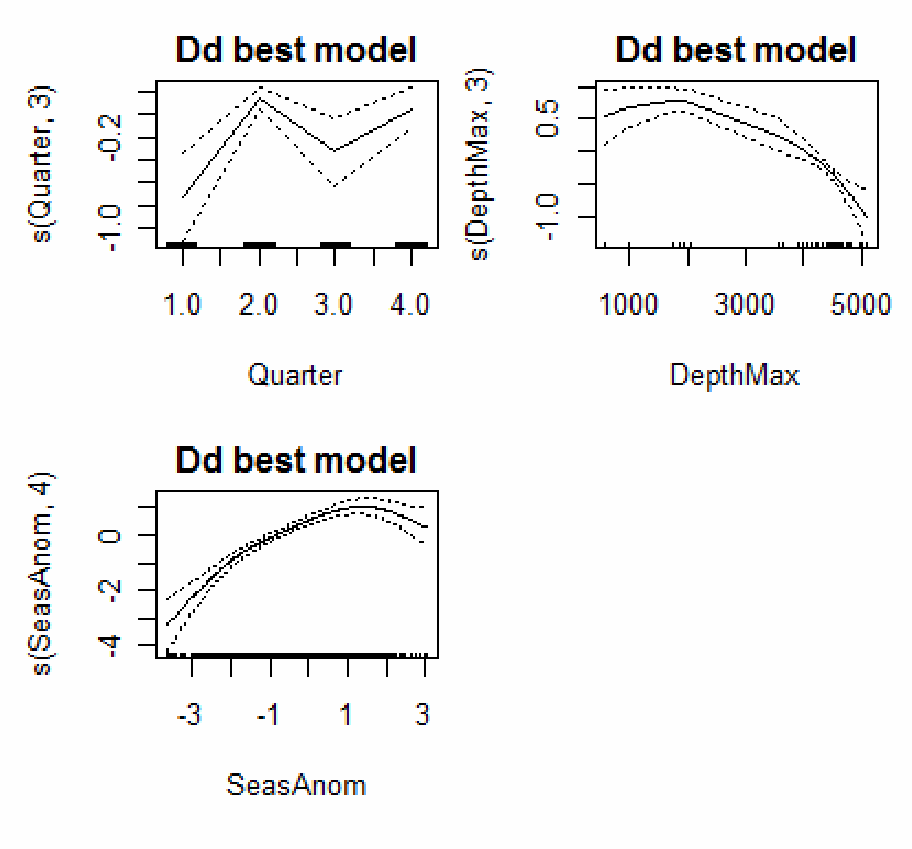


Figure 5.5 – GAM functions of short-beaked common dolphin (Dd) sightings from 1991 to 2005 for SWFSC cruises and from 2004-2009 for CalCOFI cruises, in relation to SST indices and depth variables for the best predictive models. Dashed lines are bands of two standard error.

