UNIVERSITY OF CALIFORNIA, SAN DIEGO

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

Committee in charge:

Professor John A. Hildebrand, Chair
Professor Jay P. Barlow
Professor Phil Hastings
Professor William Hodgkiss
Professor Jim J. Moore

2010

UMI Number: 3419837

All rights reserved

INFORMATION TO ALL USERS
The quality of this reproduction is dependent upon the quality of the copy submitted.

In the unlikely event that the author did not send a complete manuscript
and there are missing pages, these will be noted. Also, if material had to be removed,
a note will indicate the deletion.

UMI 3419837
Copyright 2010 by ProQuest LLC.
All rights reserved. This edition of the work is protected against
unauthorized copying under Title 17, United States Code.

ProQuest LLC
789 East Eisenhower Parkway
P.O. Box 1346
Ann Arbor, MI 48106-1346

Copyright

E. Elizabeth Henderson, 2010

All rights reserved.

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

TABLE OF CONTENTS

Signature Page……... iii

Dedication……..…….…….. iv

Table of Contents…….... v

List of Figures……... x

List of Tables…… xiii

Acknowledgements……... xv

Vita…….…… xxii

Abstract…….……..…….. xxiv

Chapter 1 Introduction……..…….…… 1

Background……..…… 4

Southern California Bight……. 4

Delphinid Vocalizations…… 7

Focal Species…… 8

Dissertation Outline...…..…… 10

Literature Cited..…….. 14

Chapter 2 The Behavioral Context of Common Dolphin (*Delphinus* sp.) Vocalizations……..… 24

Abstract……..……..…… 24

Introduction……..…… 25

Methods……...…… 28

Study Area and Survey Platforms…… 28

Behavioral and Acoustic Sampling…… 29

Call Selection……. 32

Analysis……. 35

Results……...…….. 36

Discussion...…...…….. 41

Conclusions…….. 47

Acknowledgements…….. 49

Tables……... 50

Figures…….. 52

Literature Cited…… 56

Chapter 3 Classification of Behavior Using Vocalizations of Pacific White-Sided Dolphins (*Lagenorhynchus obliquidens*)…….… 63

Abstract……..……..…… 63

Introduction……..…… 64

Methods……...…… 68

Study Area and Survey Platforms…… 68

Visual Observations and Behavioral Sampling…… 69

Acoustic Sampling and Call Selection……. 72

Analysis……. 75

Results……...…….. 77

Discussion...…...…….. 81

Conclusions…….…….. 87

Acknowledgements…….. 89

Tables……... 90

Figures…….. 92

Literature Cited…… 97

Chapter 4 The Role of Marine Mammals as Top Predators: An Analysis of Marine Mammal Occurrence and Oceanographic Patterns in the Southern California Bight…...……. 104

Abstract……..……..…… 104

Introduction……..…… 105

Methods……...…… 108

Study Area …… 108

Data Collection and Analysis…….…… 108

Oceanographic Sampling..……. 109

Zooplankton Abundance……... 110

Acoustic Estimation of Fish Biomass and Behavior…. 110

Marine Mammal Monitoring……. 113

Results……...……. 114

Marine Mammal Composition……... 114

Oceanographic Parameters……. 115

Zooplankton Abundance……...……. 116

Parameter Correlations…….…….. 118

Echosounder Data and Fish Biomass……. 120

Discussion...…...…… 122

Oceanographic Synthesis……... 122

Zooplankton Abundance…… 125

Fish Biomass……... 126

Marine Mammal Occurrence Patterns…… 127

Summary and Limitations…..…….. 130

Acknowledgements……..…….. 132

Tables……... 133

Figures…….. 134

Appendix I: Spearman rank correlation test results..…… 145

Literature Cited…… 149

Chapter 5 Effects of Sea Surface Temperature Variation on the Distribution of Small Cetaceans in the Southern California Bight: Implications for Climate Change…….… 155

Abstract……..……..…… 155

Introduction……..…… 156

Methods……...…… 159

Study Area…… 159

Surveys……...…… 161

Model Data…...……. 164

Results……...……... 168

Common dolphins……. 169

Risso's dolphins……. 171

Striped dolphins……. 172

Bottlenose dolphins…… 173

Northern right whale dolphins……... 173

Dall's porpoise……... 174

Pacific white-sided dolphins…….. 175

Discussion...…...……..….. 175

Conclusions……..….. 181

Acknowledgements……..….. 183

Tables……..…... 184

Figures……..…….. 186

Appendix I: Survey Cruise Lists…… 199

Literature Cited……..…… 201

LIST OF FIGURES

Chapter 2

Figure 2.1 Bathymetric map of the study area in Southern California Bight…… 52

Figure 2.2 Spectrograms of common dolphin whistle categories……..... 53

Figure 2.3 Behavioral categories for common dolphins ……...….... 54

Figure 2.4 Daily behavior patterns of common dolphins ……...…… 54

Figure 2.5 Group size composition for each behavior category...……..... 55

Figure 2.6 Group spacing composition for each behavior category……..… 55

Chapter 3

Figure 3.1 Bathymetric map of Southern California Bight, with an inset of San Clemente Island..…….…. 92

Figure 3.2 Spectrogram of pulsed call series…….…..…..…… 93

Figure 3.3 Summary of behavioral data..…….…… 93

Figure 3.4 Median click and clicks/individual rates for each behavior…… 94

Figure 3.5 Median group size for each behavior …….…..…….. 95

Figure 3.6 Gini variable importance measures for the final top ranked call features, with group size and calls/clicks per individual included……..…..……...…… 96

Chapter 4

Figure 4.1 The Southern California Bight, with an inset of San Clemente Island and the location of each FLIP deployment....…...…… 134

Figure 4.2 Normalized *TS* of fish and zooplankton as a function of L/λ, and Δ*Sv* for fish and zooplankton ...…… 136

Figure 4.3 Time series of (A) delphinid, (B) whale, and (C) pinniped sightings, and (D) environmental data, (E) temperature contours, and (F) fluorescence contours…….…… 138

Figure 4.4 T-S plots for 2007 and 2008 with isopycnals……. 139

Figure 4.5 Satellite-derived SST's, averaged over each of four weeks for each cruise……... 140

Figure 4.6 Zooplankton abundances (averaged in m^{-2}) from bongo net tows in 2008.……...……...…… 141

Figure 4.7 Length (in feret diameter.s) distributions for all zooplankton… 142

Figure 4.8 Time series of volume backscattering strength (*Sv*) for fish and zooplankton…….…… 143

Figure 4.9 Fish biomass density (kg/m^2), estimated using the different proportions of four fish species ……...……...…… 144

Chapter 5

Figure 5.1 The Southern California Bight study area …….……..…… 180

Figure 5.2 Effort for all surveys…….. 180

Figure 5.3 Seasonal SST anomalies from the SCB from 1981 to 2009, and the yearly moving average SST anomalies…….…… 181

Figure 5.4 ENSO and PDO SST anomalies from 1979-2009……..… 181

Figure 5.5 GAM functions of short-beaked common dolphin (Dd) sightings…….. 182

Figure 5.6 GAM functions of long-beaked common dolphin (Dc) sightings…….. 183

Figure 5.7 GAM functions of common dolphin (Dsp) sightings ….…… 184

Figure 5.8 GAM functions of striped dolphin (Sc) sightings ….. …….. 185

Figure 5.9 GAM functions of Risso's dolphin (Gg) sightings ……...……. 186

Figure 5.10 GAM functions of bottlenose dolphin (Tt) sightings …… 187

Figure 5.11 GAM functions of northern right whale dolphin (Lb) sightings…….. 188

Figure 5.12 GAM functions of Pacific white-sided dolphin (Lo) sightings... 189

Figure 5.13 GAM functions of Dall's porpoise (Pd) sightings ……..…… 190

Figure 5.14 Mean SST's for 1997 - 2000, taken from AVHRR satellite data……..……. 192

LIST OF TABLES

Chapter 2

Table 2.1 Descriptions of the group behavioral categories used for analysis……... 50

Table 2.2 Summary of effort and the number of common dolphin groups used for analysis for all surveys……. 50

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…….…. 51

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…… 51

Chapter 3

Table 3.1 Descriptions of the behavioral categories used for analysis…….. 90

Table 3.2 Summary of effort and number of Pacific white-sided dolphin groups sighted for all surveys…….…… 90

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……. 91

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…… 91

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……. 91

Chapter 4

Table 4.1 Number of sightings for each year of FLIP deployment…… 133

Table 4.2 Density estimates (kg/m^2) for each fish species, estimated from scattering volume and averaged across all echosounder measurments……... 133

Chapter 5

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…….…….. 178

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…….. 179

ACKNOWLEDGMENTS

My thanks must of course start at the beginning, with my advisor John Hildebrand, for taking me on my first FLIP trip, hiring me as an observer, and finally agreeing to take me on as a graduate student with my crazy project idea. John allowed me the freedom and opportunity to develop my ideas, run multiple cruises, and try out whatever scheme I came up with. Thanks for the acoustics knowledge, the experience, and above all, the laughter on FLIP! Thanks also to the rest of my committee members. Thanks to Jay Barlow for always being available to answer questions, bounce around ideas, give invaluable statistics advice, and read countless manuscript revisions. You have been a great mentor, and I appreciate you going above and beyond. Thanks to Jim Moore for the behavioral wisdom and conference advice. Thanks to Bill Hodgkiss for making signal processing understandable and interesting, and for always being helpful and cheerful. Finally, thanks to Phil Hastings, for the wisdom of the fishes and the wonderful blennies, your love for what you do has been an inspiration. I owe thanks to several other professors and "advisors": Sean Wiggins for teaching me Triton and spectral analysis when I was clueless and for organizing lab hookey days; Marie Roch for teaching me about classification, sharing with me her knowledge, programming skills and advice with infinite kindness and patience; Peter Franks, for the equipment loan, oceanography advice, and dynamite teaching skills; Mark Ohman for all the help sampling and analyzing zooplankton, especially lending me your gear, letting me be an honorary lab member for a few weeks, and then for letting me pick your brain to figure out what it all meant; Annie Townsend for

additional help with the net gear and sampling advice; Alison Cawood for many hours of Zooscan help; Dave Demer at SWFSC for countless hours helping me figure out how in the world to analyze my acoustic data and make heads or tails of the results; Karin Forney for all of the modeling help and advice and for answering all of my questions, no matter how small; Eric Archer and Megan Ferguson for additional statistics help and modeling advice; and Mati Kahru for help with WIM and an amazingly fast email response time. Also major thanks to Beve Kennedy, without whom nothing would ever happen in our lab, but who is always happy and helpful, and who has the best art and craft ideas; and to Monica Suiymanjaya for all her help and party-organzing skills.

I have to also thank my numerous visual and acoustic observers, crew members and collaborators. Without all of you there is no way this project would have happened, and I am grateful to all of you. First and foremost I have to thank Bill Gaines, Captain Tom Golfinos and Paul Porcioncula for all of the FLIP trips. Bill believes passionately in the FLIP and ceaselessly works to keep it in use, and bent over backward on numerous occasions to make sure my cruises actually happened. Tom is the best captain a person could ever hope for, and will say "whatever you want" with a twinkle in his eye no matter what crazy thing you want to try. Thanks for three Halloweens, one Thanksgiving, and a million laughs, Tom. σας ευχαριστώ. Paul was the best cook ever, could magically produce salads three weeks into a cruise, made sure everyone was taken care of, created the best desserts, and would still tell you to "eat some more, skinny" after you had gained ten pounds. Thanks to the other

crew members, especially Greg Viehmann and Roy Barrette, who always lent a hand with a smile on their faces and were experts at crocheting. Thanks to Michael Smith for leading visual observations for all three years, and for being so wonderful to work with. Finally, thanks to all the FLIP observers and acousticians: Megan McKenna, Katherine Kim, Greg Falxa, Alexis Rudd, Jennifer Funk, Amanda Cummins, Allan Ligon, Nadia Rubio, Ethan Roth, Gustavo Cárdenas, Velvet Voelz, Jamie Gibbon, Lamalani Siverts, Brenda deGerald, Kait Frasier, and Kristina Welch. Thanks to Cascadia Research Collective for the San Clemente Island collaboration, particularly Erin Falcone, Greg Schorr, Annie Douglas and John Calambokidis. Thanks especially to Erin for being a fantastic boat partner, the long days on the water were filled with conversation and laughter and I appreciate all of it. Additional thanks to the NUWC folks, David Moretti, Ron Morrissey, Susan Jarvis, and Nancy DiMarzo, and the Naval Postgraduate School folks, Ernie Young, Curt Collins and Tarry Rago. Finally, the funding for all of this work was provided by CNO-N45 and the Naval Postgraduate School, so big thanks to Frank Stone for all his efforts to make it happen.

Now comes the sentimental part – thanks to all my lab-mates and friends that have been a part of this journey over the last five years. I am so lucky to have ended up in a lab where I liked everyone and we all supported each other, shared ideas, and inspired one another. I have to first thank Melissa and Mario Soldevilla for twelve years of friendship and for helping me get my foot in the door. Melissa and Mario provided a wealth of advice, laughter, and friendship, and were some of my first friends “in the field”. Can’t wait for the boat, guys! Thanks to Lisa Munger, for being

the second person I knew at Scripps, my yoga and water-slide buddy, and a constant source of sunshine and giggles. Thanks to Jessica Burtenshaw for being my first officemate and for putting up with all of my first-year questions, sharing my taste in music, and for all the Sudoku, you rock. An enormous amount of thanks go out to Megan McKenna. We started the same year, took every class together, went on numerous cruises together (mostly mine, thanks for that!), and basically have been glued at the hip for the last five years, so thank goodness she is such an awesome person and has become one of my closest friends. I am looking forward to all our future adventures together. Thanks to my revolving cast of officemates – Hannah Bassett, Karli Merkens, Aly Fleming and Liz Vu. Thanks to Hannah for her wisdom beyond her years, and for trying to teach me to have a backbone like she does. Thanks to Aly for being literally the kindest, happiest person on earth and for bringing that into my life when I needed it most, and thanks to Liz Vu for being my other Liz, my running buddy, and a totally cool person, it's been a fun last year thanks to both of you! Thanks to Simone Baumann-Pickering for coming to San Diego and being a good mentor and friend, for lots of discussions and advice, and for showing me it could be done. Thanks to Chris Garsha for fixing or rebuilding all five of the computers I killed and for finally hanging out outside of the lab, to Ethan Roth for being like a brother and for the mullet, to Josh Jones for the many laughs, to Brent Hurley for every board you've built, and to Greg Campbell for the small boat co-captaining and array building. Thanks to Kait Frasier for being an awesome intern and trying to make something tangible out of my ephemeral ideas. Good luck to you, Liz and Kerri as you guys pick

up the mantle of the lab. Thanks to Amanda Cummins for many hours of visual observations, for Span-tuckey, and for lab-hopping with me - where are we going next? Thanks to Sara Kerosky for standing up in front of everyone on your first day while we sang, I knew you were cool then and there. There are so many people in our lab that it is impossible to name them all, but thanks to everyone – we work as a giant team and everyone is appreciated!

Thanks also have to go out to the absolutely amazing network of friends that have been a part of this journey for many years. First my "family", the Borg: Annie, Jess, Jenelle, Vida, Heath, Betsy, Chelsea, Holly: they have not left my side since we were fourteen, and there is no way I would be where or who I am without them. Our family has doubled and tripled in the ensuing years, and everyone has followed their dreams and have become amazing people. Thanks for the last 20 years and for the next 60. Then came my Drew crew: Maggie, Niles, Chris, Darian, Danny, Ryan, Liz, Melissa, and Cathy: my entire college experience was shaped by them and my life is still blessed to have them in it with just as much joy and laughter as we had then. My first marine biology experience was in Hawaii, where I worked with Melissa, Rebecca, Alison, and Siri, who are still my marine mammal partners in crime. Can't wait to work and play with all of them more in the future, when we get to be in charge! My time in Texas was filled with Holly, Mike, Rebecca, Darcy, and Jen, and we enjoyed it to the fullest. I would not have made it through the first round of grad school without them. Finally, I ended up in San Diego, and was somehow handed two entire groups of friends wrapped in shiny bows. First was Kim, Eric, Stacey, Mike, Shannon, Dave,

Kevin and Emily, my built-in Ocean Beach posse. Thanks for keeping me sane and giving me an outlet outside of school, and for letting me be auntie to all your beautiful children. Second was The Girlfriend Groupie Group, which lasted way longer than the band – Jen, Vern, Stefanie, Laura, Kristy, Ann, Amanda and Lisa. Thanks for being the best group of wine and brunch aficionados a girl could ask for! Last, but not least, my Scripps cohort: Megan, Talina, Geoff, Andrew and Marco. We got each other through first year departmentals, third (or so) year qualifiers, many quarters of classes and research, and many, many beer nights. The absolute best group of people to survive graduate school with, hands down.

Thank you of course to my family, my mother, Patte, my big brother, Andrew and his lovely wife and daughters Paula, Peyton and Frankie, my beautiful sisters Meagan and Sarah, my stepmother Liz, and my grandmother Polly. You have all listened, wondered, questioned, laughed and cheered at my (long) scholastic journey – thanks for all of it, we never thought it would be done but it finally is!

My amazing, wonderful and supportive husband Judd deserves more thanks than can fit on a page. He came with me to Texas and sweltered for three years, watched me tear my hair out and swear never again when I finished my Master's, and only shook his head when I told him I was doing it all over again. He has waited patiently while I have gone on cruises, to conferences, worked late, and generally not been around. Thanks Judd!

The research presented in this dissertation was possible due to funding provided by the Chief of Naval Operation-N45. Several travel grants were received

with gratitude through the Graduate Office, and a generous Scholar Award was received from P.E.O. International. Ian Higginbottom and the people at Echoview also generously donated software for my acoustic analysis.

Chapter 2, in full, has been submitted for publication in Marine Mammal Science: Henderson, E.E., Hildebrand, J.A., Smith, M. H., and Falcone, E. A. The Behavioral Context of Common Dolphin (*Delphinus* sp.) Vocalizations. The dissertation author was the primary investigator and author of this paper.

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.

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.

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.

VITA

EDUCATION

2010 Ph.D. in Oceanography
University of California, San Diego

2004 M.Sc. in Wildlife and Fisheries Management,
Texas A&M University, College Station

1999 BA, PsychoBiology, Magna Cum Laude
Drew University, Madison, NJ

TEACHING AND RESEARCH EXPERIENCE

2009 Teaching Assistant, Department of Electrical Engineering,
University of California, San Diego

2004-2005 Marine Mammal Acoustician
Scripps/Southwest Fisheries Science Center, San Diego CA

2002-2003 Teaching Assistant, Department of Marine Biology,
Texas A&M University, Galveston

2000 Research Assistant, The Dolphin Institute, Honolulu, HI

1998 Intern, Kewalo Basin Marine Mammal Laboratory,
Honolulu, HI

PUBLICATIONS

E. E. Henderson and B. Würsig. 2008. Behavior patterns of bottlenose dolphins in San Luis Pass, Texas. *Gulf of Mexico Science* 25(2):153-161.

E. A. Falcone, G.S. Schorr, A.B. Douglas, J. Calambokidis, E. E. Henderson, M.F. McKenna, J. Hildebrand, and D. Moretti. 2009. Sighting characteristics and photo-identification of Cuvier's beaked whales (*Ziphius cavirostris*) near San Clemente Island, California: a key area for beaked whales and the military? *Marine Biology* DOI: 10.1007/s00227-009-1289-8

M. S. Soldevilla, E. E. Henderson, G. S. Campbell, S. M. Wiggins, J. A. Hildebrand, and M. A. Roch. 2008. Classification of Risso's and Pacific white-sided dolphins using spectral properties of echolocation clicks. *The Journal of the Acoustical Society of America* 124(1):609-624.