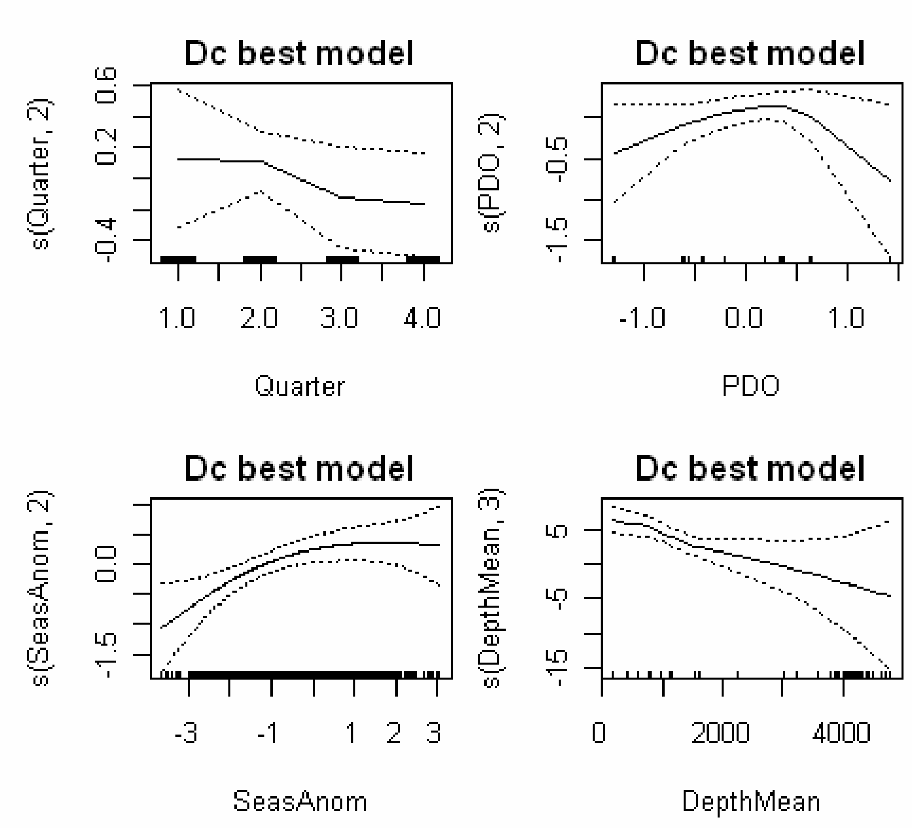


Figure 5.6 – GAM functions of long-beaked common dolphin (Dc) sightings from 1991 to 2005 for SWFSC cruises and from 2004-2009 for CalCOFI cruises, in relation to SST indices and depth variables for the best predictive models. Dashed lines are bands of two standard error.

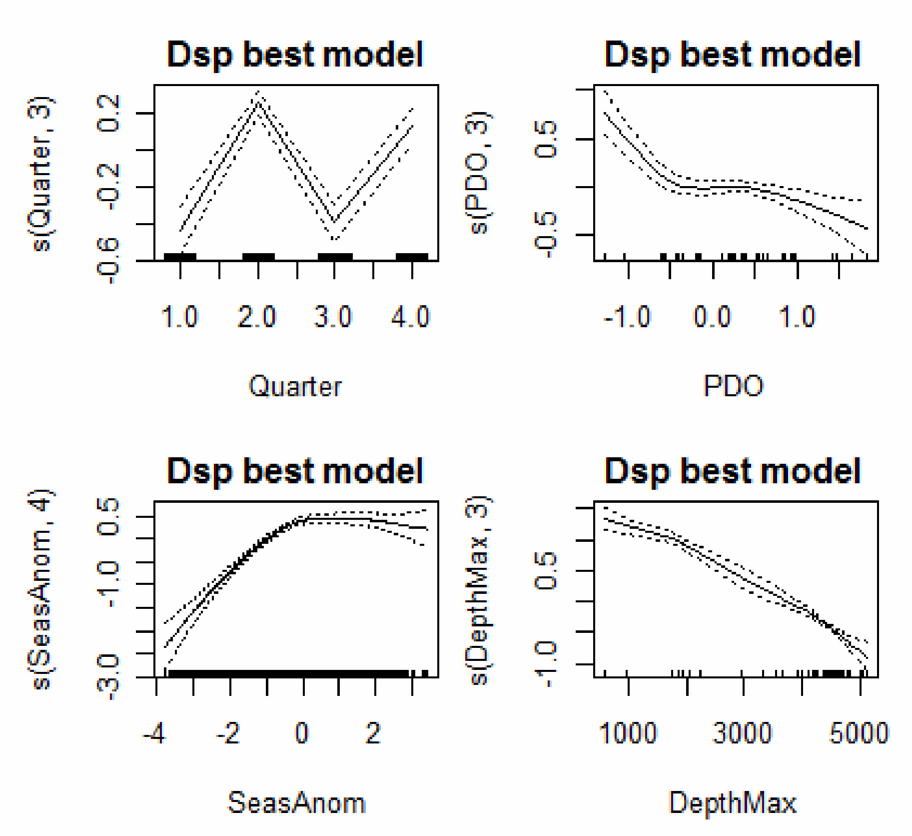


Figure 5.7 – GAM functions of common dolphin (Dsp) sightings from 1979 to 2009 in relation to SST indices and depth variables for the best predictive models. Dashed lines are bands of two standard errors.

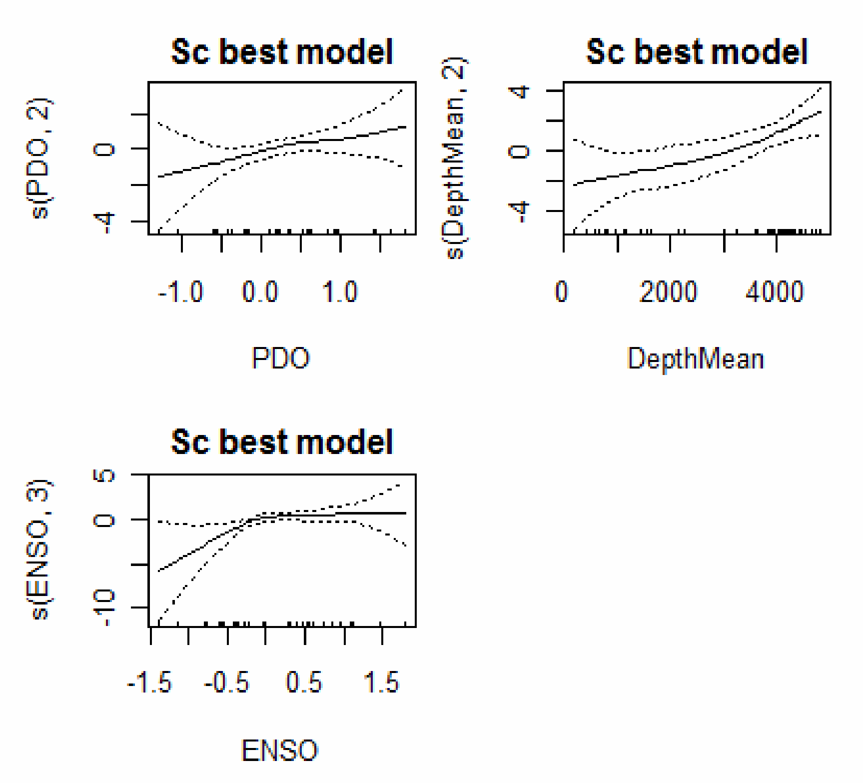


Figure 5.8 – GAM functions of striped dolphin (Sc) sightings from 1979 to 2009 in relation to SST indices and depth variables for the best predictive models. Dashed lines are bands of two standard errors.

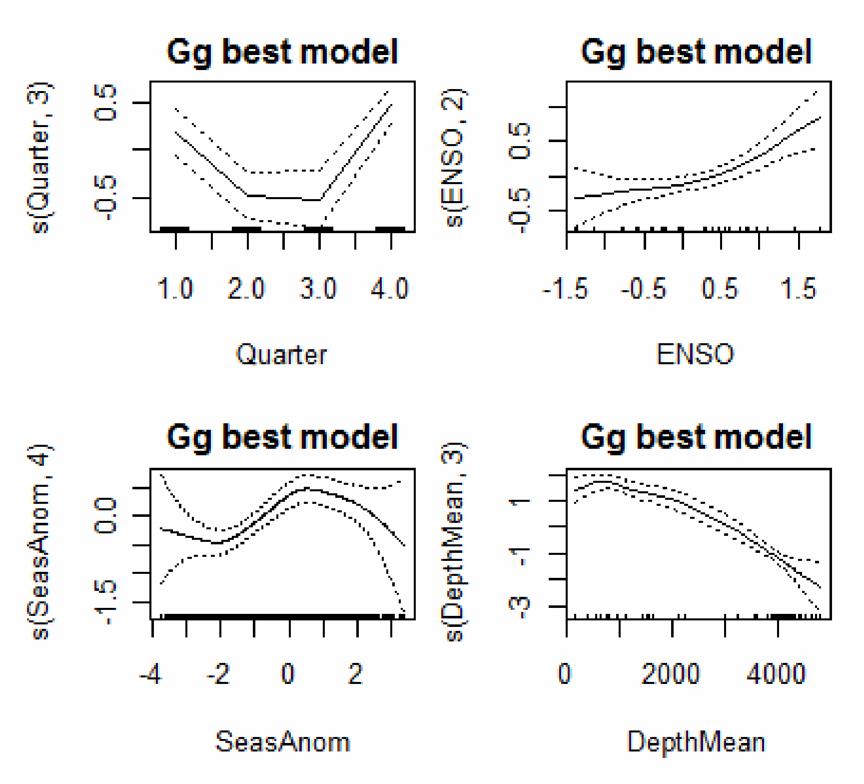


Figure 5.9 – GAM functions of Risso's dolphin (Gg) sightings from 1979 to 2009 in relation to SST indices and depth variables for the best predictive models. Dashed lines are bands of two standard errors.