M. A. Roch, M. S. Soldevilla, J. C. Burtenshaw, E. E. Henderson, and J. A. Hildebrand. 2007. Gaussian mixture model classification of odontocetes in the Southern California Bight and the Gulf of California. *The Journal of the Acoustical Society of America* 121(3):1737-1748.

M. A. Roch, M. S. Soldevilla, J. C. Burtenshaw, E. E. Henderson, S. M. Wiggins, J. A. Hildebrand. 2006. On the use of the Teager energy operator for the detection of clicks in free-ranging dolphins. *The Journal of the Acoustical Society of America* 120(5):3014-3015.

K. A. Kim, P. Hursky, M. B. Porter, J. A. Hildebrand, E. E. Henderson and S. M. Wiggins. 2006. Dolphin pods of the Southern California Offshore Range: Localization and behavior. *The Journal of the Acoustical Society of America* 119(5):3403.

E. E. Henderson. 2004. Behavior, association patterns and habitat use of a small community of bottlenose dolphins in San Luis Pass, TX. M.Sc. Thesis, Texas A&M University, Galveston, TX.

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

University of California, San Diego, 2010

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 zoo-plankton 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.

Literature Cited

Ansmann, I. C., J. C. Goold, P. G. H. Evans, M. P. Simmonds and S. G. Keith. 2007. Variation in the whistle characteristics of short-beaked common dolphins, *Delphinus delphis*, at two locations around the British Isles. Journal of the Marine Biological Association of the United Kingdom 87:19-26.

Au, D. W. K. and W. L. Perryman. 1985. Dolphin Habitats in the eastern tropical Pacific. Fishery Bulletin 83:623-643.

Au, W. W. L. 1993. The Sonar of Dolphins. Springer-Verlag Inc, New York.

Au, W. W. L. 2004. Echolocation signals of wild dolphins. Acoustical Physics 50:454-462.

Baker, C. S. and L. M. Herman. 1984. Aggressive behavior between humpack whales (*Megaptera novaeangliae*) wintering in Hawaiian waters. Canadian Journal of Zoology 62:1922-1937.

Ballance, L. T., R. L. Pitman and P. C. Fiedler. 2006. Oceanographic influences on seabirds and cetaceans of the eastern tropical Pacific: A review. Progress in Oceanography 69:360-390.

Barlow, J. and K. A. Forney. 2007. Abundance and population density of cetaceans in the California Current ecosystem. Fishery Bulletin 105:509-526.

Baumann-Pickering, S. 2009. Species identification and measurement of activity in odontocete species of Palmyra Atoll by acoustic monitoring. PhD. Eberhard Karls Universitat Tubingen,

Baumgartner, M. F. 1997. The distribution of Risso's dolphin (*Grampus griseus*) with respect to the physiography of the northern Gulf of Mexico. Marine Mammal Science 13:614-638.

Benoit-Bird, K. and W. W. L. Au. 2001. Foraging Behavior of the Hawaiian Spinner Dolphin, *Stenella longirostris*. Page 22 14th Biennial Conference on the Biology of Marine Mammals. Society for Marine Mammalogy, Vancouver.

Brownell, R. L., W. A. Walker and K. A. Forney. 1999. Pacific white-sided dolphins *Lagenorhynchus obliquidens* Gill, 1865. Pages 57-84 *in* S.H. Ridgway and R. Harrison, eds. Handbook of Marine Mammals,. Academic Press, London, San Diego.

Caldeira, R. M. A., P. Marchesiello, N. P. Nezlin, P. M. DiGiacomo and J. C. McWilliams. 2005. Island wakes in the Southern California Bight. Journal of Geophysical Research 110:C11012.

Caldwell, M. C. and D. K. Caldwell. 1971. Statistical evidence for individual signature whistles in Pacific white-sided dolphins, *Lagenorhynchus obliquidens*. Cetology 3:1-9.

Checkley Jr., D. M. and J. A. Barth. 2009. Patterns and processes in the Calfornia Current System. Progress in Oceanography 83:49-64.

Christal, J. and H. Whitehead. 2001. Social affiliations within sperm whale (*Physeter macrocephalus*) groups. Ethology 107:323-340.

Clapham, P. J. 1996. The social and reproductive biology of humpback whales:an ecological perspective. Mammal Review 26:27-49.

Craig, A. S. and L. M. Herman. 2000. Habitat preferences of female humpback whales (*Megaptera novaeangliae*) in the Hawaiian islands are associated with reproductive status. Marine Ecology-Progress Series 193:209-216.

Cross, J. N. and L. G. Allen. 1993. Fishes. Pages 459-540 *in* M.D. Dailey, D.J. Reish and J.W. Anderson, eds. Ecology of the Southern California Bight: A synthesis and interpretation. University of California Press, Berkeley.

Davis, R. W., N. Jaquet, D. Gendron, U. Markaida, G. Bazzino and W. Gilly. 2007. Diving behavior of sperm whales in relation to behavior of a major prey species, the jumbo squid, in the Gulf of California, Mexico. Marine Ecology Progress Series 333:291-302.

Dawson, S. 1991a. Clicks and Communication: The behavioural and social contexts of Hector's dolphin vocalizations. Ethology 88:265-276.

Dawson, S. M. 1991b. Clicks and Communication - the Behavioral and Social Contexts of Hector Dolphin Vocalizations. Ethology 88:265-276.

Defran, R. H., D. W. Weller, D. L. Kelly and M. A. Espinosa. 1999. Range characteristics of Pacific coast bottlenose dolphins (*Tursiops truncatus)* in the Southern California Bight. Marine Mammal Science 15:381-393.

Di Lorenzo, E., N. Schneider, K. M. Cobb, P. J. S. Franks, K. Chhak, A. J. Miller, J. C. McWilliams, S. J. Bograd, H. Arango, E. Curchitser, T. M. Powell and P. Riviere. 2008. North Pacific Gyre Oscillation links ocean climate and ecosystem change. Geophysical Research Letters 35:6.

Dohl, T. P., M. L. Bonnell and R. G. Ford. 1986. Distribution and abundance of common dolphin, *Delphinus delphus*, in the Southern California Bight: A quantitative assessment based upon aerial transect data. Fishery Bulletin 84:333-343.

Evans, W. E. 1982. Distribution and differentiation of stock of *Delphinus delphis* Linnaeus in the Northeastern Pacific. Mammals in the Sea 4: Small Cetaceans, Seals, Sirenians and Otters:45-66.

Evans, W. E., W. W. Sutherland and R. G. Beil. 1964. The directional characteristics of delphinid sounds. Pages 353-369 *in* W.N. Tavolga, ed. Marine Bio-acoustics. Pergamon Press, Oxford, New York.

Ferguson, M. C., J. Barlow, P. C. Fiedler, S. B. Reilly and T. Gerrodette. 2006. Spatial models of delphinid (family Delphinidae) encounter rate and group size in the eastern tropical Pacific Ocean. Ecological Modelling 193:645-662.

Ford, J. K. B. 1989. Acoustic behavior of resident killer whales (*Orcinus orca*) off Vancouver Island, British Columbia. Canadian Journal of Zoology 67:727-745.

Forney, K. A. 2000. Environmental models of cetacean abundance: reducing uncertainty in population trends. Conservation Biology 14:1271-1286.

Forney, K. A. and J. Barlow. 1998. Seasonal patterns in the abundance and distribution of California cetaceans, 1991-1992. Marine Mammal Science 14:460-489.

Fristrup, K. M. and W. A. Watkins. 1994. Marine animal sound classification. Woods Hole Oceanographic Institution WHOI-94-13.

Hanson, M. T. and R. H. Defran. 1993. The behavior and feeding ecology of the Pacific coast bottlenose dolphin, *Tursiops truncatus*. Aquatic Mammals 19:127-142.

Hastie, G. D., R. J. Swift, G. Slesser, P. M. Thompson and W. R. Turrell. 2005. Environmental models for predicting oceanic dolphin habitat in the Northeast Atlantic. Ices Journal of Marine Science 62:760-770.

Heise, K. 1997. Diet and feeding behavior of Pacific white-sided dolphins (*Lagenorhyncus obliquidens*) as revealed through the collection of prey fragments and stomach content analysis. Report of the International Whaling Commission 47:807-815.

Henderson, E. E. and B. Würsig. 2007. Behavior patterns of bottlenose dolphins in San Luis Pass, Texas. Gulf of Mexico Science 2:153-161.

Herman, L. M. and W. N. Tavolga. 1980. The communication systems of cetaceans. Pages 149–209 *in* L.M. Herman, ed. Cetacean Behavior: Mechanisms and Functions. Wiley, New York.

Herzing, D. L. 1996. Vocalizations and associated underwater behavior of free-ranging Atlantic spotted dolphins, *Stenella frontalis* and Bottlenose dolphins, *Tursiops truncatus*. Aquatic Mammals 22:61-80.

Heyning, J. E. and W. F. Perrin. 1994. Evidence for two species of common dolphin (Genus *Delphinus*) from the Eastern North Pacific. Contributions in Science 442:1-35.

Hickey, B. M. 1993. Physical Oceanography. Pages 19-70 *in* M.D. Dailey, D.J. Reish and J.W. Anderson, eds. Ecology of the Southern California Bight: A synthesis and interpretation. University of California Press, Los Angeles.

Hickey, B. M., E. L. Dobbins and S. E. Allen. 2003. Local and remote forcing of currents and temperature in the central Southern California Bight. Journal of Geophysical Research 108:26-21-26-26-26.

Hoelzel, A. R. 1993. Foraging behavior and social group dynamics in Puget Sound killer whales. Animal Behaviour 45:581-591.

Hui, C. A. 1979. Undersea topography and distribution of dolphins of the genus *Delphinus* in the Southern California Bight. JOURNAL OF MAMMALOGY 60:521-527.

Johnson, M., L. S. Hickmott, N. Aguilar de Soto and P. T. Madsen. 2008. Echolocation behavior adapted to prey in foraging Blainville's beaked whale (*Mesoplodon densirostris*). Proceedings of the Royal Society Biological Sciences Series B 275:133-139.

Johnson, M., P. T. Madsen, W. M. X. Zimmer and N. T. Aguilar de Soto, P. L. 2006. Foraging Blainville's beaked whales (*Mesoplodon densirostris*) produce distinct click types matched to different phases of echolocation. The Journal of Experimental Biology 209:5038-5050.

Lammers, M. O. and W. W. L. Au. 2003. Directionality in the whistles of Hawaiian spinner dolphins (Stenella longirostris): A signal feature to cue direction of movement? Marine Mammal Science 19:249-264.

Lammers, M. O., W. W. L. Au and D. L. Herzing. 2003. The broadband social acoustic signaling behavior of spinner and spotted dolphins. Journal of the Acoustical Society of America 114:1629-1639.

Learmonth, J. A., C. D. MacLeod, M. B. Santos, G. J. Pierce, H. Q. P. Crick and R. A. Robinson. 2006. Potential effects of climate change on marine mammals. Oceanography and Marine Biology: An Annual Review 44:431-464.

Leatherwood, S., R. R. Reeves, A. E. Bowles, B. S. Stewart and K. R. Goodrich. 1984. Distribution, seasonal movements and abundance of Pacific white-sided dolphins in the Eastern North Pacific. Scientific Report of Whales Research Institute 35:129-157.

Li, S. H., K. X. Wang, D. Wang and T. Akamatsu. 2005. Echolocation signals of the free-ranging Yangtze finless porpoise (*Neophocaena phocaenoides asiaeorientialis*). Journal of the Acoustical Society of America 117:3288-3296.

Logerwell, E. A., B. Lavaniegos and P. E. Smith. 2001. Spatially-explicit bioenergetics of Pacific sardine in the Southern California Bight: are mesoscale eddies areas of exceptional prerecruit production? Progress in Oceanography 49:391-406.

Logerwell, E. A. and P. E. Smith. 2001. Mesoscale eddies and survival of late stage Pacific sardine (*Sardinops sagax*) larvae. Fisheries Oceanography 10:13-25.

Lux, C. A., A. S. Costa and A. E. Dizon. 1997. Mitochondrial DNA population structure of the Pacific white-sided dolphin. Report of the International Whaling Commission 47:645-652.

MacLeod, C. D. 2009. Global climate change, range changes and potential implications for the conservation of marine cetaceans: a review and synthesis. Endangered Species Research 7:125-136.

MacLeod, C. D., C. R. Weir, M. Begoña Santos and T. E. Dunn. 2008. Temperature-based summer habitat partitioning between white-beaked and common dolphins around the United Kingdom and Republic of Ireland. Journal of the Marine Biological Association of the United Kingdom 88:1193-1198.

Madsen, P. T., M. Johnson, N. A. de Soto, W. M. X. Zimmer and P. Tyack. 2005. Biosonar performance of foraging beaked whales (Mesoplodon densirostris). Journal of Experimental Biology 208:181-194.

Mantua, N. J. and S. R. Hare. 2002. The Pacific Decadal Oscillation. Journal of Oceanography 58:35-44.

McGowan, J. A. 1985. El Niño 1983 in the Southern California Bight. Pages 166-184 *in* W.S. Wooster and D.L. Fluharty, eds. El Niño North: Niño effects in the Eastern Subarctic Pacific Ocean. Washington Sea Grant Program, University of Washington, Seattle.

Mellinger, D. K., S. L. Nieukirk, H. Matsumoto, S. L. Heimlich, R. P. Dziak, J. Haxel, M. Fowler, C. Meinig and H. V. Miller. 2007. Seasonal occurrence of North Atlantic right whale (*Eubalaena glacialis*) vocalizations at two sites on the Scotian Shelf. Marine Mammal Science 23:856-867.

Moore, S. E. and S. H. Ridgway. 1995. Whistles produced by common dolphins from the Southern California Bight. Aquatic Mammals 21.1:55-63.

Murray, S. O., E. Mercado and H. L. Roitblat. 1998. Characterizing the graded structure of false killer whale (Pseudorca crassidens) vocalizations. Journal of the Acoustical Society of America 104:1679-1688.

Neumann, D. R. 2001. The activity budget of free-ranging common dolphins (Delphinus delphis) in the northwestern Bay of Plenty, New Zealand. Aquatic Mammals 27:121-136.

Nichol, L. M. and D. M. Shackleton. 1996. Seasonal movements and foraging behaviour of northern resident killer whales (Orcinus orca) in relation to the inshore distribution of salmon (Oncorhynchus spp) in British Columbia. Canadian Journal of Zoology-Revue Canadienne De Zoologie 74:983-991.

Norris, K. S., B. Würsig, R. S. Wells, M. Würsig, S. Brownlee, C. M. Johnson and J. Solon. 1985. The Behavior of the Hawaiian Spinner Dolphin, *Stenella longirostris*.

Norton, J., D. McLain, R. Brainard and D. Husby. 1985. 1982-1983 El Niño event off Baja and Alta California and its ocean climate context. Pages 44-72 *in* W.S. Wooster and D.L. Fluharty, eds. El Niño north: Niño effects in the eastern subarctic Pacific Ocean University of Washington, Seattle, WA.

Ohizumi, H., M. Yoshioka, K. Mori and N. Miyazaki. 1998. Stomach contents of common dolphins (*Delphinus delphis*) in the pelagic Western North Pacific. Marine Mammal Science 14:835-844.

Oleson, E. M. 2005. Calling behavior of blue and fin whales off California. PhD. University of California, San Diego, San Diego.

Oleson, E. M., S. M. Wiggins and J. A. Hildebrand. 2007. Temporal separation of blue whale call types on a southern California feeding ground. Animal Behaviour 74:881-894.

Osnes-Erie, L. D. 1999. Food habits of common dolphin (*Delphinus delphis* and *D. capensis*) off California. Master's thesis. San Jose State University, Moss Landing.

Oswald, J. N., J. Barlow and T. F. Norris. 2003. Acoustic identification of nine delphinid species in the eastern tropical Pacific Ocean. Marine Mammal Science 19:20-37.

Perrin, W. F. 2002. Common Dolphins. Pages 245-248 *in* W.F. Perrin, B. Würsig and J. Thewissen, G. M., eds. Encyclopedia of Marine Mammals. Academic Press, San Diego.

Rankin, S., J. Oswald, J. Barlow and M. Lammers. 2007. Patterned burst-pulse vocalizations of the northern right whale dolphin, *Lissodelphis borealis*. Journal of the Acoustical Society of America 121:1213-1218.

Redfern, J. V., M. C. Ferguson, E. A. Becker, K. D. Hyrenbach, C. Good, J. Barlow, K. Kaschner, M. F. Baumgartner, K. A. Forney and L. T. Ballance. 2006. Techniques for cetacean-habitat modeling. Marine Ecology-Progress Series 310:271-295.

Reid, J. L., G. I. Roden and J. G. Wyllie. 1958. Studies of the California Current System. CalCOFI Report:28-56.

Reilly, S. B. and V. G. Thayer. 1990. Blue whales (*Balaenoptera musculus*) distribution in the eastern tropical Pacific. Marine Mammal Science 6:265-277.

Richardson, W., C. J. Greene, C. Malme and D. Thomson. 1995. Marine Mammals and Noise. Academic Press, San Diego.

Roch, M. A., M. S. Soldevilla, J. C. Burtenshaw, E. E. Henderson and J. A. Hildebrand. 2007. Gaussian mixture model classification of odontocetes in the Southern California Bight and the Gulf of California. Journal of the Acoustical Society of America 121:1737-1748.

Selzer, L. A. and P. M. Payne. 1988. The distribution of white-sided (*Lagenorhyncus acutus*) and common dolphins (*Delphinus delphus*) vs. environmental features of the continental shelf of the northeastern United States. Marine Mammal Science 4:141-153.

Sette, O. E. and J. D. Isaacs. 1960. The changing Pacific Ocean in 1957 and 1958. CalCOFI Report 7:13-217.

Shane, S. H., R. S. Wells and B. Würsig. 1986. Ecology, Behavior and social organization of the bottlenose dolphin: a review. Marine Mammal Science 2:34-63.

Silber, G. K. 1986. The relationship of social vocalizations to surface behavior and aggression in the Hawaiian humpback whale (*Megaptera novaeangliae*). Canadian Journal of Zoology 64:2075-2079.

Simmonds, M. P. and W. J. Eliott. 2009. Climate change and cetaceans: concerns and recent developments. Journal of the Marine Biological Association of the United Kingdom 89:203-210.

Simon, M., P. K. McGregor and F. Ugarte. 2007. The relationship between the acoustic behavior and surface activity of killer whales (*Orcinus orca*) that feed on herring *(Clupea harengus*). Acta Ethology 10:47-53.

Smith, P. E. 1995. A warm decade in the Southern California Bight. CalCOFI Report 36:120-126.

Smith, R. C., P. Dustan, D. Au, K. S. Baker and E. A. Dunlap. 1986. Distribution of cetacean and sea-surface chlorophyll concentration in the California Current. Marine Biology 91:385-402.

Soldevilla, M. S., E. E. Henderson, G. S. Campbell, S. M. Wiggins, J. A. Hildebrand and M. A. Roch. 2008. Classification of Risso's and Pacific white-sided dolphins using spectral properties of echolocation clicks. The Journal of the Acoustical Society of America 124:609-624.