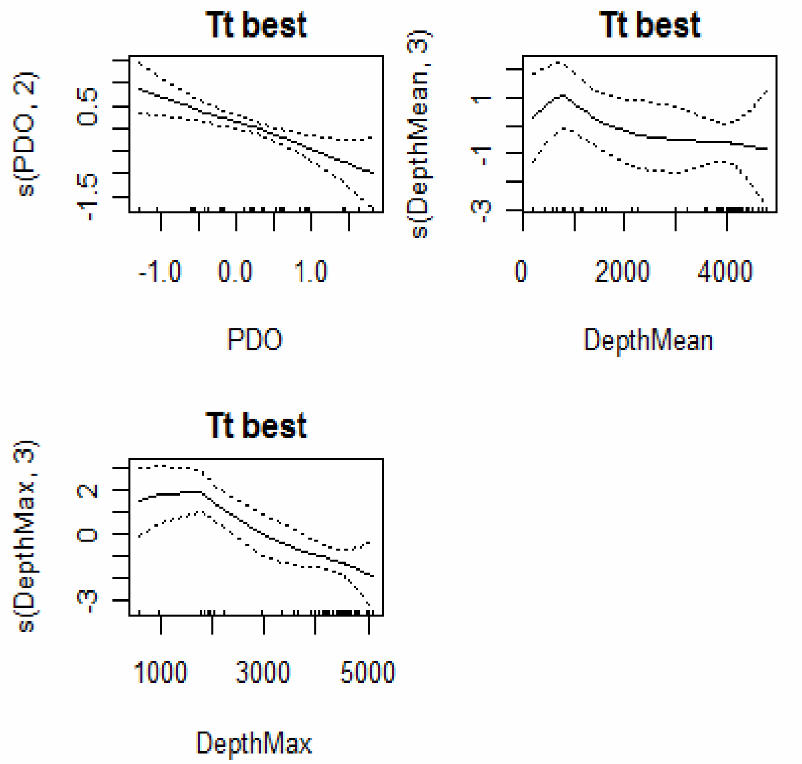


Figure 5.10 – GAM functions of bottlenose dolphin (Tt) sightings from 1979 to 2009 in relation to SST indices and depth variables for the best predictive models. Dashed lines are bands of two standard errors.