Soldevilla, M. S., S. M. Wiggins and J. A. Hildebrand. 2010. Spatio-temporal comparison of Pacific white-sided dolphin echolocation click types. Aquatic Biology 9:49-62.

Star, J. L. and M. M. Mullin. 1981. Zooplankton assemblages in three areas of the North Pacific as revealed by continuous horizontal transects. Deep-Sea Research 28A:1303-1322.

Stockin, K. A., V. Binedell, N. Wiseman, D. H. Brunton and M. B. Orams. 2009. Behavior of free-ranging common dolphins (*Delphinus* sp.) in the Hauraki Gulf, New Zealand. Marine Mammal Science 25:283-301.

Stroud, R. K., C. H. Fiscus and H. Kajimura. 1981. Food of the Pacific white-sided dolphin, *Lagenorhyncus obliquidens*, Dall's porpoise, *Phocoenoides dalli*, and nothern fur seal, *Callorhinus ursinus*, off California and Washington. Fishery Bulletin 78:951-959.

Strub, P. T. and C. James. 2000. Altimeter-derived variability of surface velocities in the California current system: 2. Seasonal circulation and eddy statistics. Deep-Sea Research II 47:831-870.

Van Parijs, S. M. and P. J. Corkeron. 2001. Vocalizations and behaviour of Pacific humpback dolphins *Sousa chinensis*. Ethology 107:701-716.

Verfuss, U. K., L. A. Miller and H. U. Schnitzler. 2005. Spatial orientation in echolocating harbour porpoises (*Phocoena phocoena*). Journal of Experimental Biology 208:3385-3394.

Walker, W. A. and L. L. Jones. 1993. Food habits of northern right whale dolphin, Pacific white-sided dolphin, and northern fur seal caught in the high seas driftnet fisheries of the North Pacific Ocean, 1990. International North Pacific Fisheries Commission Bulletin 53:285-295.

Walker, W. A., S. Leatherwood, K. R. Goodrick, W. F. Perrin and R. K. Stroud. 1986. Geographic variation and biology of the Pacific white-sided dolphin, *Lagenorhynchus obliquidens*, in the north-eastern Pacific. Pages 441–465 *in* M.M. Bryden and R. Harrison, eds. Research on Dolphins. Clarendon Press, Oxford.

Wang, C. and P. C. Fiedler. 2006. ENSO variability and the eastern tropical Pacific: A review. Progress in Oceanography 69:239-266.

Watkins, W. A. 1964. The harmonic interval: fact or artifact in spectral analysis of pulse trains. Pages 15-43 *in* W.N. Tavolga, ed. Marine Bio-Acoustics. Pergamon Press, Oxford, New York.

Watkins, W. A. and D. Wartzok. 1985. Sensory biophysics of marine mammals. Marine Mammal Science 1:219-260.

Weilgart, L. S. and H. Whitehead. 1990. Vocalizations of the North Atlantic pilot whale (*Globicephala melas*) as related to behavioral contexts. Behavioral Ecology and Sociobiology 26:399-402.

Wells, R. S. 1991. The role of long-term study in understanding the social structure of a bottlenose dolphin community. Pages 199-225 *in* K. Pryor and K.S. Norris, eds. Dolphin societies - discoveries and puzzles. University of California Press, Berkeley.

Whitehead, H. and L. Weilgart. 2000. The Sperm Whale. Pages 154-172 *in* J. Mann, R.C. Connor, P.L. Tyack and H. Whitehead, eds. Cetacean societies: Field studies of dolphins and whales. The University of Chicago Press, Chicago.

Whitten, J. L. and J. A. Thomas. 2001. Whistle repertoire of Pacific white-sided dolphins (*Lagenorhynchus obliquidens*) at the John G. Shedd Aquarium. The Journal of the Acoustical Society of America 109:2391.

Wiggins, S. 2003. Autonomous acoustic recording packages (ARPs) for long-term monitoring of whale sounds. Marine Technology Society Journal 37:13-22.

Wiggins, S. M. and J. A. Hildebrand. 2007. High-frequency Acoustic Recording Package (HARP) for broad-band, long-term marine mammal monitoring. Pages 551-557 International Symposium on Underwater Technology 2007 and International Workshop on Scientific Use of Submarine Cables & Related Technologies 2007. Institute of Electrical and Electronics Engineers, Tokyo, Japan.

Würsig, B., R. R. Reeves and J. G. Ortega-Ortiz. 2002. Global climate change and marine mammals. Pages 589-608 *in* W.E. Evans and J.A. Raga, eds. Marine mammals: biology and conservation. Kluwer Academic/Plenum Publishers.

CHAPTER 2

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

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

and Erin A. Falcone

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.

Acknowledgements

Funding for this research was provided by CNO-N45 and the Naval Postgraduate School; we thank Frank Stone, Ernie Young and Curt Collins for support and assistance. We thank our San Clemente Island collaborators: the Cascadia Research Collective, particularly John Calambokidis and Greg Schorr; the Scripps Whale Acoustics Lab, especially Megan McKenna, Greg Campbell, and all the shore-based lab members who assisted in localizing animals; and NUWC, including David Moretti, Ron Morrissey, Susan Jarvis, and Nancy DiMarzo. We also thank the many members of the FLIP observation teams without whom this work could not have been done, including Sean Wiggins, Katherine Kim, Greg Falxa, Alexis Rudd, Jennifer Funk, Amanda Cummins, Allan Ligon, Nadia Rubio, Ethan Roth, Gustavo Cárdenas, Velvet Voelz, Jamie Gibbon, Lamalani Siverts, Brenda deGerald, Kait Frasier, and Kristina Welch; and the FLIP crew members, particularly Bill Gaines, Captain Tom Golfinos, Paul Porcioncula, and Greg Viehmann. Thanks to Eric Archer for assistance on random forest models, and to Phil Hastings, Jay Barlow and Jim Moore for helpful comments.

Chapter 2, in full, has been submitted for publication in Marine Mammal Science: Henderson, E.E., Hildebrand, J.A., Smith, M. H., and Falcone, E. A. The Behavioral Context of Common Dolphin (*Delphinus* sp.) Vocalizations. The dissertation author was the primary investigator and author of this paper.

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%

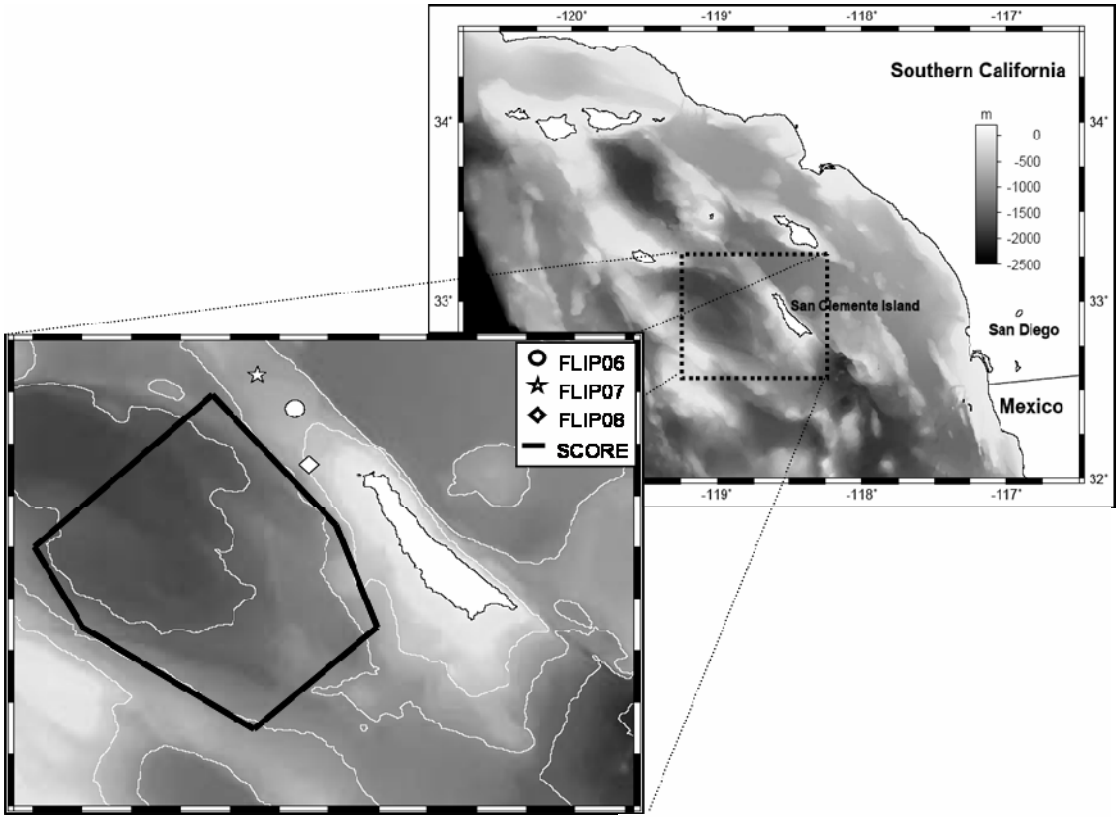


Figure 2.1 - Bathymetric map of the study area in Southern California Bight. The shapes indicate the locations of FLIP moorings in 2006, 2007 and 2008, northwest of San Clemente Island. The dark line indicates the border of the San Clemente Offshore Range (SCORE).

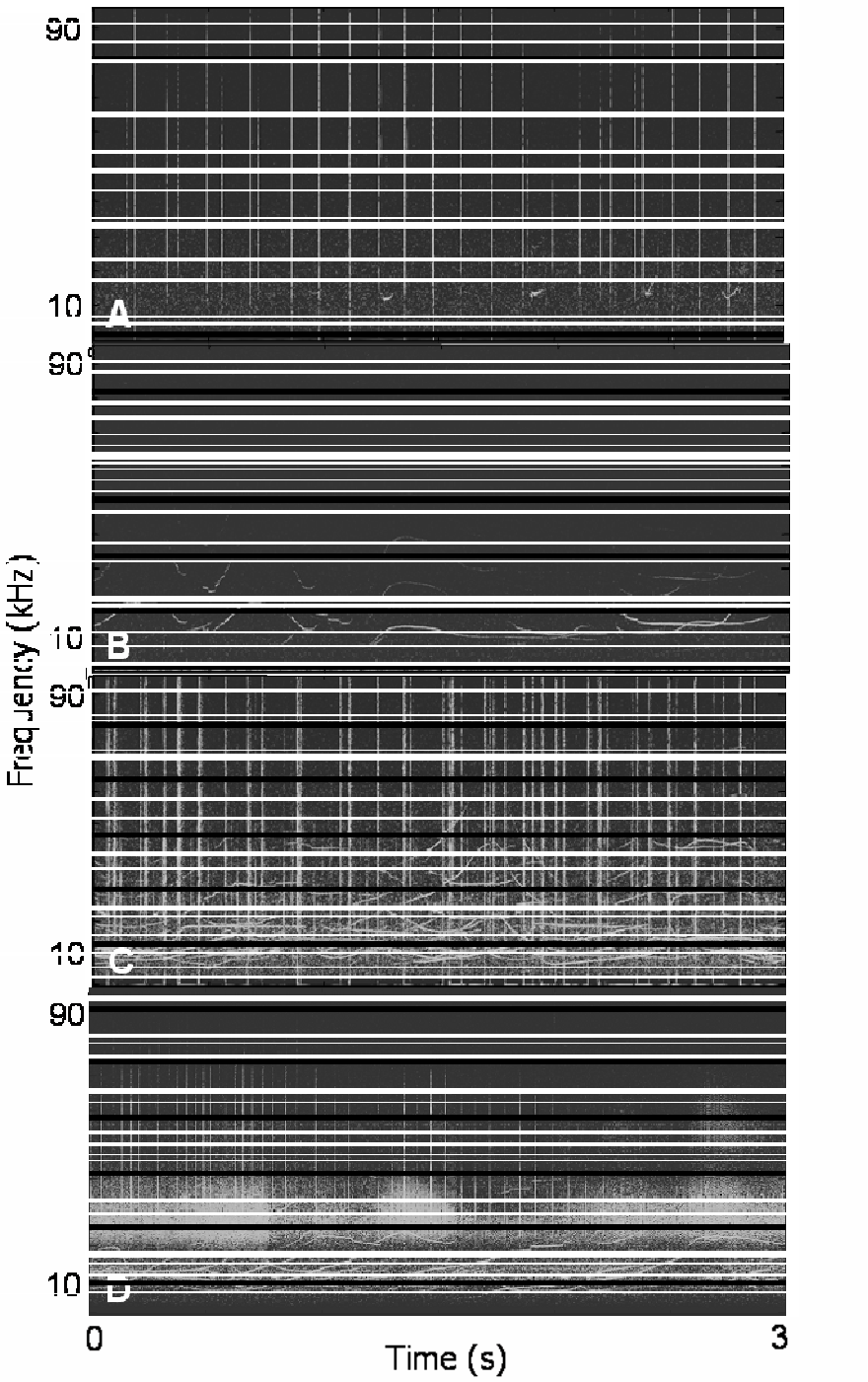


Figure 2.2 - Spectrograms of common dolphin whistle categories: (A) shows distinct individual whistles with no harmonics; (B) shows whistles with harmonics that are still individually distinct from each other; (C) and (D) show overlapped whistle bouts, with whistles that cannot to be uniquely identified.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

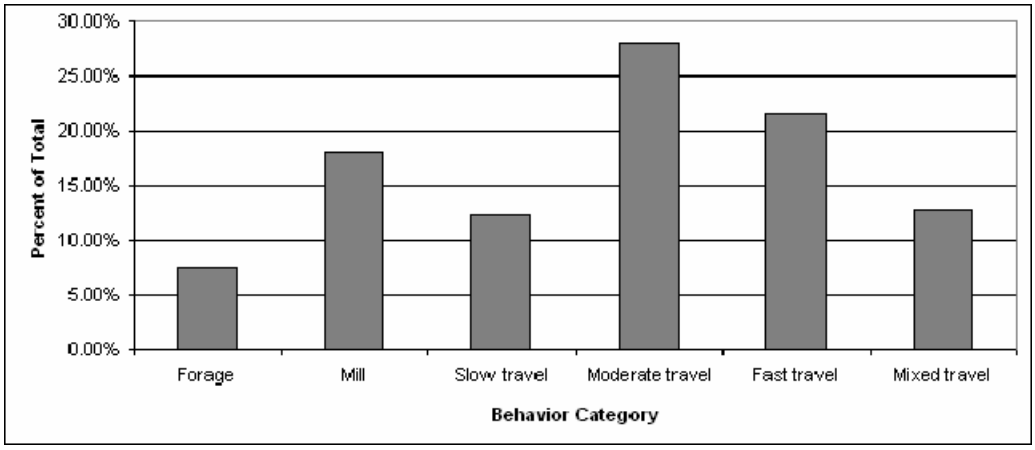


Figure 2.3 - Behavioral categories for common dolphins. The bars show the percent time animals were observed in each behavioral state.

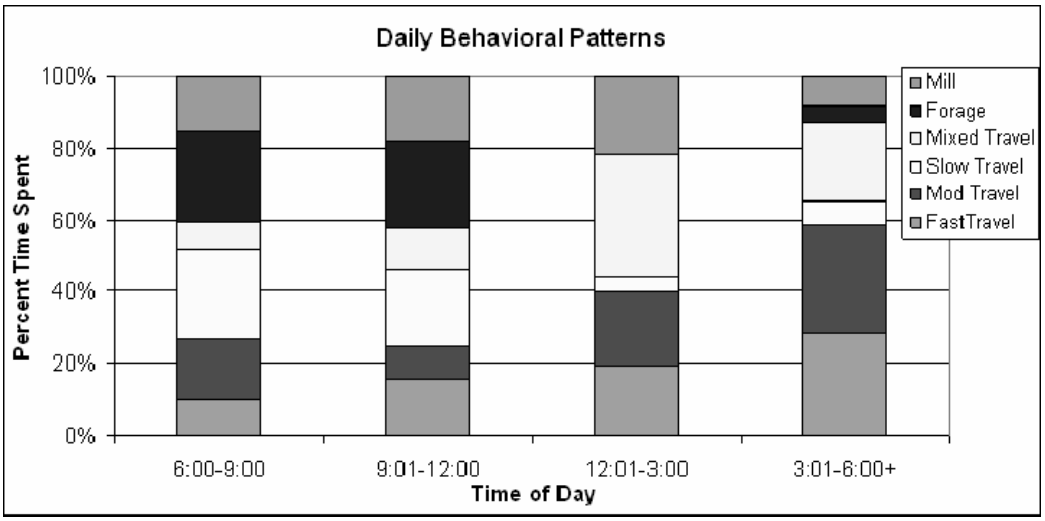


Figure 2.4 - Daily behavior patterns of common dolphins. Observed rates of all behaviors in each time period were significantly different from expected using Chi-Square analyses.

Figure 2.5 - Group size composition for each behavior category.

Figure 2.6 - Group spacing composition for each behavior category.

Literature Cited

Altmann, J. 1974. Observational study of behavior sampling methods. Behaviour 49:227-267.

Ansmann, I. C., J. C. Goold, P. G. H. Evans, M. P. Simmonds and S. G. Keith. 2007. Variation in the whistle characteristics of short-beaked common dolphins, *Delphinus delphis*, at two locations around the British Isles. Journal of the Marine Biological Association of the United Kingdom 87:19-26.

Au, D. W. K. and W. L. Perryman. 1985. Dolphin Habitats in the eastern tropical Pacific. Fishery Bulletin 83:623-643.

Au, W. W. L. 1993. The Sonar of Dolphins. Springer-Verlag Inc, New York.

Au, W. W. L. 2004. Echolocation signals of wild dolphins. Acoustical Physics 50:454-462.

Bass, A. H., D. A. Bodnar and J. R. McKibben. 1997. From neurons to behavior: vocal-acoustic communication in teleost fish. Biology Bulletin 192:158-160.

Belwood, J. J. and J. H. Fullard. 1984. Echolocation and foraging behavior in the Hawaiian hoary bat, *Lasiurus cinereus semotus*. Canadian Journal of Zoology 62:2113-2120.

Benoit-Bird, K. J. and W. W. L. Au. 2003. Prey dynamics affect foraging by a pelagic predator (*Stenella longirostris*) over a range of spatial and temporal scales. Behavioral Ecology and Sociobiology 53:364-373.

Benoit-Bird, K. J. and W. W. L. Au. 2009. Phonation behavior of cooperatively foraging spinner dolphins. Journal of the Acoustical Society of America 125:539-546.

Benson, S. R., D. A. Croll, B. B. Marinovic, F. P. Chavez and J. T. Harvey. 2002. Changes in the cetacean assemblage of a coastal upwelling ecosystem during El Niño 1997-98 and La Niña 1999. Progress in Oceanography 54:279-291.

Brieman, L. 2001. Random Forests. Machine Learning 45:5-32.

Brownlee, S. 1983. Correlations between sounds and behavior in the Hawaiian spinner dolphin (*Stenella longirositris*). Master's thesis. University of California, Santa Cruz, Santa Cruz.

Caldwell, M. C. and D. K. Caldwell. 1968. Vocalization of Naive Captive Dolphins in Small Groups. Science 159:1121-1123.

Charlton, B. D., Z. Zhihe and R. J. Snyder. 2009. The information content of giant panda, *Ailuropoda melanoleuca*, bleats: acoustic cues to sex, age and size. Animal Behaviour 78:893-898.

Clarke, A. S. 1990. Vocal communication in captive golden monkeys (*Rhinopithecus roxellanae*). Primates 31:601-606.

Crawford, J. D., M. Hagedorn and C. D. Hopkins. 1986. Acoustic communication in an electric fish, *Pollimyrus isidori* (Mormyridae). Journal of Comparative Physiology A 159:297-310.

Crockford, C. and C. Boesch. 2003. Context-specific calls in wild chimpanzees, *Pan troglodytes verus*: analysis of barks. Animal Behaviour 66:115-125.

Dawson, S. 1991. Clicks and Communication: The behavioural and social contexts of Hector's dolphin vocalizations. Ethology 88:265-276.

Dohl, T. P., M. L. Bonnell and R. G. Ford. 1986. Distribution and abundance of common dolphin, *Delphinus delphus*, in the Southern California Bight: A quantitative assessment based upon aerial transect data. Fishery Bulletin 84:333-343.

Evans, W. E. 1982. Distribution and differentiation of stock of *Delphinus delphis* Linnaeus in the Northeastern Pacific. Mammals in the Sea 4: Small Cetaceans, Seals, Sirenians and Otters:45-66.

Falcone, E. A., G. S. Schorr, E. E. Henderson, M. F. McKenna, D. Moretti, A. Douglas, J. Calambokidis and J. A. Hildebrand. 2009. Sighting characteristics and photo-identification of Cuvier's beaked whales (Ziphius cavirostris) near San Clemente Island, California: a key area for beaked whales and the military? Marine Biology 156:2631-2640.

Farley, T. D. 1995. Geographic variation in dorsal fin color of short-beaked common dolphins, *Delphinus delphis,* in the Eastern Pacific Ocean. Administrative Report LJ-95-06:1-17.

Fisher, F. H. and F. N. Spiess. 1963. Flip-Floating Instrument Platform. The Journal of the Acoustical Society of America 35:1633-1644.

Forney, K. A. and J. Barlow. 1998. Seasonal patterns in the abundance and distribution of California cetaceans, 1991-1992. Marine Mammal Science 14:460-489.

Gallo-Reynoso, J. P. 1991. Group behavior of common dolphins (*Delphinus delphus*) during prey capture. Anales Inst. Biol. Nac. Auton. Mexico, Ser. Zool. 62:253-262.

Goold, J. C. 2000. A diel pattern in vocal activity of short-beaked common dolphins, *Delphinus delphis*. Marine Mammal Science 16:240-244.

Hanson, M. T. and R. H. Defran. 1993. The behavior and feeding ecology of the Pacific coast bottlenose dolphin, *Tursiops truncatus*. Aquatic Mammals 19:127-142.

Henderson, E. E. and B. Würsig. 2007. Behavior patterns of bottlenose dolphins in San Luis Pass, Texas. Gulf of Mexico Science 2:153-161.

Heyning, J. E. and W. F. Perrin. 1994. Evidence for two species of common dolphin (Genus *Delphinus*) from the Eastern North Pacific. Contributions in Science 442:1-35.

Jaccard, J., M. A. Becker and G. Wood. 1984. Pairwise multiple comparison procedures: A review. Psychological Bulletin 96:589-596.

Janik, V. M. 2000. Food-related bray calls in wild bottlenose dolphins (*Tursiops truncatus*). Proceedings of the Royal Society Biological Sciences Series B 267:923-927.

Jarvis, S., D. Moretti, R. Morrissey and N. DiMarzio. 2003. Passive monitoring and localization of marine mammals in open ocean environments using widely spaced bottom mounted hydrophones. The Journal of the Acoustical Society of America 114:2405-2406.

Krishna, S. N. and S. B. Krishna. 2005. Female courtship calls of the litter frog (*Rana curtipes*) in the tropical forests of Western Ghats, South India. Amphibia-Reptilia 26:431-435.

Kruskal, W. and W. A. Wallis. 1952. Use of ranks in one-criterion variance analysis. Journal of the American Statistical Association 47:583-621.

Lammers, M. O. and W. W. L. Au. 2003. Directionality in the whistles of Hawaiian spinner dolphins (Stenella longirostris): A signal feature to cue direction of movement? Marine Mammal Science 19:249-264.

Leighton, T. G., S. G. Richards and P. R. White. 2004. Trapped within a wall of sound. Acoustics bulletin 29:24-29.

Liaw, A. and M. Wiener. 2002. Classification and Regression by Random Forest. R News 2:18-22.

MacLeod, C. D., C. R. Weir, M. Begoña Santos and T. E. Dunn. 2008. Temperature-based summer habitat partitioning between white-beaked and common dolphins around the United Kingdom and Republic of Ireland. Journal of the Marine Biological Association of the United Kingdom 88:1193-1198.

Mann, J. 1999. Behavioral sampling methods for cetaceans: A review and critique. Marine Mammal Science 15:102-122.

McCowan, B. and I. Rommeck. 2006. Bioacoustic monitoring of aggression in group-housed rhesus macaques. Journal of Applied Animal Welfare Science 9:261-268.

Mellinger, D. K. 2001. Ishmael 1.0 User's Guide. NOAA Technical Report OAR-PMEL-120. NOAA Pacific Marine Environmental Laboratory.

Mennill, D. J. and S. L. Vehrencamp. 2008. Context-dependent functions of avian duets revealed by microphone-array recordings and multispeaker playback. Current Biology 18:1314-1319.

Meynier, L., C. Pusineri, J. Spitz, M. B. Santos, G. J. Pierce and V. Ridoux. 2008. Intraspecific dietary variation in the short-beaked common dolphin *Delphinus delphis* in the Bay of Biscay: importance of fat fish. Marine Ecology-Progress Series 354:277-287.

Moore, S. E. and S. H. Ridgway. 1995. Whistles produced by common dolphins from the Southern California Bight. Aquatic Mammals 21.1:55-63.

Moretti, D., S. Jarvis, N. DiMarzio and R. Morrissey. 2004. Passive detection, data association, and localization of marine mammal calls using traditional 3D hyperbolic tracking algorithms. The Journal of the Acoustical Society of America 116:2606-2606.

Naguib, M. and V. M. Janik. 2009. Vocal communication in birds and mammals. Advances in the Study of Behavior 40:1-322.

Neumann, D. R. 2001a. The activity budget of free-ranging common dolphins (Delphinus delphis) in the northwestern Bay of Plenty, New Zealand. Aquatic Mammals 27:121-136.

Neumann, D. R. 2001b. Seasonal movements of short-beaked common dolphins (Delphinus delphis) in the north-western Bay of Plenty, New Zealand: Influence of sea surface temperature and El Nino/La Nina. New Zealand Journal of Marine and Freshwater Research 35:371-374.

Neumann, D. R. and M. B. Orams. 2003. Feeding behaviours of short-beaked common dolphins, *Delphinus delphis*, in New Zealand. Aquatic Mammals 29.1:137-149.

Norris, K. S. and T. P. Dohl. 1980. Behavior of the Hawaiian spinner dolphin, *Stenella longirostris*. Fishery Bulletin 77:821-849.

Norris, K. S., B. Wursig, R. S. Wells and M. Wursig. 1994. The Hawaiian Spinner Dolphin. University of California Press, Berkeley.

Ohizumi, H., M. Yoshioka, K. Mori and N. Miyazaki. 1998. Stomach contents of common dolphins (*Delphinus delphis*) in the pelagic Western North Pacific. Marine Mammal Science 14:835-844.

Osnes-Erie, L. D. 1999. Food habits of common dolphin (*Delphinus delphis* and *D. capensis*) off California. Master's thesis. San Jose State University, Moss Landing.

Oswald, J. N., J. Barlow and T. F. Norris. 2003. Acoustic identification of nine delphinid species in the eastern tropical Pacific Ocean. Marine Mammal Science 19:20-37.

Reeves, R. R., B. S. Stewart, P. J. Clapham and J. A. Powell. 2002. Guide to Marine Mammals of the World. Alfred A Knopf, New York.

Reilly, S. B. 1990. Seasonal changes in distribution and habitat differences among dolphins in the eastern tropical Pacific. Marine Ecology-Progress Series 66:1-11.

Richardson, W. J., K. J. Finley, G. W. Miller, R. A. Davis and W. R. Koski. 1995. Feeding, Social, and Migration behavior of bowhead whales, *Balaena mysticetus,* in Baffin Bay vs. the Beaufort Sea - Regions with different amounts of human activity. Marine Mammal Science 11:1-45.

Richman, B. 1980. Did human speech originate in coordinated vocal music? Semiotica 32:233-244.

Ridgway, S. H. 1983. Dolphin hearing and sound production in health and illness. Pages 247-296 *in* R.R. Fay and G. Gourevitch, eds. Hearing and other senses: presentations in honor of E. G. Weaver. The Amphora Press, Groton, CT.

Roberts, T. J. 2003. Learning about vocal communication in birds. Journal of the Bombay Natural History Society 100:390-393.

Roch, M. A., M. S. Soldevilla, J. C. Burtenshaw, E. E. Henderson and J. A. Hildebrand. 2007. Gaussian mixture model classification of odontocetes in the Southern California Bight and the Gulf of California. Journal of the Acoustical Society of America 121:1737-1748.

Rosel, P. E., A. E. Dizon and J. E. Heyning. 1994. Genetic analysis of sympatric morphotypes of common dolphins (genus *Delphinus*). Marine Biology 119:159-167.

Shane, S. H. 1990. Comparison of bottlenose dolphin behavior in Texas and Florida, with a critique of methods for studying dolphin behavior. Pages 541-558 *in* S. Leatherwood and R.R. Reeves, eds. The Bottlenose Dolphin. Academic Press, Inc., San Diego, CA.

Simeonovska-Nikolova, D. M. and V. M. Bogoev. 2008. Vocal communication in the striped field mouse, *Apodemus agrarius*, in dyadic encounters and intraspecific cage groups. Journal of Natural History 42:289-299.

Simon, M., P. K. McGregor and F. Ugarte. 2007. The relationship between the acoustic behavior and surface activity of killer whales (*Orcinus orca*) that feed on herring *(Clupea harengus*). Acta Ethology 10:47-53.

Simon, M., F. Ugarte, M. Wahlberg and L. A. Miller. 2006. Icelandic killer whales *Orcinus orca* use a pulsed call suitable for manipulating the schooling behaviour of herring *Clupea harengus*. Bioacoustics 16:57-74.

Siroky, D. S. 2008. Navigating Random Forests. Statistics Surveys 0:1-14.

Sjare, B. L. and T. G. Smith. 1986. The relationship between behavioral activity and underwater vocalizations of the white whale, *Delphinapterus leucas*. Canadian Journal of Zoology 64:2824-2831.

Soldevilla, M. S., E. E. Henderson, G. S. Campbell, S. M. Wiggins, J. A. Hildebrand and M. A. Roch. 2008. Classification of Risso's and Pacific white-sided dolphins using spectral properties of echolocation clicks. The Journal of the Acoustical Society of America 124:609-624.

Stockin, K. A., V. Binedell, N. Wiseman, D. H. Brunton and M. B. Orams. 2009. Behavior of free-ranging common dolphins (*Delphinus* sp.) in the Hauraki Gulf, New Zealand. Marine Mammal Science 25:283-301.

Taruski, A. G. 1979. The whistle repertoire of the North Atlantic pilot whale (*Globicephala melaena*) and its relationship to behavior and environment. Pages 345-368 *in* H.E. Winn and B.L. Olla, eds. Behavior of marine animals: Current perspectives in research. Plenum Press, New York.

Tershy, B. R., D. Breese and S. Alvarez-Borrego. 1991. Increase in cetacean and seabird numbers in the Canal de Ballenas during an El Niño-Southern Oscillation event. Marine Ecology-Progress Series 69:299-302.

Thorson, J., T. Weber and F. Huber. 1982. Auditory behavior of the cricket II. Simplicity of calling-song recognition in *Gryllus*, and anomalous phonotaxis at abnormal carrier frequencies. Journal of Comparative Physiology A 146:361-378.

Van Parijs, S. M. and P. J. Corkeron. 2001. Vocalizations and Behaviour of Pacific humpback dolphins (*Sousa chinensis*). Ethology 107:701-716.

Vergne, A. L., M. B. Pritz and N. Mathevon. 2009. Acoustic communication in crocodilians: from behaviour to brain. Biological Reviews (Cambridge) 84:391-411.

Weilgart, L. S. and H. Whitehead. 1990. Vocalizations of the North Atlantic pilot whale (*Globicephala melas*) as related to behavioral contexts. Behavioral Ecology and Sociobiology 26:399-402.

Wells, K. D. 1977. The social behaviour of anuran amphibians. Animal Behaviour 25:666-693.

Wiggins, S. 2003. Autonomous acoustic recording packages (ARPs) for long-term monitoring of whale sounds. Marine Technology Society Journal 37:13-22.

Wiggins, S. M. and J. A. Hildebrand. 2007. High-frequency Acoustic Recording Package (HARP) for broad-band, long-term marine mammal monitoring. Pages 551-557 International Symposium on Underwater Technology 2007 and International Workshop on Scientific Use of Submarine Cables & Related Technologies 2007. Institute of Electrical and Electronics Engineers, Tokyo, Japan.

Würsig, B., F. Cipriano and M. Würsig. 1991. Dolphin movement patterns: Information from radio and theodolite tracking studies. Pages 79-111 *in* K. Pryor and K.S. Norris, eds. Dolphin Societies: Discoveries and puzzles. University of California Press, Ltd., Berkeley and Los Angeles, California.

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

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.

Acknowledgements

We are grateful to SWFSC and PRBO for the use of their datasets, without which this analysis could not have been conducted, and to all of the visual observers over the years who gathered the data. Thanks also to Nate Mantua and Steven Hare for permission to use their PDO Index, and to NOAA for permission to use their ENSO Index. Thanks to Megan Ferguson and Elizabeth Becker for assistance with the modeling, and to Mati Kahru for help with the satellite sea surface temperature data and WIM.

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%

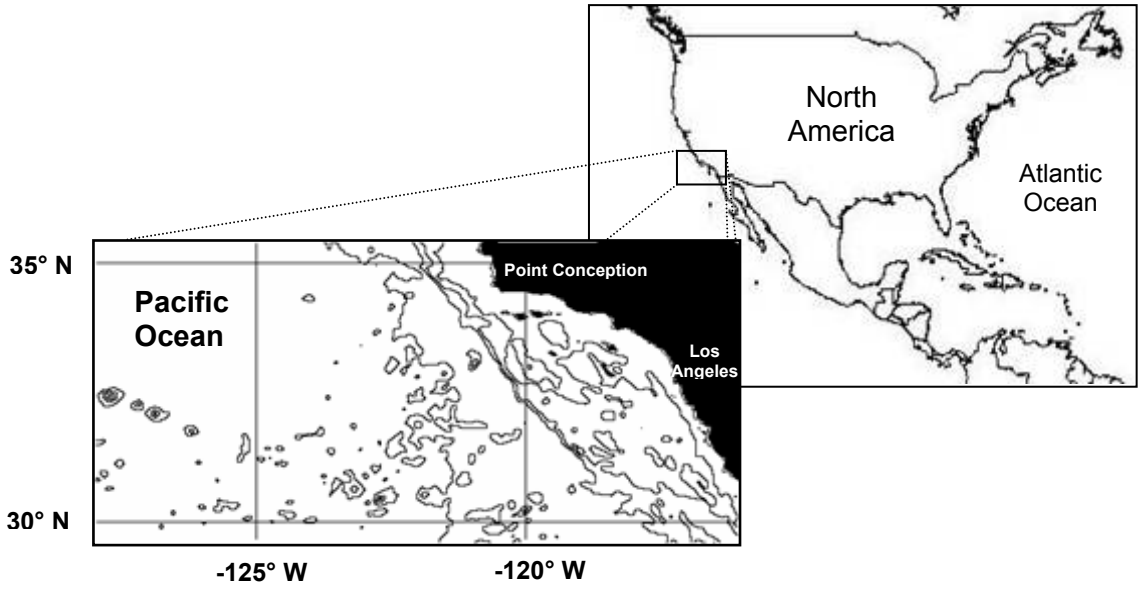


Figure 5.1 – The Southern California Bight study area, located in the Eastern North Pacific Ocean, south of Point Conception and incorporating the Channel Islands. 500-m depth contours are plotted.

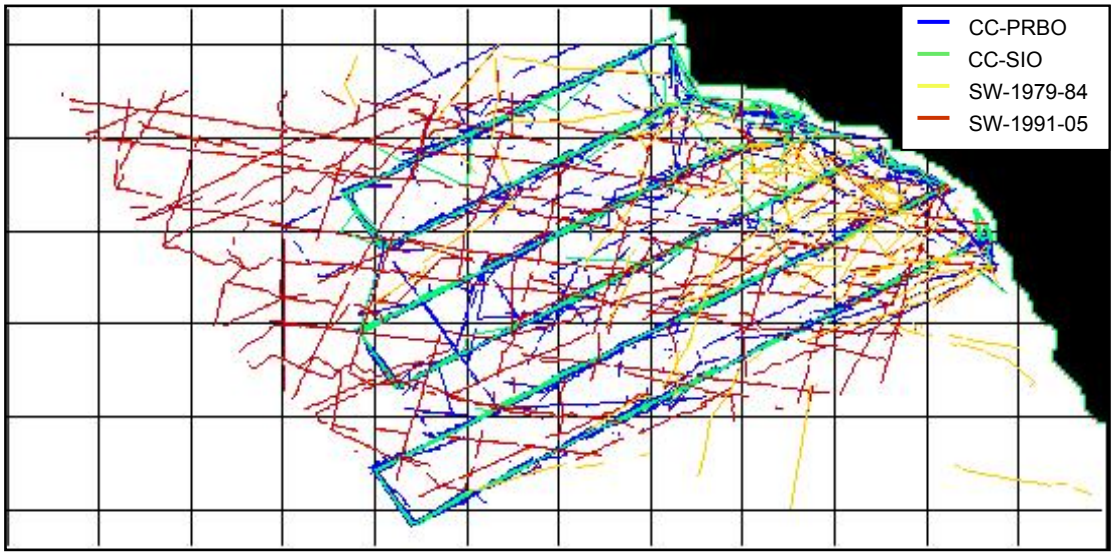


Figure 5.2 – Transect lines surveyed for all studies. CalCOFI - PRBO surveys are in purple, CalCOFI - SIO surveys are in blue, SWFSC surveys from 1979-1984 are in red and SWFSC surveys from 1991-2005 are in orange. Black lines indicate latitude and longitude in 1 degree increments, used to create the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

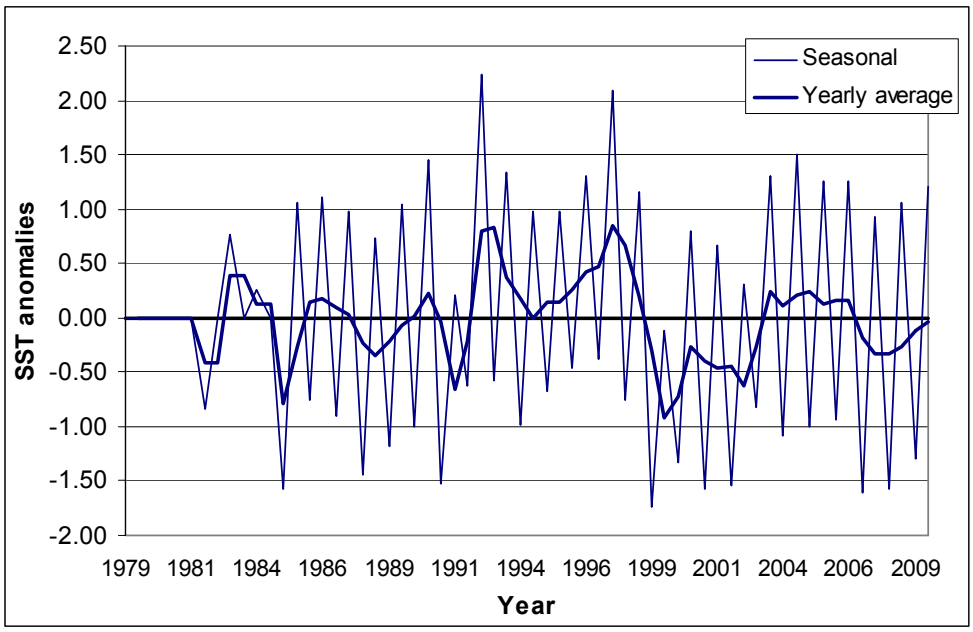


Figure 5.3 - Seasonal SST anomalies from the SCB from 1981 to 2009, and the yearly moving average SST anomalies.