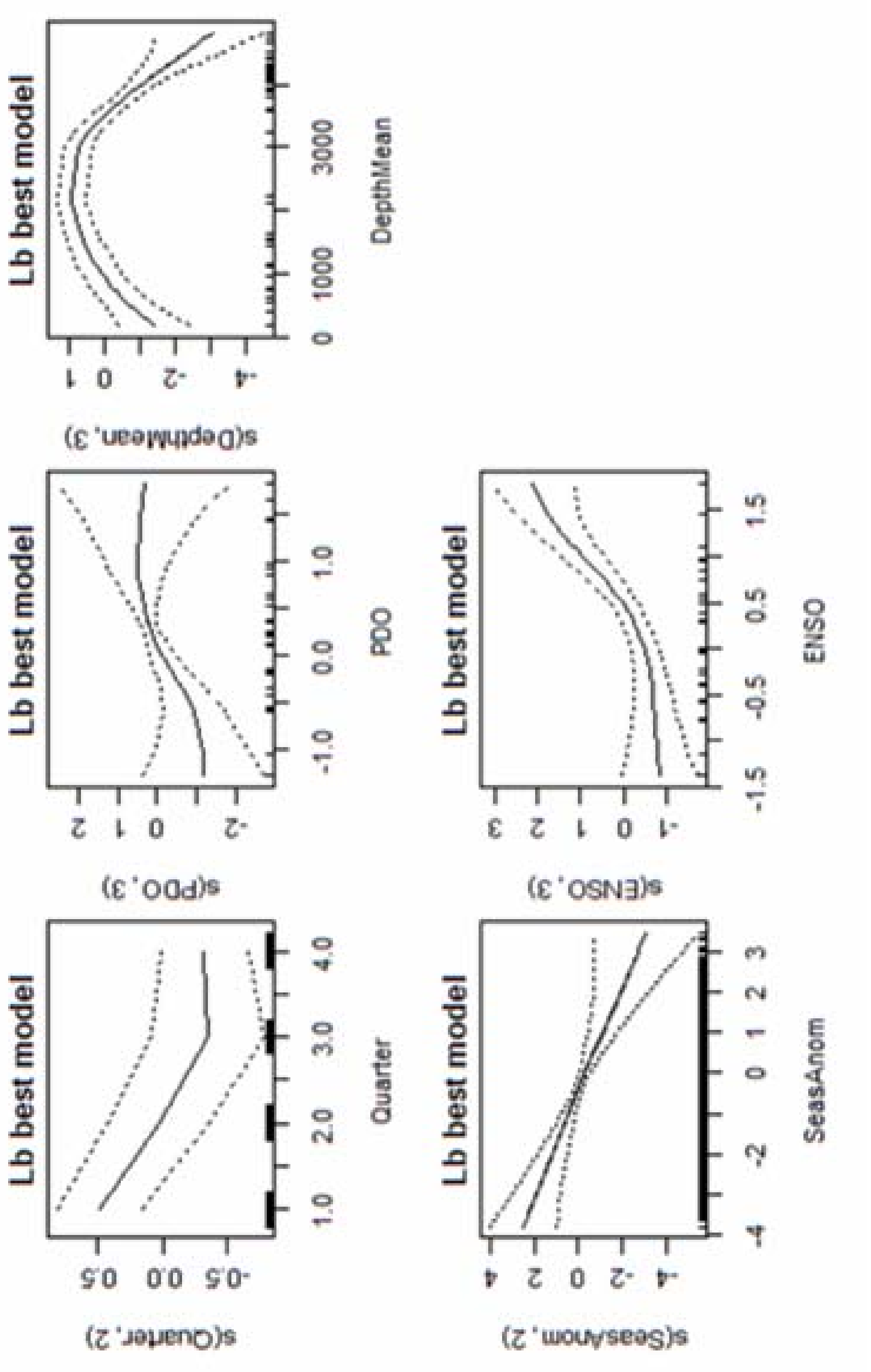


Figure 5.11 – GAM functions of northern right whale dolphin (Lb) sightings from 1979 to 2009 in relation to SST indices and depth variables for the best predictive models. Dashed lines are bands of two standard errors.

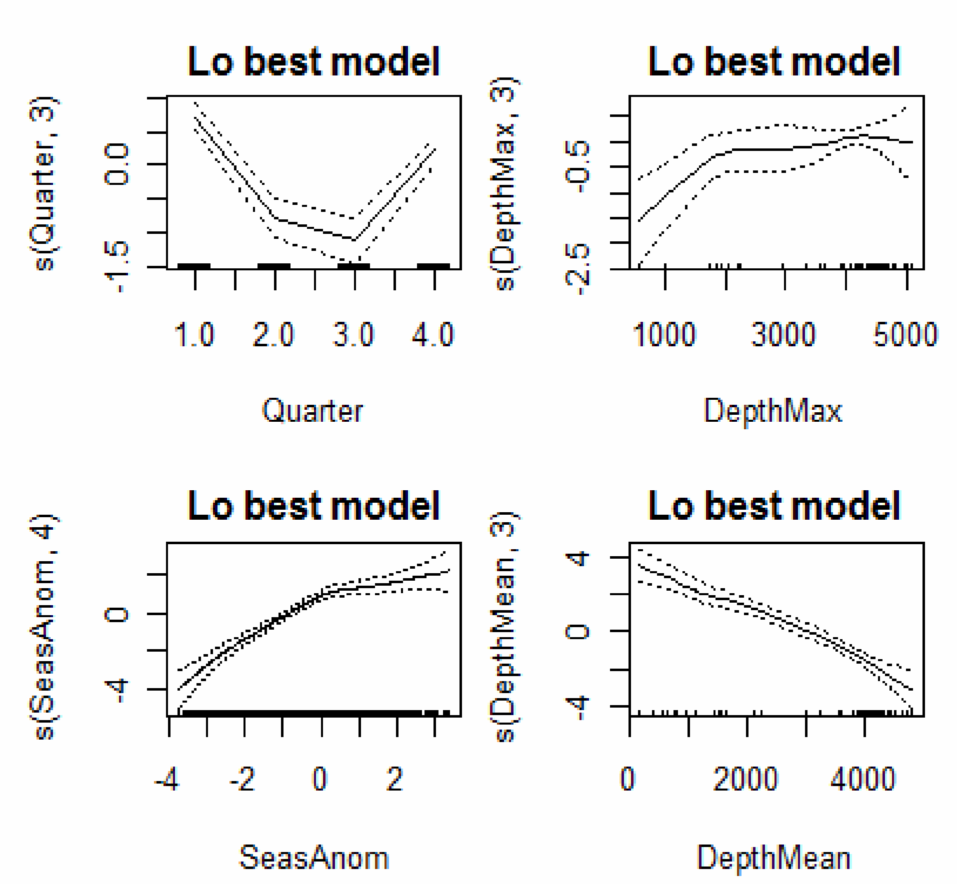


Figure 5.12 – GAM functions of Pacific white-sided dolphin (Lo) sightings from 1979 to 2009 in relation to SST indices and depth variables for the best predictive models. Dashed lines are bands of two standard errors.

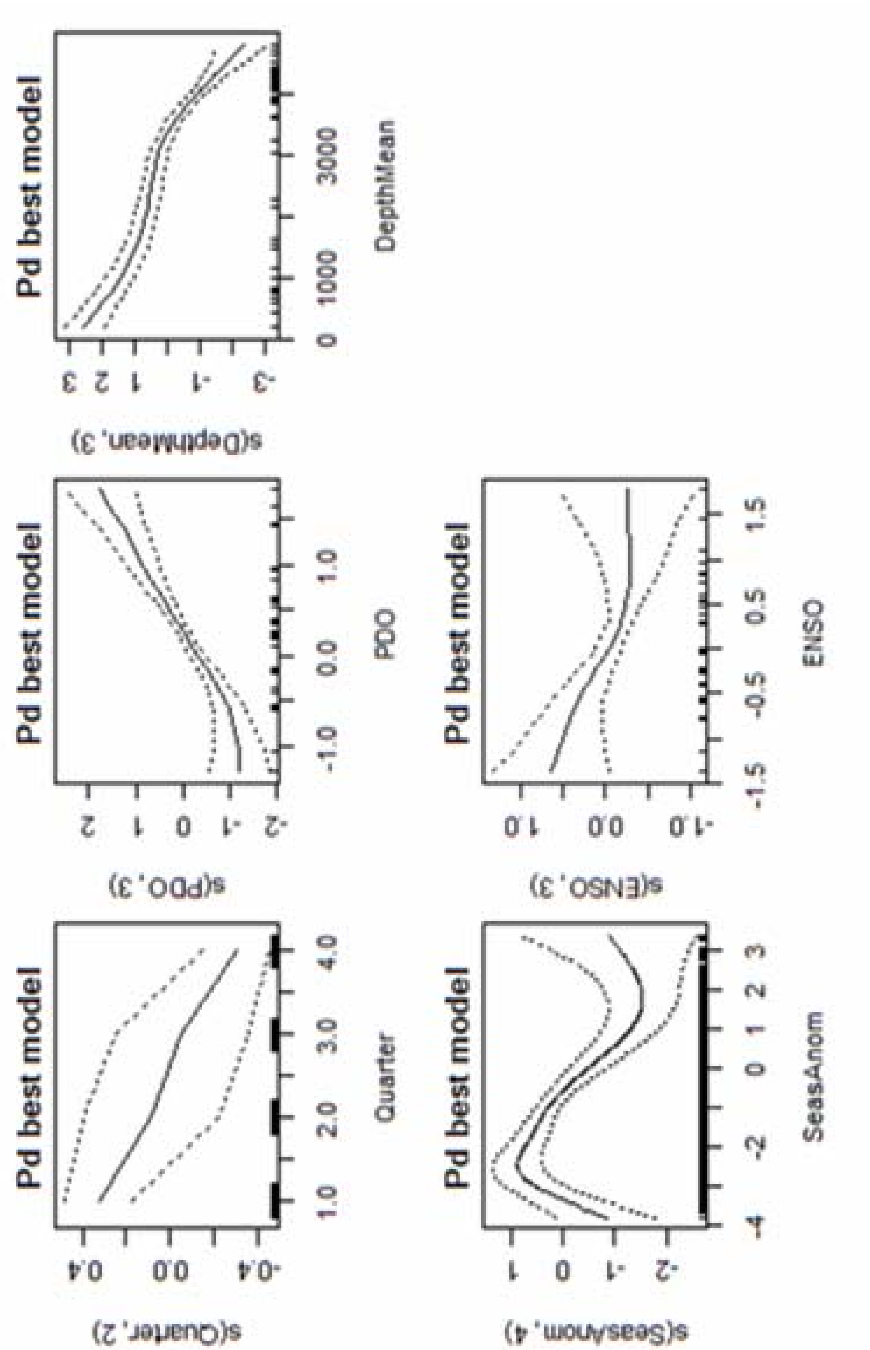
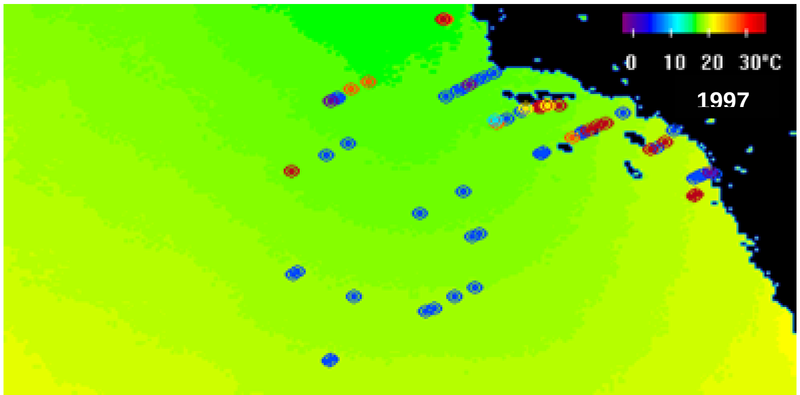
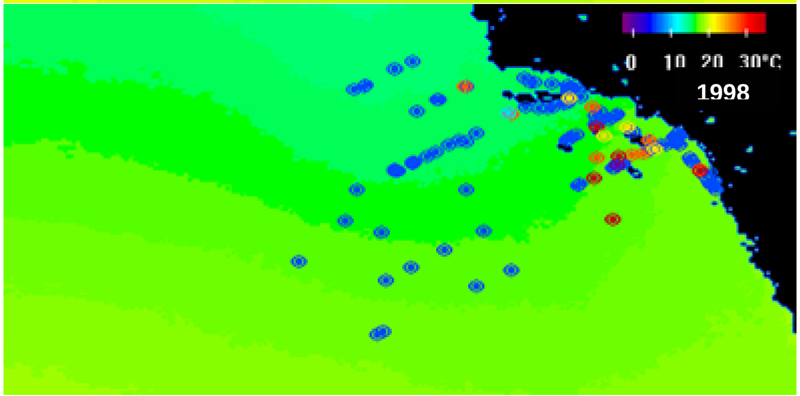