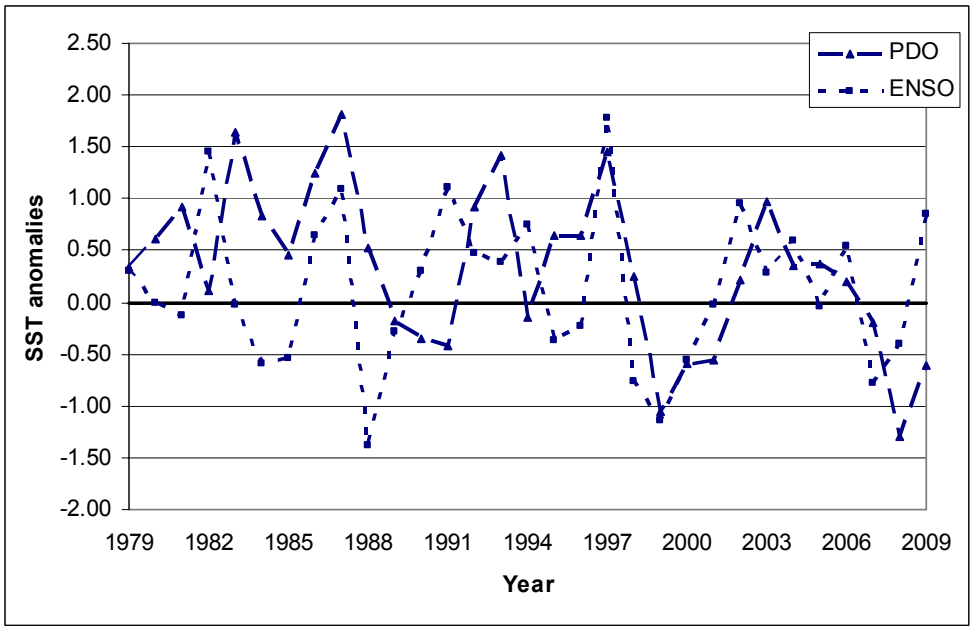


Figure5.4 - ENSO and PDO SST anomalies from 1979-2009. PDO SST anomalies were calculated using data from 1900-2009, while ENSO anomalies were calculated using a three month running mean from 1950-2009.

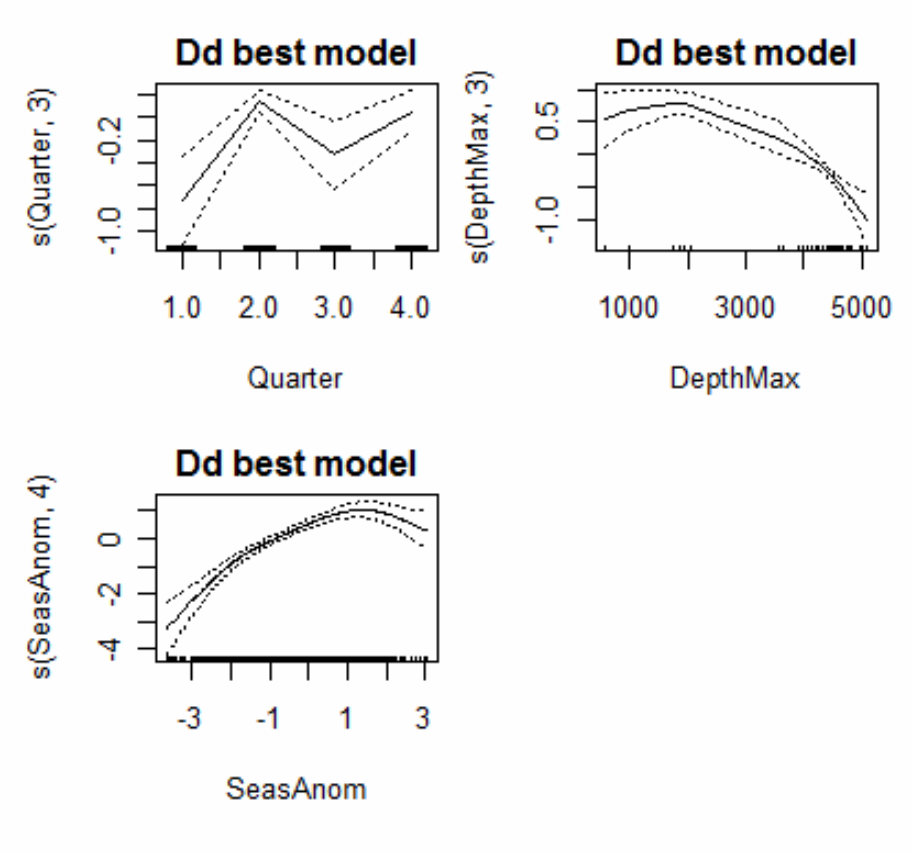


Figure 5.5 – GAM functions of short-beaked common dolphin (Dd) sightings from 1991 to 2005 for SWFSC cruises and from 2004-2009 for CalCOFI cruises, in relation to SST indices and depth variables for the best predictive models. Dashed lines are bands of two standard error.

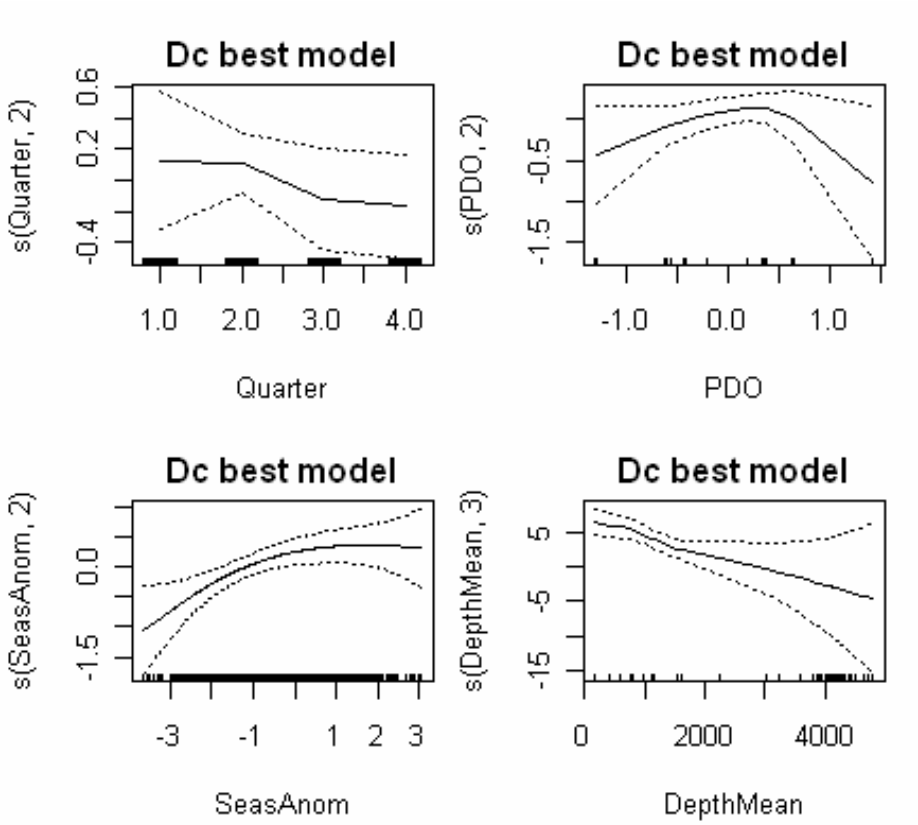


Figure 5.6 – GAM functions of long-beaked common dolphin (Dc) sightings from 1991 to 2005 for SWFSC cruises and from 2004-2009 for CalCOFI cruises, in relation to SST indices and depth variables for the best predictive models. Dashed lines are bands of two standard error.

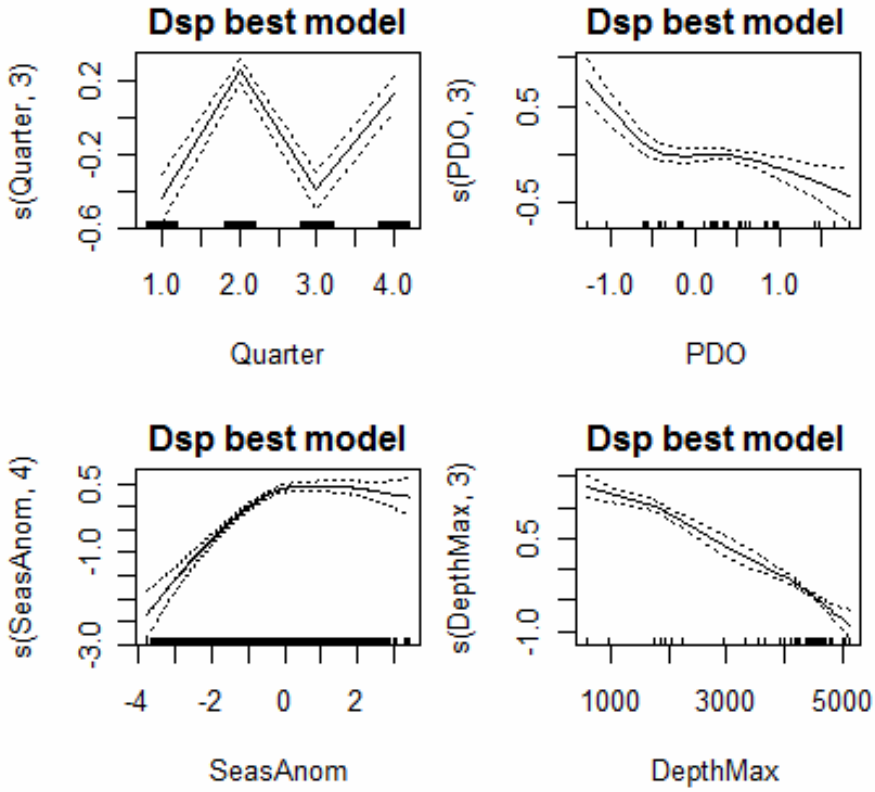


Figure 5.7 – GAM functions of common dolphin (Dsp) sightings from 1979 to 2009 in relation to SST indices and depth variables for the best predictive models. Dashed lines are bands of two standard errors.

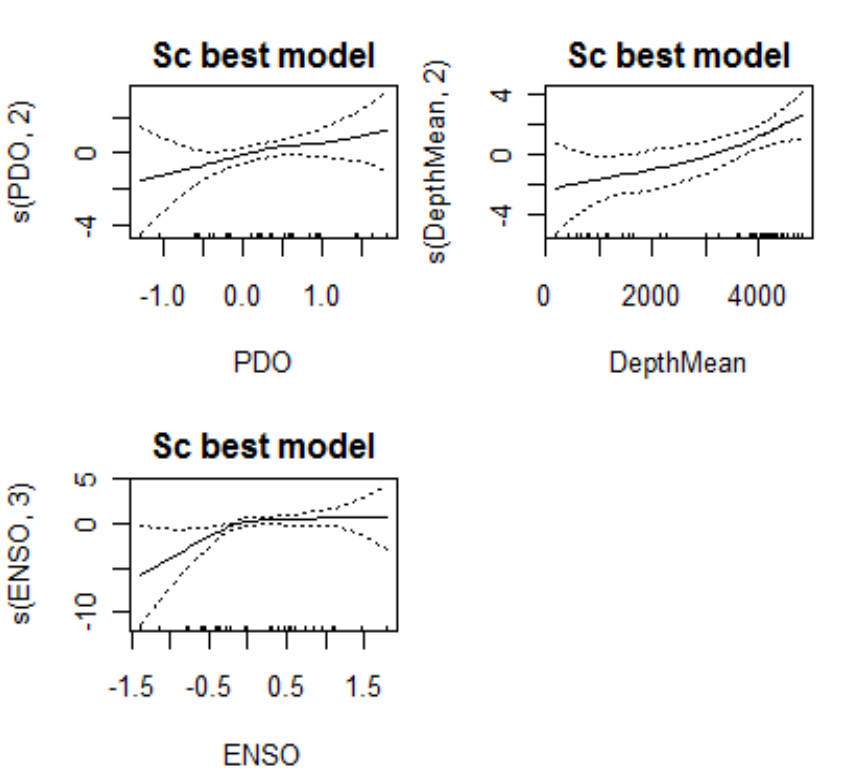


Figure 5.8 – GAM functions of striped dolphin (Sc) sightings from 1979 to 2009 in relation to SST indices and depth variables for the best predictive models. Dashed lines are bands of two standard errors.

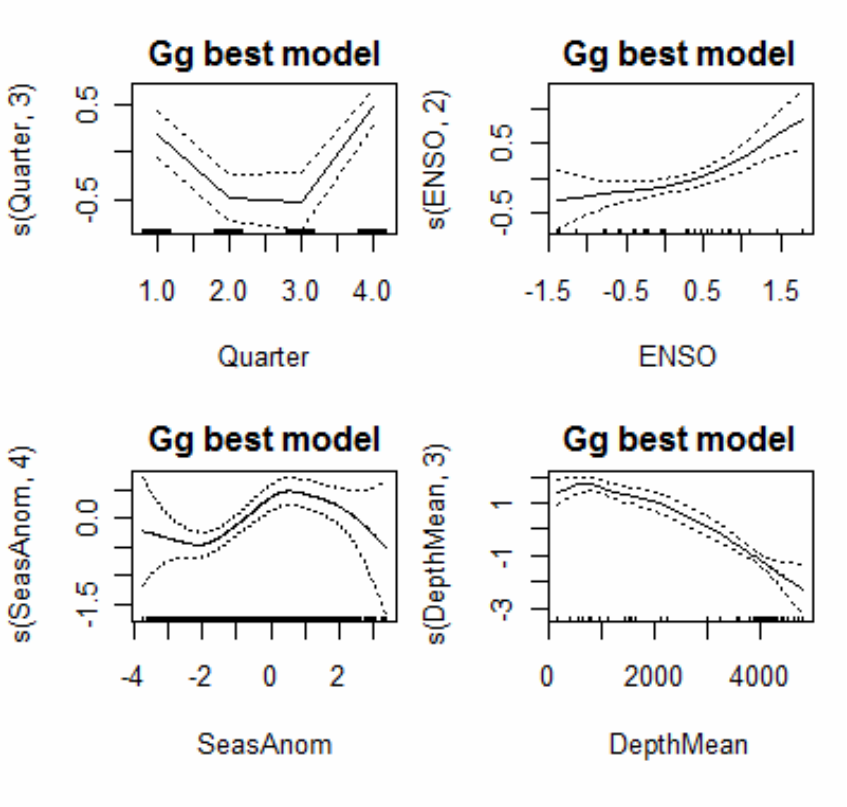


Figure 5.9 – GAM functions of Risso's dolphin (Gg) sightings from 1979 to 2009 in relation to SST indices and depth variables for the best predictive models. Dashed lines are bands of two standard errors.

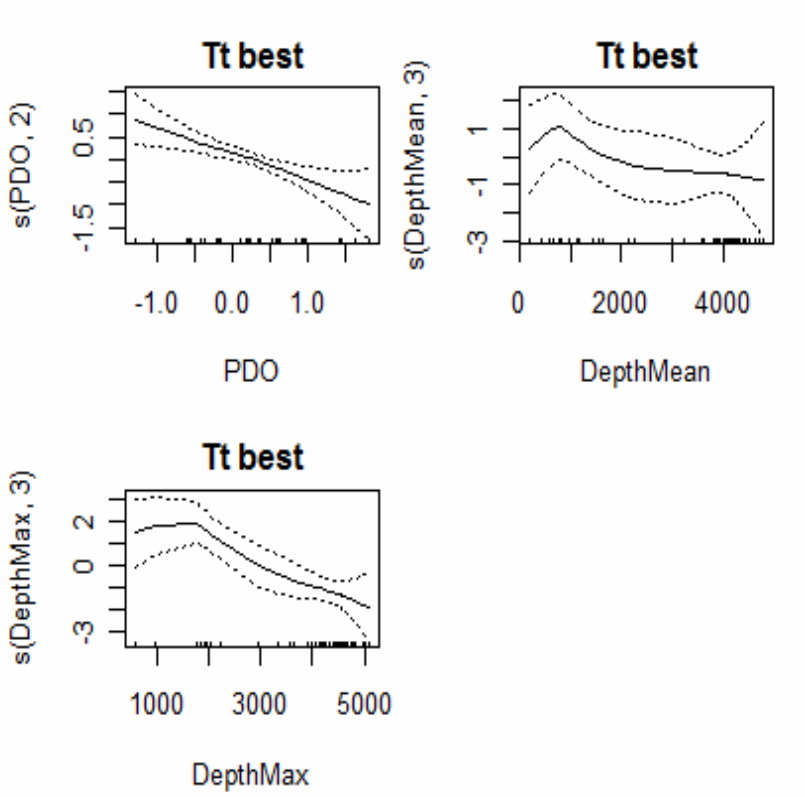


Figure 5.10 – GAM functions of bottlenose dolphin (Tt) sightings from 1979 to 2009 in relation to SST indices and depth variables for the best predictive models. Dashed lines are bands of two standard errors.

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.