Figure 5.13 – GAM functions of Dall's porpoise (Pd) sightings from 1979 to 2009 in relation to SST indices and depth variables for the best predictive models. Dashed lines are bands of two standard errors.

Figure 5.14 - Mean SST's for 1997 - 2000, taken from AVHRR satellite data. Dark blue circles are common dolphins, orange circles are Pacific white-sided dolphins, red circles are Risso's dolphins, yellow circles are bottlenose dolphins, light blue circles are northern right whale dolphins, and purple circles are Dall's porpoise. Sighting data are all from PRBO CalCOFI cruises.


0 10 20 30°C
1997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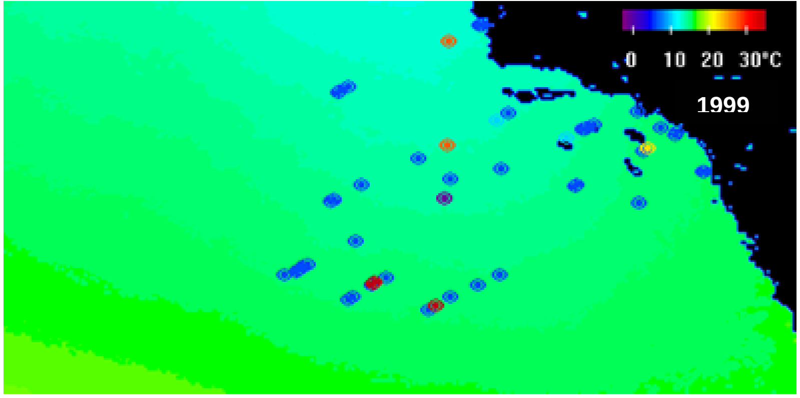
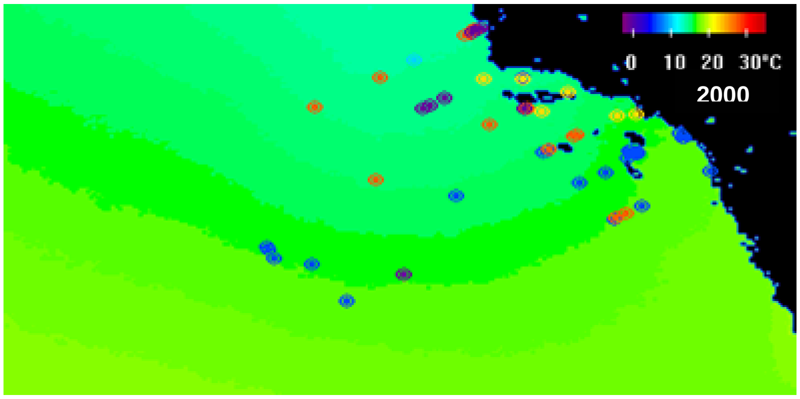
1998


0 10 20 30°C
1999


0 10 20 30°C
2000

Appendix I – Survey Cruise Lists

CalCOFI Cruise List

Cruise	Year	Season
CAC198705	1987	Spring
CAC198709	1987	Summer
CAC198711	1987	Fall
CAC198801	1988	Winter
CAC198804	1988	Spring
CAC198808	1988	Summer
CAC198810	1988	Fall
CAC198901	1989	Winter
CAC198904	1989	Spring
CAC198907	1989	Summer
CAC198911	1989	Fall
CAC199003	1990	Winter
CAC199004	1990	Spring
CAC199007	1990	Summer
CAC199011	1990	Fall
CAC199101	1991	Winter
CAC199103	1991	Spring
CAC199107	1991	Summer
CAC199109	1991	Fall
CAC199201	1992	Winter
CAC199204	1992	Spring
CAC199207	1992	Summer
CAC199209	1992	Fall
CAC199301	1993	Winter
CAC199303	1993	Spring
CAC199308	1993	Summer
CAC199310	1993	Fall
CAC199401	1994	Winter
CAC199403	1994	Spring
CAC199410	1994	fall
CAC199501	1995	Winter
CAC199504	1995	Spring
CAC199507	1995	Summer
CAC199510	1995	Fall
CAC199604	1996	Spring
CAC199608	1996	Summer
CAC199610	1996	Fall
CAC199701	1997	Winter
CAC199707	1997	Summer
CAC199709	1997	Fall
CAC199712	1997	El Nino1
CAC199801	1998	Winter
CAC199803	1998	El Nino2
CAC199804	1998	Spring
CAC199805	1998	El Nino3
CAC199806	1998	El Nino4
CAC199807	1998	Summer
CAC199809	1998	Fall
CAC199810	1998	El Nino5
CAC199904	1999	Spring
CAC199908	1999	Summer
CAC199910	1999	Fall
CAC200004	2000	Spring
CAC200007	2000	Summer
CAC200010	2000	Fall
CAC200101	2001	Winter
CAC200104	2001	Spring
CAC200107	2001	Summer
CAC200110	2001	Fall
CAC200201	2002	Winter
CAC200203	2002	Spring
CAC200207	2002	Summer
CAC200211	2002	Fall
CAC200301	2003	Winter
CAC200304	2003	Spring
CAC200307	2003	Summer
CAC200310	2003	Fall
CAC200401	2004	Winter
CAC200404	2004	Spring
CC0407	2004	Summer
CC0411	2004	Fall
CC0501	2005	Winter
CC0504	2005	Spring
CC0507	2005	Summer
CC0511	2005	Fall
CC0602	2006	Winter
CC0604	2006	Spring
CC0607	2006	Summer
CC0610	2006	Fall
CC0701	2007	Winter
CC0704	2007	Spring
CC0707	2007	Summer
CC0711	2007	Fall
CC0801	2008	Winter
CC0803	2008	Spring
CC0808	2008	Summer
CC0810	2008	Fall
CC0901	2009	Winter
CC0903	2009	Spring
CC0907	2009	Summer
CC0911	2009	Fall

SWFSC Cruise List

Cruise Name	Year	Duration
0564	1979	Sept-Oct
0646	1980	June-July
0798	1982	April
0674	1983	Dec
0905	1984	Dec
CAMMS	1991	July-Oct
PODS	1993	July-Oct
ORCAWALE	1996	Aug-Nov
ORCAWALE	2001	July-Dec
CSCAPE	2005	Aug-Dec

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