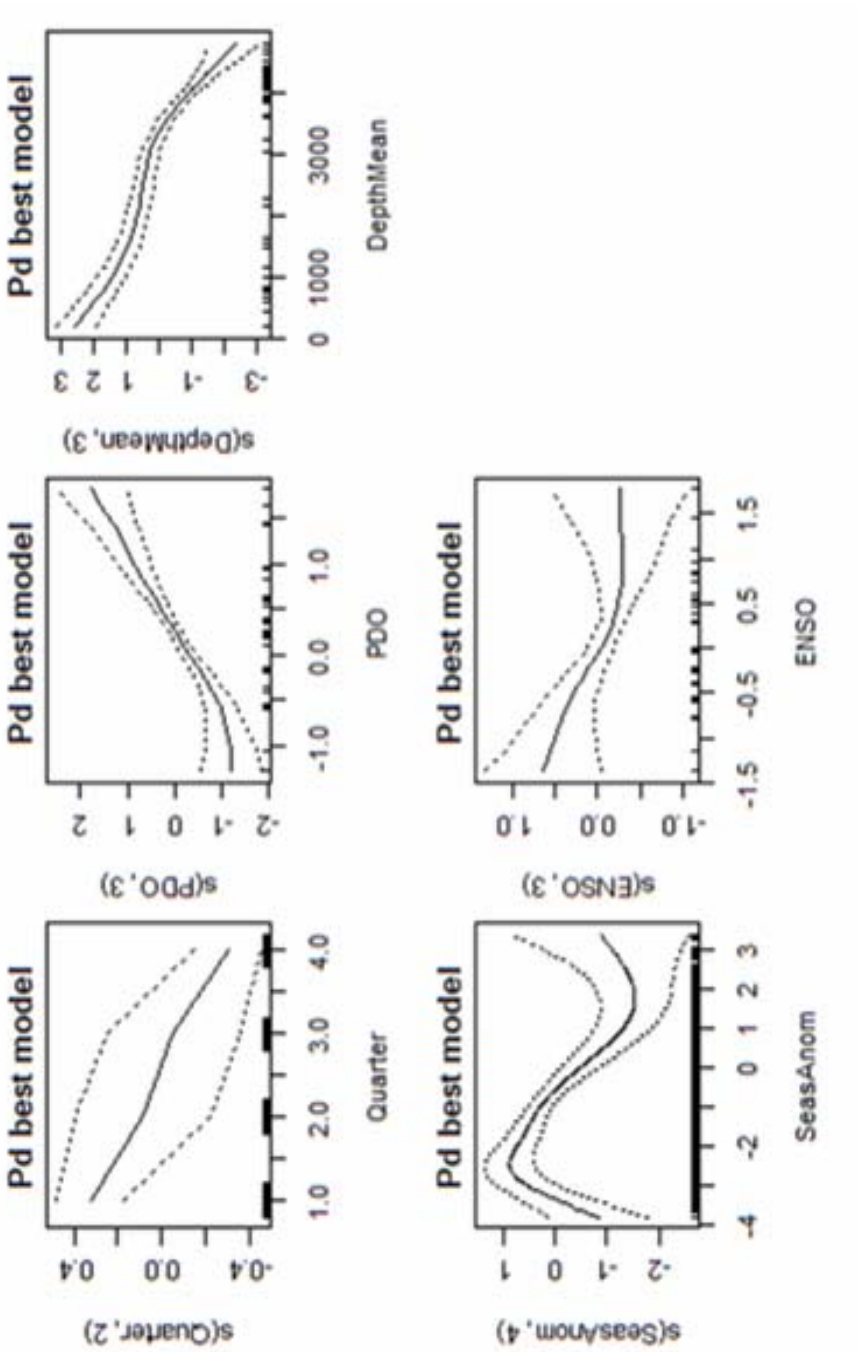
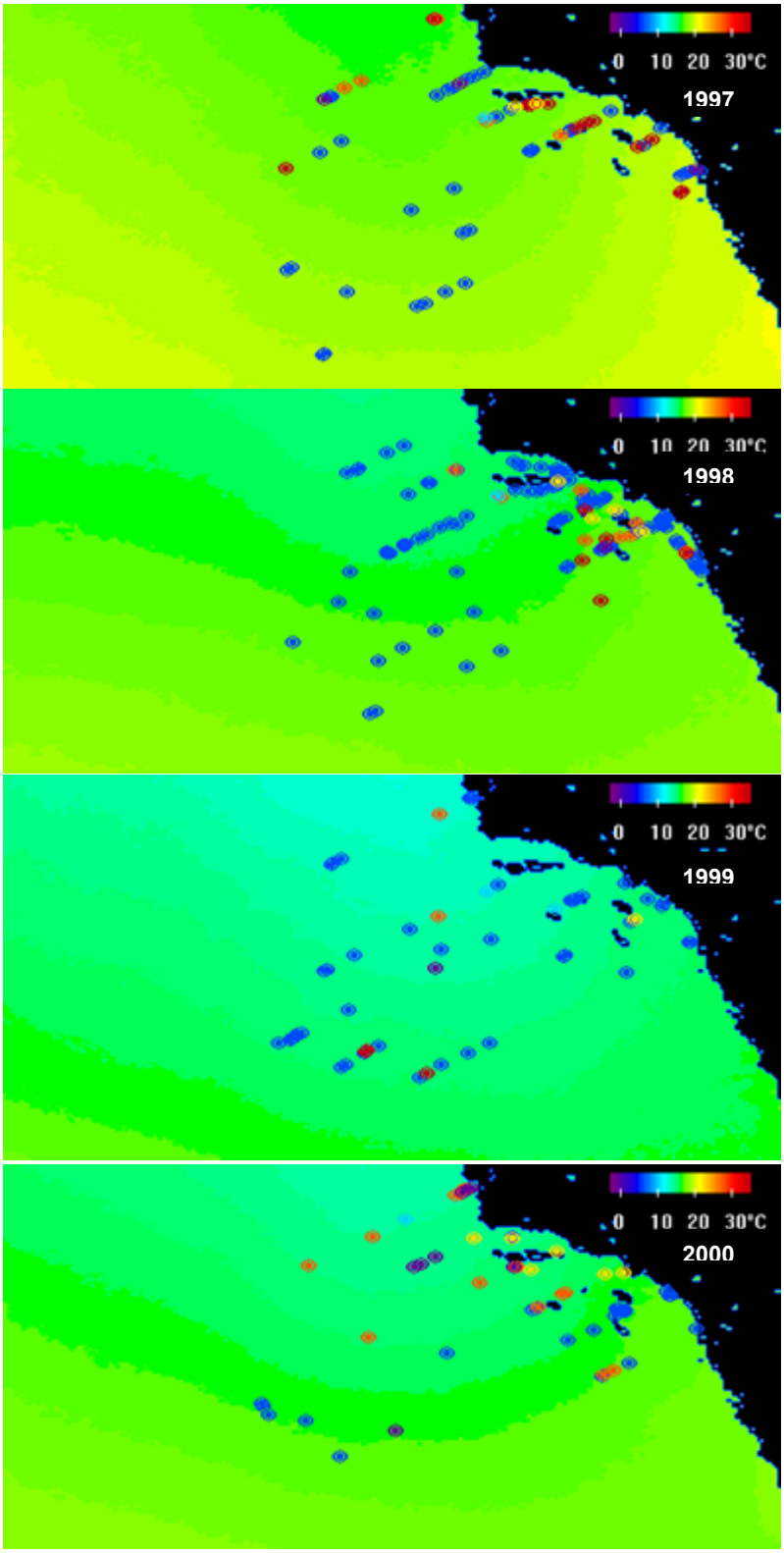


Figure 5.13 – GAM functions of Dall's porpoise (Pd) sightings from 1979 to 2009 in relation to SST indices and depth variables for the best predictive models. Dashed lines are bands of two standard errors.

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
0 10 20 30°C
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

Literature Cited

Agostini, V. N., R. C. Francis, A. B. Hollowed, S. D. Pierce, C. Wilson and A. N. Hendrix. 2006. The relationship between Pacific hake (*Merluccius productus*) distribution and poleward subsurface flow in the California Current System. Canadian Journal of Fisheries and Aquatic Sciences 63:2648-2659.

Agostini, V. N., A. N. Hendrix, A. B. Hollowed, C. D. Wilson, S. D. Pierce and R. C. Francis. 2008. Climate-ocean variability and Pacific hake: A geostatistical modeling approach. Journal of Marine Systems 71:237-248.

Akaike, H. 1976. An information criterion (AIC). Math Science 14:5-9.

Altmann, J. 1974. Observational study of behavior sampling methods. Behaviour 49:227-267.

Ansmann, I. C., J. C. Goold, P. G. H. Evans, M. P. Simmonds and S. G. Keith. 2007. Variation in the whistle characteristics of short-beaked common dolphins, *Delphinus delphis*, at two locations around the British Isles. Journal of the Marine Biological Association of the United Kingdom 87:19-26.

Au, D. W. K. and W. L. Perryman. 1985. Dolphin Habitats in the eastern tropical Pacific. Fishery Bulletin 83:623-643.

Au, W. W. L. 1993. The Sonar of Dolphins. Springer-Verlag Inc, New York.

Au, W. W. L. 2004. Echolocation signals of wild dolphins. Acoustical Physics 50:454-462.

Bailey, K. M., R. C. Francis and P. R. Stevens. 1982. The life history and fishery of Pacific whiting, *Merluccius productus*. CalCOFI Report 23:81-98.

Baird, R. W. and H. Whitehead. 2000. Social organization of mammal-eating killer whales: group stability and dispersal patterns. Canadian Journal of Zoology 78:2096-2105.

Baker, C. S. and L. M. Herman. 1984. Aggressive behavior between humpack whales (*Megaptera novaeangliae*) wintering in Hawaiian waters. Canadian Journal of Zoology 62:1922-1937.

Baldwin, J. M. 1896. A new factor in evolution. American Naturalist 30:441-451.

Ballance, L. T., R. L. Pitman and P. C. Fiedler. 2006. Oceanographic influences on seabirds and cetaceans of the eastern tropical Pacific: A review. Progress in Oceanography 69:360-390.

Bane, J. M., Y. H. Spitz, R. M. Letelier and W. T. Peterson. 2007. Jet stream intraseasonal oscillations drive dominant ecosystem variations in Oregon's summertime coastal upwelling system. Proceedings of the National Academy of Science USA 104:13262-13267.

Barange, M., I. Hampton and M. Soule. 1996. Empirical determination of *in situ* target strengths of three loosely aggregated pelagic fish species. ICES Journal of Marine Science 53:225-232.

Barlow, J. and K. A. Forney. 2007. Abundance and population density of cetaceans in the California Current ecosystem. Fishery Bulletin 105:509-526.

Bass, A. H., D. A. Bodnar and J. R. McKibben. 1997. From neurons to behavior: vocal-acoustic communication in teleost fish. Biology Bulletin 192:158-160.

Baumann-Pickering, S. 2009. Species identification and measurement of activity in odontocete species of Palmyra Atoll by acoustic monitoring. PhD. Eberhard Karls Universitat Tubingen,

Baumgartner, M. F. 1997. The distribution of Risso's dolphin (*Grampus griseus*) with respect to the physiography of the northern Gulf of Mexico. Marine Mammal Science 13:614-638.

Baumgartner, M. F. and D. M. Fratantoni. 2008. Diel periodicity in both sei whale vocalization rates and the vertical migration of their copepod prey observed from ocean gliders. Limnology and Oceanography 53:2197-2209.

Becker, E. A. 2007. Predicting seasonal patterns of California cetacean density based on remotely sensed environmental data. University of California, Santa Barbara, United States -- California.

Belwood, J. J. and J. H. Fullard. 1984. Echolocation and foraging behavior in the Hawaiian hoary bat, *Lasiurus cinereus semotus*. Canadian Journal of Zoology 62:2113-2120.

Benoit-Bird, K. and W. W. L. Au. 2001. Foraging Behavior of the Hawaiian Spinner Dolphin, *Stenella longirostris*. Page 22 14th Biennial Conference on the Biology of Marine Mammals. Society for Marine Mammalogy, Vancouver.

Benoit-Bird, K., W. W. L. Au and R. Kastelein. 2006. Testing the odontocete acoustic prey debilitation hypothesis: No stunning results. Pages 1118-1123. ASA.

Benoit-Bird, K. J. 2003. Dynamics of the Hawai'ian mesopelagic boundary community and their effects on predator foraging behavior. University of Hawai'i, United States -- Hawaii.

Benoit-Bird, K. J. and W. W. L. Au. 2003. Prey dynamics affect foraging by a pelagic predator (*Stenella longirostris*) over a range of spatial and temporal scales. Behavioral Ecology and Sociobiology 53:364-373.

Benoit-Bird, K. J. and W. W. L. Au. 2009. Phonation behavior of cooperatively foraging spinner dolphins. Journal of the Acoustical Society of America 125:539-546.

Benson, S. R., D. A. Croll, B. B. Marinovic, F. P. Chavez and J. T. Harvey. 2002. Changes in the cetacean assemblage of a coastal upwelling ecosystem during El Niño 1997-98 and La Niña 1999. Progress in Oceanography 54:279-291.

Bertrand, A., M. A. Barbieri, J. Cordova, C. Hernandez, F. Gomez and F. Leiva. 2004. Diel vertical behaviour, predator-prey relationships, and occupation of space by jack mackerel (Trachurus murphyi) off Chile. ICES Journal of Marine Science 61:1105-1112.

Braune, P., S. Schmidt and E. Zimmermann. 2008. Acoustic divergence in the communication of cryptic species of nocturnal primates (*Microcebus* ssp.). BMC Biology 6:1-10.

Brieman, L. 2001. Random Forests. Machine Learning 45:5-32.

Brinton, E. 1967. Vertical Migration and Avoidance Capability of Euphausiids in California Current. Limnology and Oceanography 12:451-&.

Brodeur, R. D., J. P. Fisher, R. L. Emmett, C. A. Morgan and E. Casillas. 2005. Species composition and community structure of pelagic nekton off Oregon and Washington under variable oceanographic conditions. Marine Ecology Progress Series 298:41-57.

Brownell, R. L., W. A. Walker and K. A. Forney. 1999. Pacific white-sided dolphins *Lagenorhynchus obliquidens* Gill, 1865. Pages 57-84 *in* S.H. Ridgway and R. Harrison, eds. Handbook of Marine Mammals,. Academic Press, London, San Diego.

Brownlee, S. 1983. Correlations between sounds and behavior in the Hawaiian spinner dolphin (*Stenella longirositris*). Master's thesis. University of California, Santa Cruz, Santa Cruz.

Buckland, S. T., D. R. Anderson, K. P. Burnham and J. L. Laake. 1993. Distance sampling: Estimating abundance of biological populations. Chapman & Hall, reprinted 1999 by RUWPA, University of St. Andrews, Scotland., London.

Burgess, L. 2006. Foraging ecology of common dolphins (*Delphinus* sp.) in the Hauraki Gulf, New Zealand. Master of Science. Massey University, Albany, New Zealand.

Burnham, K. P., D. R. Anderson and J. L. Laake. 1980. Estimation of density from line transect sampling of biological populations. Wildlife Monograms:1-202.

Calambokidis, J., G. H. Steiger, K. Rasmussen, J. Urban, K. C. Balcomb, P. L. de Guevara, M. Salinas, J. K. Jacobsen, C. S. Baker, L. M. Herman, S. Cerchio and J. D. Darling. 2000. Migratory destinations of humpback whales that feed

off California, Oregon and Washington. Marine Ecology-Progress Series 192:295-304.

Caldeira, R. M. A., P. Marchesiello, N. P. Nezlin, P. M. DiGiacomo and J. C. McWilliams. 2005. Island wakes in the Southern California Bight. Journal of Geophysical Research 110:C11012.

Caldwell, M. C. and D. K. Caldwell. 1968. Vocalization of Naive Captive Dolphins in Small Groups. Science 159:1121-1123.

Caldwell, M. C. and D. K. Caldwell. 1971. Statistical evidence for individual signature whistles in Pacific white-sided dolphins, *Lagenorhynchus obliquidens*. Cetology 3:1-9.

Cartamil, D. P. and C. G. Lowe. 2004. Diel movement patterns of ocean sunfish *Mola mola* off southern California. Marine Ecology Progress Series 266:245-253.

Charlton, B. D., Z. Zhihe and R. J. Snyder. 2009. The information content of giant panda, *Ailuropoda melanoleuca*, bleats: acoustic cues to sex, age and size. Animal Behaviour 78:893-898.

Checkley Jr., D. M. and J. A. Barth. 2009. Patterns and processes in the Calfornia Current System. Progress in Oceanography 83:49-64.

Christal, J. and H. Whitehead. 2001. Social affiliations within sperm whale (*Physeter macrocephalus*) groups. Ethology 107:323-340.

Clapham, P. J. 1996. The social and reproductive biology of humpback whales:an ecological perspective. Mammal Review 26:27-49.

Clapham, P. J., S. Leatherwood, I. Szczepaniak and R. L. Brownell. 1997. Catches of humpback and other whales from shore stations at Moss Landing and Trinidad, California, 1919-1926. Marine Mammal Science 13:368-394.

Clarke, A. S. 1990. Vocal communication in captive golden monkeys (*Rhinopithecus roxellanae*). Primates 31:601-606.

Connor, R. C. 2001. Individual foraging specializations in marine mammals: Culture and ecology. Behavioral and Brain Sciences 24:329-+.

Craig, A. S. and L. M. Herman. 2000. Habitat preferences of female humpback whales (*Megaptera novaeangliae*) in the Hawaiian islands are associated with reproductive status. Marine Ecology-Progress Series 193:209-216.

Crawford, J. D., M. Hagedorn and C. D. Hopkins. 1986. Acoustic communication in an electric fish, *Pollimyrus isidori* (Mormyridae). Journal of Comparative Physiology A 159:297-310.

Crockford, C. and C. Boesch. 2003. Context-specific calls in wild chimpanzees, *Pan troglodytes verus*: analysis of barks. Animal Behaviour 66:115-125.

Croll, D. A., B. Marinovic, S. R. Benson, F. P. Chavez, N. Black, R. Ternullo and B. R. Tershy. 2005. From wind to whales: trophic links in a coastal upwelling system. Marine Ecology Progress Series 289:117-130.

Croll, D. A., B. R. Tershy, R. P. Hewitt, D. A. Demer, P. C. Fiedler, S. E. Smith, W. Armstrong, J. M. Popp, T. Kiekhefer, V. R. Lopez, J. R. Urban and D. Gendron. 1998. An integrated approach to the foraging ecology of marine birds and mammals. Deep Sea Research Part II: Topical Studies in Oceanography 45:1353-1371.

Cross, J. N. and L. G. Allen. 1993. Fishes. Pages 459-540 *in* M.D. Dailey, D.J. Reish and J.W. Anderson, eds. Ecology of the Southern California Bight: A synthesis and interpretation. University of California Press, Berkeley.

Davis, R. W., N. Jaquet, D. Gendron, U. Markaida, G. Bazzino and W. Gilly. 2007. Diving behavior of sperm whales in relation to behavior of a major prey species, the jumbo squid, in the Gulf of California, Mexico. Marine Ecology Progress Series 333:291-302.

Dawson, S. 1991a. Clicks and Communication: The behavioural and social contexts of Hector's dolphin vocalizations. Ethology 88:265-276.

Dawson, S. M. 1991b. Clicks and Communication - the Behavioral and Social Contexts of Hector Dolphin Vocalizations. Ethology 88:265-276.

Defran, R. H., D. W. Weller, D. L. Kelly and M. A. Espinosa. 1999. Range characteristics of Pacific coast bottlenose dolphins (*Tursiops truncatus)* in the Southern California Bight. Marine Mammal Science 15:381-393.

Demer, D. A., J. P. Zwolinski, K. A. Byers, G. R. Cutter, J. S. Renfree and T. S. Sessions. 2010. Acoustic-trawl surveys of Pacific sardine (*Sardinops sagax*) in the California Current ecosystem. Southwest Fisheries Science Center.

Di Lorenzo, E., N. Schneider, K. M. Cobb, P. J. S. Franks, K. Chhak, A. J. Miller, J. C. McWilliams, S. J. Bograd, H. Arango, E. Curchitser, T. M. Powell and P. Riviere. 2008. North Pacific Gyre Oscillation links ocean climate and ecosystem change. Geophysical Research Letters 35:6.

Dohl, T. P., M. L. Bonnell and R. G. Ford. 1986. Distribution and abundance of common dolphin, *Delphinus delphus*, in the Southern California Bight: A quantitative assessment based upon aerial transect data. Fishery Bulletin 84:333-343.

Dudzinski, K. M. 1996. Communication and behavior in the Atlantic spotted dolphin (*Stenella frontalis*); Relationships between vocal and behavioral activities. PhD. Texas A&M University, College Station.

Edelaar, P. 2008. Assortative mating also indicates that common crossbill *Loxia curvirostra* vocal types are species. Journal of Avian Biology 39:9-12.

Eschmann, C., R. Moore and K. A. I. Nekaris. 2008. Calling patterns of western purple-faced langurs (Mammalia: Primates: Cercopithecidea: *Trachypithecus vetulus nestor*) in a degraded human landscape in Sri Lanka. Contributions to Zoology 77:57-65.

Evans, W. E. 1973. Echolocation by Marine Delphinids and One Species of Freshwater Dolphin. Journal of the Acoustical Society of America 54:191-199.

Evans, W. E. 1982. Distribution and differentiation of stock of *Delphinus delphis* Linnaeus in the Northeastern Pacific. Mammals in the Sea 4: Small Cetaceans, Seals, Sirenians and Otters:45-66.

Evans, W. E., W. W. Sutherland and R. G. Beil. 1964. The directional characteristics of delphinid sounds. Pages 353-369 *in* W.N. Tavolga, ed. Marine Bio-acoustics. Pergamon Press, Oxford, New York.

Falcone, E. A., G. S. Schorr, E. E. Henderson, M. F. McKenna, D. Moretti, A. Douglas, J. Calambokidis and J. A. Hildebrand. 2009. Sighting characteristics and photo-identification of Cuvier's beaked whales (Ziphius cavirostris) near San Clemente Island, California: a key area for beaked whales and the military? Marine Biology 156:2631-2640.

Farley, T. D. 1995. Geographic variation in dorsal fin color of short-beaked common dolphins, *Delphinus delphis,* in the Eastern Pacific Ocean. Administrative Report LJ-95-06:1-17.

Ferguson, M. C., J. Barlow, P. C. Fiedler, S. B. Reilly and T. Gerrodette. 2006. Spatial models of delphinid (family Delphinidae) encounter rate and group size in the eastern tropical Pacific Ocean. Ecological Modelling 193:645-662.

Fiedler, P. C. 2002. Ocean environment. Pages 824-830 *in* W.F. Perrin, B. Wursig and J.G.M. Thewissen, eds. Encyclopedia of Marine Mammals. Academic Press, San Diego.

Fiedler, P. C., S. B. Reilly, R. P. Hewitt, D. Demer, V. A. Philbrick, S. Smith, W. Armstrong, D. A. Croll, B. R. Tershy and B. R. Mate. 1998. Blue whale habitat and prey in the California Channel Islands. Deep-Sea Research Part Ii-Topical Studies in Oceanography 45:1781-1801.

Fisher, F. H. and F. N. Spiess. 1963. Flip-Floating Instrument Platform. The Journal of the Acoustical Society of America 35:1633-1644.

Flinn, R. D., A. W. Trites, E. J. Gregr and R. I. Perry. 2002. Diets of fin, sei and sperm whales in British Columbia: an analysis of commercial whaling records, 1963-1967. Marine Mammal Science 18:663-679.

Foerschler, M. I. and E. K. V. Kalko. 2009. Vocal types in crossbill populations (*Loxia* spp.) of southwest Europe. Journal of Ornithology 150:17-27.

Ford, J. K. B. 1989. Acoustic behavior of resident killer whales (*Orcinus orca*) off Vancouver Island, British Columbia. Canadian Journal of Zoology 67:727-745.

Forney, K. A. 2000. Environmental models of cetacean abundance: reducing uncertainty in population trends. Conservation Biology 14:1271-1286.

Forney, K. A. and J. Barlow. 1998. Seasonal patterns in the abundance and distribution of California cetaceans, 1991-1992. Marine Mammal Science 14:460-489.

Friedlaender, A. S., P. N. Halpin, S. S. Qian, G. L. Lawson, P. H. Wiebe, D. Thiele and A. J. Read. 2006. Whale distribution in relation to prey abundance and oceanographic processes in shelf waters of the Western Antarctic Peninsula. Marine Ecology-Progress Series 317:297-310.

Fristrup, K. M. and W. A. Watkins. 1994. Marine animal sound classification. Woods Hole Oceanographic Institution WHOI-94-13.

Frost, B. W. and L. E. McCrone. 1979. Vertical distribution, diel vertical migration, and abundance of some mesopelagic fishes in the eastern subarctic Pacific Ocean in summer. Fishery Bulletin 76:751-770.

Furusawa, M. 1991. Designing quantitative echosounders. Journal of the Acoustical Society of America 90:26-36.

Gallo-Reynoso, J. P. 1991. Group behavior of common dolphins (*Delphinus delphus*) during prey capture. Anales Inst. Biol. Nac. Auton. Mexico, Ser. Zool. 62:253-262.

Gannon, D. P., N. B. Barros, D. P. Nowacek, A. J. Read, D. M. Waples and R. S. Wells. 2005. Prey detection by bottlenose dolphins, *Tursiops truncatus*: an experimental test of the passive listening hypothesis. Animal Behaviour 69:709-720.

Gerhardt, H. C. 1994. The Evolution of Vocalization in Frogs and Toads. Annual Review of Ecology and Systematics 25:293-324.

Gerrodette, T. and J. Forcada. 2002. Estimates of abundance of northeastern offshore spotted, coastal spotted, and eastern spinner dolphins in the eastern tropical Pacific Ocean. Southwest Fisheries Science Center, La Jolla, California.

Goold, J. C. 2000. A diel pattern in vocal activity of short-beaked common dolphins, *Delphinus delphis*. Marine Mammal Science 16:240-244.

Gorsky, G., M. D. Ohman, M. Picheral, S. Gasparini, L. Stemmann, J. B. Romagnan, A. Cawood, S. Pesant, C. Garcia-Comas and F. Prejger. 2010. Digital zooplankton image analysis using the Zooscan integrated system. Journal of Plankton Research 32:285-303.

Götz, T., U. K. Verfuss and H. U. Schnitzler. 2006. 'Eavesdropping' in wild rough-toothed dolphins (*Steno bredanensis*)? Biology Letters 2:5-7.

Gowans, S., H. Whitehead and S. K. Hooker. 2001. Social organization in northern bottlenose whales, Hyperoodon ampullatus: not driven by deep-water foraging? Animal Behaviour 62:369-377.

Gregr, E. J. and A. W. Trites. 2001. Predictions of critical habitat for five whale species in the waters of coastal British Columbia. Canadian Journal of Fisheries and Aquatic Sciences 58:1265-1285.

Hanson, M. T. and R. H. Defran. 1993. The behavior and feeding ecology of the Pacific coast bottlenose dolphin, *Tursiops truncatus*. Aquatic Mammals 19:127-142.

Harrison, R. G. 1991. Molecular-Changes at Speciation. Annual Review of Ecology and Systematics 22:281-308.

Hastie, G. D., R. J. Swift, G. Slesser, P. M. Thompson and W. R. Turrell. 2005. Environmental models for predicting oceanic dolphin habitat in the Northeast Atlantic. Ices Journal of Marine Science 62:760-770.

Hastie, T. and R. Tibshirani. 1986. Generalized Additive Models. Statistical Science 1:297-310.

Hawkins, A. D. 1993. Underwater sound and fish behaviour *in* T.J. Pitcher, ed. Behaviour of Teleost Fishes. Chapman & Hall, London.

Heath, C. B. 2002. California, Galapagos, and Japanese sea lions. Pages 180-186 *in* W.F. Perrin, B. Wursig and J. Thewissen, G. M., eds. Encyclopedia of Marine Mammals. Academic Press, San Diego.

Heise, K. 1997. Diet and feeding behavior of Pacific white-sided dolphins (*Lagenorhyncus obliquidens*) as revealed through the collection of prey fragments and stomach content analysis. Report of the International Whaling Commission 47:807-815.

Henderson, E. E., J. A. Hildebrand and M. H. Smith. 2009. Behavior and vocalization patterns of common dolphins (*Delphinus* sp.) in the Southern California Bight 18th Biennial Conference on the Biology of Marine Mammals, Quebec, Canada.

Henderson, E. E. and B. Würsig. 2007. Behavior patterns of bottlenose dolphins in San Luis Pass, Texas. Gulf of Mexico Science 2:153-161.

Herman, L. M. 1979. Humpback whales in Hawaiian waters: A study in historical ecology. Pacific Science 33:1-15.

Herman, L. M. and W. N. Tavolga. 1980. The communication systems of cetaceans. Pages 149–209 *in* L.M. Herman, ed. Cetacean Behavior: Mechanisms and Functions. Wiley, New York.

Herzing, D. L. 1996. Vocalizations and associated underwater behavior of free-ranging Atlantic spotted dolphins, *Stenella frontalis* and Bottlenose dolphins, *Tursiops truncatus*. Aquatic Mammals 22:61-80.

Heyning, J. E. and W. F. Perrin. 1994. Evidence for two species of common dolphin (Genus *Delphinus*) from the Eastern North Pacific. Contributions in Science 442:1-35.

Hickey, B. M. 1993. Physical Oceanography. Pages 19-70 *in* M.D. Dailey, D.J. Reish and J.W. Anderson, eds. Ecology of the Southern California Bight: A synthesis and interpretation. University of California Press, Los Angeles.

Hickey, B. M., E. L. Dobbins and S. E. Allen. 2003. Local and remote forcing of currents and temperature in the central Southern California Bight. Journal of Geophysical Research 108:26-21-26-26-26.

Hindell, M. A. 2002. Elephant seals. Pages 370-373 *in* W.F. Perrin, B. Wursig and J. Thewissen, G. M., eds. Encyclopedia of marine mammals. Academic Press, San Diego.

Hoelzel, A. R. 1993. Foraging behavior and social group dynamics in Puget Sound killer whales. Animal Behaviour 45:581-591.

Hubbs, C. L. 1948. Changes in the fish fauna of western North America correlated with changes in ocean temperature. Journal of Marine Research 7:459-382.

Hui, C. A. 1979. Undersea topography and distribution of dolphins of the genus *Delphinus* in the Southern California Bight. JOURNAL OF MAMMALOGY 60:521-527.

Hurrell, J. W. and H. Van Loon. 2004. Decadal variations in climate associated with the North Atlantic Oscillation. Climate Change 36:301-326.

Hyrenbach, K. D. and R. R. Veit. 2003. Ocean warming and seabird communities of the southern California Current System (1987-98): response at multiple temporal scales. Deep Sea Research Part II: Topical Studies in Oceanography 50:2537-2565.

IWC. 1997. Report of the IWC workshop on climate change and cetaceans. Report of the International Whaling Commission 47:293-313.

Jaccard, J., M. A. Becker and G. Wood. 1984. Pairwise multiple comparison procedures: A review. Psychological Bulletin 96:589-596.

Janik, V. M. 2000a. Food-related bray calls in wild bottlenose dolphins (*Tursiops truncatus*). Proceedings of the Royal Society Biological Sciences Series B 267:923-927.

Janik, V. M. 2000b. Food-related bray calls In wild bottlenose dolphins (*Tursiops truncatus*). Proceedings of the Royal Society of London Series B-Biological Sciences 267:923-927.

Jarvis, S., D. Moretti, R. Morrissey and N. DiMarzio. 2003. Passive monitoring and localization of marine mammals in open ocean environments using widely spaced bottom mounted hydrophones. The Journal of the Acoustical Society of America 114:2405-2406.

Johnson, M., L. S. Hickmott, N. Aguilar de Soto and P. T. Madsen. 2008. Echolocation behavior adapted to prey in foraging Blainville's beaked whale (*Mesoplodon densirostris*). Proceedings of the Royal Society Biological Sciences Series B 275:133-139.

Johnson, M., P. T. Madsen, W. M. X. Zimmer and N. T. Aguilar de Soto, P. L. 2006. Foraging Blainville's beaked whales (*Mesoplodon densirostris*) produce distinct click types matched to different phases of echolocation. The Journal of Experimental Biology 209:5038-5050.

Jones, G. 1997. Acoustic signals and speciation: the roles of natural and sexual selection in the evolution of cryptic species. Advances in the Study of Behavior 26:317-354.

Kingston, T., M. C. Lara, G. Jones, Z. Akbar, T. H. Kunz and C. J. Schneider. 2001. Acoustic divergence in two cryptic *Hipposideros* species: A role for social selection? Proceedings Royal Society of London Series B Biological Sciences 268:1381-1386.

Kinzey, D., P. Olson and T. Gerrodette. 2000. Marine mammal data collection procedures on research ship line-transect surveys by the Southwest Fisheries Science Center. Southwest Fisheries Science Center.

Krishna, S. N. and S. B. Krishna. 2005. Female courtship calls of the litter frog (*Rana curtipes*) in the tropical forests of Western Ghats, South India. Amphibia-Reptilia 26:431-435.

Kruskal, W. and W. A. Wallis. 1952. Use of ranks in one-criterion variance analysis. Journal of the American Statistical Association 47:583-621.

Lammers, M. O. and W. W. L. Au. 2003. Directionality in the whistles of Hawaiian spinner dolphins (Stenella longirostris): A signal feature to cue direction of movement? Marine Mammal Science 19:249-264.

Lammers, M. O., W. W. L. Au and D. L. Herzing. 2003. The broadband social acoustic signaling behavior of spinner and spotted dolphins. Journal of the Acoustical Society of America 114:1629-1639.

Lammers, M. O., M. Schotten and W. W. L. Au. 2006. The spatial context of free-ranging Hawaiian spinner dolphins (*Stenella longirostris*) producing acoustic signals. The Journal of the Acoustical Society of America 119:1244.

Learmonth, J. A., C. D. MacLeod, M. B. Santos, G. J. Pierce, H. Q. P. Crick and R. A. Robinson. 2006. Potential effects of climate change on marine mammals. Oceanography and Marine Biology: An Annual Review 44:431-464.

Leatherwood, S., R. R. Reeves, A. E. Bowles, B. S. Stewart and K. R. Goodrich. 1984. Distribution, seasonal movements and abundance of Pacific white-sided dolphins in the Eastern North Pacific. Scientific Report of Whales Research Institute 35:129-157.

Lehodey, P., J. Alheit, M. Barange, T. Baumgartner, G. Beaugrand, K. Drinkwater, J.-M. Fromentin, S. R. Hare, G. Ottersen, R. I. Perry, C. V. D. L. Roy, C. D. and F. Werner. 2006. Climate variability, fish, and fisheries. Journal of Climate - Special Section 19:5009-5030.

Leighton, T. G., S. G. Richards and P. R. White. 2004. Trapped within a wall of sound. Acoustics bulletin 29:24-29.

Li, S. H., K. X. Wang, D. Wang and T. Akamatsu. 2005. Echolocation signals of the free-ranging Yangtze finless porpoise (*Neophocaena phocaenoides asiaeorientialis*). Journal of the Acoustical Society of America 117:3288-3296.

Liaw, A. and M. Wiener. 2002. Classification and Regression by Random Forest. R News 2:18-22.

Lluch-Belda, D., D. B. Lluch-Cota and S. E. Lluch-Cota. 2003. Scales of interannual variability in the California Current System: Associated physical mechanisms and likely ecological impacts. CalCOFI Report 44:76-85.

Logerwell, E. A., B. Lavaniegos and P. E. Smith. 2001. Spatially-explicit bioenergetics of Pacific sardine in the Southern California Bight: are mesoscale eddies areas of exceptional prerecruit production? Progress in Oceanography 49:391-406.

Logerwell, E. A. and P. E. Smith. 2001. Mesoscale eddies and survival of late stage Pacific sardine (*Sardinops sagax*) larvae. Fisheries Oceanography 10:13-25.

Lowry, M. S., C. W. Oliver and J. B. Wexler. 1986. The food habits of California sea lions at San Clemente Island, California; April 1983 through September 1985. NOAA Administrative Report LJ-86-33.

Lux, C. A., A. S. Costa and A. E. Dizon. 1997. Mitochondrial DNA population structure of the Pacific white-sided dolphin. Report of the International Whaling Commission 47:645-652.

MacLeod, C. D. 2009. Global climate change, range changes and potential implications for the conservation of marine cetaceans: a review and synthesis. Endangered Species Research 7:125-136.

MacLeod, C. D., S. M. Bannon, G. J. Pierce, C. Schweder, J. A. Learmonth, J. S. Herman and R. J. Reid. 2005. Climate change and the cetacean community of north-west Scotland. Biological Conservation 124:477-483.

MacLeod, C. D., C. R. Weir, M. Begoña Santos and T. E. Dunn. 2008. Temperature-based summer habitat partitioning between white-beaked and common

dolphins around the United Kingdom and Republic of Ireland. Journal of the Marine Biological Association of the United Kingdom 88:1193-1198.

Madsen, P. T., M. Johnson, N. A. de Soto, W. M. X. Zimmer and P. Tyack. 2005. Biosonar performance of foraging beaked whales (Mesoplodon densirostris). Journal of Experimental Biology 208:181-194.

Mann, J. 1999. Behavioral sampling methods for cetaceans: A review and critique. Marine Mammal Science 15:102-122.

Mantua, N. J. and S. R. Hare. 2002. The Pacific Decadal Oscillation. Journal of Oceanography 58:35-44.

Mayr, E. 1977. Darwin and Natural-Selection. American Scientist 65:321-327.

McCowan, B. and I. Rommeck. 2006. Bioacoustic monitoring of aggression in group-housed rhesus macaques. Journal of Applied Animal Welfare Science 9:261-268.

McGowan, J. A. 1985. El Niño 1983 in the Southern California Bight. Pages 166-184 *in* W.S. Wooster and D.L. Fluharty, eds. El Niño North: Niño effects in the Eastern Subarctic Pacific Ocean. Washington Sea Grant Program, University of Washington, Seattle.

McGowan, J. A., S. J. Bograd, R. J. Lynn and A. J. Miller. 2003. The biological response to the 1977 regime shift in the California Current. Deep-Sea Research II 50:2567-2582.

Mellinger, D. K. 2001. Ishmael 1.0 User's Guide. NOAA Technical Report OAR-PMEL-120. NOAA Pacific Marine Environmental Laboratory.

Mellinger, D. K., S. L. Nieukirk, H. Matsumoto, S. L. Heimlich, R. P. Dziak, J. Haxel, M. Fowler, C. Meinig and H. V. Miller. 2007. Seasonal occurrence of North Atlantic right whale (*Eubalaena glacialis*) vocalizations at two sites on the Scotian Shelf. Marine Mammal Science 23:856-867.

Mennill, D. J. and S. L. Vehrencamp. 2008. Context-dependent functions of avian duets revealed by microphone-array recordings and multispeaker playback. Current Biology 18:1314-1319.

Mesnick, S. L., B. L. Taylor, R. G. Le Duc, S. E. Trevino, G. M. O'Corry-Crowe and A. E. Dizon. 1999. Culture and Genetic evolution in whales. Science 284:2055a.

Meynier, L., C. Pusineri, J. Spitz, M. B. Santos, G. J. Pierce and V. Ridoux. 2008. Intraspecific dietary variation in the short-beaked common dolphin *Delphinus delphis* in the Bay of Biscay: importance of fat fish. Marine Ecology-Progress Series 354:277-287.

Moore, S. E. and S. H. Ridgway. 1995. Whistles produced by common dolphins from the Southern California Bight. Aquatic Mammals 21.1:55-63.

Moretti, D., S. Jarvis, N. DiMarzio and R. Morrissey. 2004. Passive detection, data association, and localization of marine mammal calls using traditional 3D hyperbolic tracking algorithms. The Journal of the Acoustical Society of America 116:2606-2606.

Muck, P. 1989. Relationships between anchoveta spawning strategies and the spatial variability of sea surface temperature off Peru. IMPARE, Callao, Peru.

Mullin, M. M., E. R. Brooks, F. M. H. Reid, J. Napp and E. F. Stewart. 1985. Vertical structure of nearshore plankton off southern California: a storm and a larval fish food web. Fishery Bulletin 83:151-170.

Munger, L. M., D. Camacho, A. Havron, G. Campbell, J. Calambokidis, A. Douglas and J. A. Hildebrand. 2009. Baleen whale distribution relative to surface temperature and zooplankton abundance off Southern California, 2004-2008. CalCOFI Report 50:155-168.

Murray, S. O., E. Mercado and H. L. Roitblat. 1998. Characterizing the graded structure of false killer whale (Pseudorca crassidens) vocalizations. Journal of the Acoustical Society of America 104:1679-1688.

Naguib, M. and V. M. Janik. 2009. Vocal communication in birds and mammals. Advances in the Study of Behavior 40:1-322.

Neumann, D. R. 2001a. The activity budget of free-ranging common dolphins (Delphinus delphis) in the northwestern Bay of Plenty, New Zealand. Aquatic Mammals 27:121-136.

Neumann, D. R. 2001b. Seasonal movements of short-beaked common dolphins (Delphinus delphis) in the north-western Bay of Plenty, New Zealand: Influence of sea surface temperature and El Nino/La Nina. New Zealand Journal of Marine and Freshwater Research 35:371-374.

Neumann, D. R. and M. B. Orams. 2003. Feeding behaviours of short-beaked common dolphins, *Delphinus delphis*, in New Zealand. Aquatic Mammals 29.1:137-149.

Nichol, L. M. and D. M. Shackleton. 1996. Seasonal movements and foraging behaviour of northern resident killer whales (Orcinus orca) in relation to the inshore distribution of salmon (Oncorhynchus spp) in British Columbia. Canadian Journal of Zoology-Revue Canadienne De Zoologie 74:983-991.

Ñiquen, M. and M. Bouchon. 2004. Impact of El Niño events on pelagic fisheries in Peruvian waters. Deep-Sea Research II 51:563-574.

Nishimoto, M. M. and L. Washburn. 2002. Patterns of coastal eddy circulation and abundance of pelagic juvenile fish in the Santa Barbara Channel, California, USA. Marine Ecology Progress Series 241:183-199.

Norris, K. S. and T. P. Dohl. 1980. Behavior of the Hawaiian spinner dolphin, *Stenella longirostris*. Fishery Bulletin 77:821-849.

Norris, K. S., B. Wursig, R. S. Wells and M. Wursig. 1994. The Hawaiian Spinner Dolphin. University of California Press, Berkeley.

Norris, K. S., B. Würsig, R. S. Wells, M. Würsig, S. Brownlee, C. M. Johnson and J. Solon. 1985. The Behavior of the Hawaiian Spinner Dolphin, *Stenella longirostris*.

Norton, J., D. McLain, R. Brainard and D. Husby. 1985. 1982-1983 El Niño event off Baja and Alta California and its ocean climate context. Pages 44-72 *in* W.S. Wooster and D.L. Fluharty, eds. El Niño north: Niño effects in the eastern subarctic Pacific Ocean University of Washington, Seattle, WA.

Ohizumi, H., M. Yoshioka, K. Mori and N. Miyazaki. 1998. Stomach contents of common dolphins (*Delphinus delphis*) in the pelagic Western North Pacific. Marine Mammal Science 14:835-844.

Ohman, M. D. 1990. The demographic benefits of diel vertical migration by zooplankton. Ecological Monographs 60:257-281.

Oleson, E. M. 2005. Calling behavior of blue and fin whales off California. PhD. University of California, San Diego, San Diego.

Oleson, E. M., S. M. Wiggins and J. A. Hildebrand. 2007a. Temporal separation of blue whale call types on a southern California feeding ground. Animal Behaviour 74:881-894.

Oleson, E. M., S. M. Wiggins and J. A. Hildebrand. 2007b. Temporal separation of blue whale call types on a southern California feeding ground. Animal Behaviour 74:881-894.

Osnes-Erie, L. D. 1999. Food habits of common dolphin (*Delphinus delphis* and *D. capensis*) off California. Master's thesis. San Jose State University, Moss Landing.

Oswald, J. N., J. Barlow and T. F. Norris. 2003. Acoustic identification of nine delphinid species in the eastern tropical Pacific Ocean. Marine Mammal Science 19:20-37.

Ott, R. L. and M. Longnecker. 2001. An introduction to statistical methods and data analysis. Duxbury, Pacific Grove, California.

Perrin, W. F. 2002. Common Dolphins. Pages 245-248 *in* W.F. Perrin, B. Würsig and J. Thewissen, G. M., eds. Encyclopedia of Marine Mammals. Academic Press, San Diego.

Pyle, P. and L. Gilbert. 1996. Occurrence Patterns and Trends of Cetaceans Recorded from Southeast Farallon Island, California, 1973 to 1994. Northwestern Naturalist 77:1-8.

Rankin, S., J. Oswald, J. Barlow and M. Lammers. 2007. Patterned burst-pulse vocalizations of the northern right whale dolphin, *Lissodelphis borealis*. Journal of the Acoustical Society of America 121:1213-1218.

Redfern, J. V., M. C. Ferguson, E. A. Becker, K. D. Hyrenbach, C. Good, J. Barlow, K. Kaschner, M. F. Baumgartner, K. A. Forney and L. T. Ballance. 2006. Techniques for cetacean-habitat modeling. Marine Ecology-Progress Series 310:271-295.

Reeves, R. R., B. S. Stewart, P. J. Clapham and J. A. Powell. 2002. Guide to Marine Mammals of the World. Alfred A Knopf, New York.

Reid, J. L., G. I. Roden and J. G. Wyllie. 1958. Studies of the California Current System. CalCOFI Report:28-56.

Reilly, S. B. 1990. Seasonal changes in distribution and habitat differences among dolphins in the eastern tropical Pacific. Marine Ecology-Progress Series 66:1-11.

Reilly, S. B. and P. C. Fiedler. 1994. Interannual Variability of Dolphin Habitats in the Eastern Tropical Pacific .1. Research Vessel Surveys, 1986-1990. Fishery Bulletin 92:434-450.

Reilly, S. B. and V. G. Thayer. 1990. Blue whales (*Balaenoptera musculus*) distribution in the eastern tropical Pacific. Marine Mammal Science 6:265-277.

Rendell, L. and H. Whitehead. 2001. Culture in whales and dolphins. Behavioral and Brain Sciences 24:309-382.

Richardson, W., C. J. Greene, C. Malme and D. Thomson. 1995a. Marine Mammals and Noise. Academic Press, San Diego.

Richardson, W. J., K. J. Finley, G. W. Miller, R. A. Davis and W. R. Koski. 1995b. Feeding, Social, and Migration behavior of bowhead whales, *Balaena mysticetus,* in Baffin Bay vs. the Beaufort Sea - Regions with different amounts of human activity. Marine Mammal Science 11:1-45.

Richman, B. 1980. Did human speech originate in coordinated vocal music? Semiotica 32:233-244.

Ridgway, S. H. 1983. Dolphin hearing and sound production in health and illness. Pages 247-296 *in* R.R. Fay and G. Gourevitch, eds. Hearing and other senses: presentations in honor of E. G. Weaver. The Amphora Press, Groton, CT.

Roberts, T. J. 2003. Learning about vocal communication in birds. Journal of the Bombay Natural History Society 100:390-393.

Roch, M. A., M. S. Soldevilla, J. C. Burtenshaw, E. E. Henderson and J. A. Hildebrand. 2007. Gaussian mixture model classification of odontocetes in the Southern California Bight and the Gulf of California. Journal of the Acoustical Society of America 121:1737-1748.

Rosel, P. E., A. E. Dizon and J. E. Heyning. 1994. Genetic analysis of sympatric morphotypes of common dolphins (genus *Delphinus*). Marine Biology 119:159-167.

Rykaczewski, R. R. and D. M. Checkley, Jr. 2008. Influence of ocean winds on the pelagic ecosystem in upwelling regions. Proceedings of the National Academy of Sciences of the United States of America 105:1965-1970.

Santora, J. A., C. S. Reiss, V. J. Loeb and R. R. Veit. 2010. Spatial association between hotspots of baleen whales and demographic patterns of Antarctic krill *Euphausia superba* suggests size-dependent predation. Marine Ecology Progress Series 405:255-269.

Schellart, N. A. M. and A. N. Popper. 1992. Functional Aspects of the Evolution of the Auditory System of Actinopterygian Fish. Pages 295-322 Webster, D. B., R. R. Fay and a. N. Popper.

Seddon, N. 2005. Ecological adaptation and species recognition drives vocal evolution in neotropical suboscine birds. Evolution 59:200-215.

Selzer, L. A. and P. M. Payne. 1988. The distribution of white-sided (*Lagenorhyncus acutus*) and common dolphins (*Delphinus delphus*) vs. environmental features of the continental shelf of the northeastern United States. Marine Mammal Science 4:141-153.

Sette, O. E. and J. D. Isaacs. 1960. The changing Pacific Ocean in 1957 and 1958. CalCOFI Report 7:13-217.

Shane, S. H. 1990. Comparison of bottlenose dolphin behavior in Texas and Florida, with a critique of methods for studying dolphin behavior. Pages 541-558 *in* S. Leatherwood and R.R. Reeves, eds. The Bottlenose Dolphin. Academic Press, Inc., San Diego, CA.

Shane, S. H. 1994. Occurrence and habitat use of marine mammals at Santa Catalina Island, California from 1983-91. Bulletin of Southern California Academy of Science 93:13-29.

Shane, S. H. 1995. Relationship between pilot whales and Risso's dolphins at Santa Catalina Island, California, USA. Marine Ecology-Progress Series 123:5-11.

Shane, S. H., R. S. Wells and B. Würsig. 1986. Ecology, Behavior and social organization of the bottlenose dolphin: a review. Marine Mammal Science 2:34-63.

Silber, G. K. 1986. The relationship of social vocalizations to surface behavior and aggression in the Hawaiian humpback whale (*Megaptera novaeangliae*). Canadian Journal of Zoology 64:2075-2079.

Simard, Y., D. Lavoie and F. J. Saucier. 2002. Channel head dynamics: capelin (*Mallotus villosus*) aggregation in the tidally driven upwelling system of the Saguenay – St. Lawrence Marine Park's whale feeding ground. Canadian Journal of Fisheries and Aquatic Sciences 59:197-210.

Simeonovska-Nikolova, D. M. and V. M. Bogoev. 2008. Vocal communication in the striped field mouse, *Apodemus agrarius*, in dyadic encounters and intraspecific cage groups. Journal of Natural History 42:289-299.

Simmonds, M. P. and W. J. Eliott. 2009. Climate change and cetaceans: concerns and recent developments. Journal of the Marine Biological Association of the United Kingdom 89:203-210.

Simmonds, M. P. and S. J. Isaac. 2007. The impacts of climate change on marine mammals: early signs of significant problems. Oryx 41:19-26.

Simmonds, M. P. and S. J. Mayer. 1997. An evaluation of environmental and other factors in some recent marine mammal mortalities in Europe: implications for conservation and management. Environmental Review 5:89-98.

Simon, M., P. McGregor and F. Ugarte. 2007a. The relationship between the acoustic behaviour and surface activity of killer whales (Orcinus orca) that feed on herring (Clupea harengus). Acta ethologica 10:47-53.

Simon, M., P. K. McGregor and F. Ugarte. 2007b. The relationship between the acoustic behavior and surface activity of killer whales (*Orcinus orca*) that feed on herring *(Clupea harengus*). Acta Ethology 10:47-53.

Simon, M., F. Ugarte, M. Wahlberg and L. A. Miller. 2006. Icelandic killer whales *Orcinus orca* use a pulsed call suitable for manipulating the schooling behaviour of herring *Clupea harengus*. Bioacoustics 16:57-74.

Siroky, D. S. 2008. Navigating Random Forests. Statistics Surveys 0:1-14.

Sjare, B. L. and T. G. Smith. 1986. The relationship between behavioral activity and underwater vocalizations of the white whale, *Delphinapterus leucas*. Canadian Journal of Zoology 64:2824-2831.

Smith, A. L. and V. L. Friesen. 2007. Differentiation of sympatric populations of the band-rumped storm-petrel in the Galapagos Islands: an examination of genetics, morphology, and vocalizations. Molecular Ecology 16:1593-1603.

Smith, P. E. 1995. A warm decade in the Southern California Bight. CalCOFI Report 36:120-126.

Smith, P. E. and R. W. Eppley. 1982. Primary Production and the Anchovy Population in the Southern-California Bight - Comparison of Time-Series. Limnology and Oceanography 27:1-17.

Smith, R. C., P. Dustan, D. Au, K. S. Baker and E. A. Dunlap. 1986. Distribution of cetacean and sea-surface chlorophyll concentration in the California Current. Marine Biology 91:385-402.

Soldevilla, M. S. 2008. Risso's and Pacific White-sided Dolphins in the Southern California Bight: Using Echolocation Clicks to Study Dolphin Ecology. PhD. University of California, San Diego, La Jolla, California.

Soldevilla, M. S., E. E. Henderson, G. S. Campbell, S. M. Wiggins, J. A. Hildebrand and M. A. Roch. 2008. Classification of Risso's and Pacific white-sided dolphins using spectral properties of echolocation clicks. The Journal of the Acoustical Society of America 124:609-624.

Soldevilla, M. S., S. M. Wiggins, J. Calambokidis, A. Douglas, E. M. Oleson and J. A. Hildebrand. 2006. Marine mammal monitoring and habitat invesitgations during CalCOFI surveys. CalCOFI Report 47:79-91.

Soldevilla, M. S., S. M. Wiggins and J. A. Hildebrand. 2010. Spatio-temporal comparison of Pacific white-sided dolphin echolocation click types. Aquatic Biology 9:49-62.

Stafford, K. M., J. J. Citta, S. E. Moore, M. A. Daher and J. E. George. 2009. Environmental correlates of blue and fin whale call detections in the North Pacific Ocean from 1997 to 2002. Marine Ecology-Progress Series 395:37-53.

Star, J. L. and M. M. Mullin. 1981. Zooplankton assemblages in three areas of the North Pacific as revealed by continuous horizontal transects. Deep-Sea Research 28A:1303-1322.

Stenseth, N. C., A. Mysterud, G. Ottersen, J. W. Hurrell, K.-S. Chan and M. Lima. 2002. Ecological Effects of Climate Fluctuations. Science 297:1292-1296.

Stockin, K. A., V. Binedell, N. Wiseman, D. H. Brunton and M. B. Orams. 2009. Behavior of free-ranging common dolphins (*Delphinus* sp.) in the Hauraki Gulf, New Zealand. Marine Mammal Science 25:283-301.

Stroud, R. K., C. H. Fiscus and H. Kajimura. 1981. Food of the Pacific white-sided dolphin, *Lagenorhyncus obliquidens*, Dall's porpoise, *Phocoenoides dalli*, and nothern fur seal, *Callorhinus ursinus*, off California and Washington. Fishery Bulletin 78:951-959.

Strub, P. T. and C. James. 2000. Altimeter-derived variability of surface velocities in the California current system: 2. Seasonal circulation and eddy statistics. Deep-Sea Research II 47:831-870.

Suzuki, R. and A. Takaya. 2007. The dynamic changes in roles of learning through the Baldwin Effect. Artificial Life 13:31-43.

Taruski, A. G. 1979. The whistle repertoire of the North Atlantic pilot whale (*Globicephala melaena*) and its relationship to behavior and environment. Pages 345-368 *in* H.E. Winn and B.L. Olla, eds. Behavior of marine animals: Current perspectives in research. Plenum Press, New York.

Tasker, M. L., P. H. Jones, T. Dixon and B. F. Blake. 1984. Counting Seabirds at Sea from Ships: A Review of Methods Employed and a Suggestion for a Standardized Approach. The Auk 101:567-577.

Tershy, B. R., D. Breese and S. Alvarez-Borrego. 1991. Increase in cetacean and seabird numbers in the Canal de Ballenas during an El Niño-Southern Oscillation event. Marine Ecology-Progress Series 69:299-302.

Thomson, R. E. and S. E. Allen. 2000. Time series acoustic observations of macrozooplankton diel migration and associated pelagic fish abundance. Canadian Journal of Fisheries and Aquatic Science 57:1919-1931.

Thorson, J., T. Weber and F. Huber. 1982. Auditory behavior of the cricket II. Simplicity of calling-song recognition in *Gryllus*, and anomalous phonotaxis at abnormal carrier frequencies. Journal of Comparative Physiology A 146:361-378.

Tibby, R. B. 1937. The relation between surface water temperature and the distribution of spawn of the Calfornia sardine. California Fish and Game:132-137.

Tynan, C. T., D. G. Ainley, J. A. Barth, T. J. Cowles, S. D. Pierce and L. B. Spear. 2005. Cetacean distributions relative to ocean processes in the northern California Current System. Deep-Sea Research Part Ii-Topical Studies in Oceanography 52:145-167.

Van Parijs, S. M. and P. J. Corkeron. 2001a. Vocalizations and Behaviour of Pacific humpback dolphins (*Sousa chinensis*). Ethology 107:701-716.

Van Parijs, S. M. and P. J. Corkeron. 2001b. Vocalizations and behaviour of Pacific humpback dolphins *Sousa chinensis*. Ethology 107:701-716.

Verfuss, U. K., L. A. Miller, P. K. D. Pilz and H. U. Schnitzler. 2009. Echolocation by two foraging harbour porpoises (*Phocoena phocoena*). The Journal of Experimental Biology 212.

Verfuss, U. K., L. A. Miller and H. U. Schnitzler. 2005. Spatial orientation in echolocating harbour porpoises (*Phocoena phocoena*). Journal of Experimental Biology 208:3385-3394.

Vergne, A. L., M. B. Pritz and N. Mathevon. 2009. Acoustic communication in crocodilians: from behaviour to brain. Biological Reviews (Cambridge) 84:391-411.

Walker, W. A. and L. L. Jones. 1993. Food habits of northern right whale dolphin, Pacific white-sided dolphin, and northern fur seal caught in the high seas driftnet fisheries of the North Pacific Ocean, 1990. International North Pacific Fisheries Commission Bulletin 53:285-295.

Walker, W. A., S. Leatherwood, K. R. Goodrick, W. F. Perrin and R. K. Stroud. 1986. Geographic variation and biology of the Pacific white-sided dolphin, *Lagenorhynchus obliquidens*, in the north-eastern Pacific. Pages 441–465 *in* M.M. Bryden and R. Harrison, eds. Research on Dolphins. Clarendon Press, Oxford.

Wang, C. and P. C. Fiedler. 2006. ENSO variability and the eastern tropical Pacific: A review. Progress in Oceanography 69:239-266.

Wang, X. J., R. Murtugudde and R. Le Borgne. 2010. Climate driven decadal variations of biological production and plankton biomass in the equatorial Pacific Ocean: is this a regime shift? Biogeosciences Discussions 7:2169-2193.

Watkins, W. A. 1964. The harmonic interval: fact or artifact in spectral analysis of pulse trains. Pages 15-43 *in* W.N. Tavolga, ed. Marine Bio-Acoustics. Pergamon Press, Oxford, New York.

Watkins, W. A. and D. Wartzok. 1985. Sensory biophysics of marine mammals. Marine Mammal Science 1:219-260.

Weilgart, L. S. and H. Whitehead. 1990. Vocalizations of the North Atlantic pilot whale (*Globicephala melas*) as related to behavioral contexts. Behavioral Ecology and Sociobiology 26:399-402.

Wells, K. D. 1977. The social behaviour of anuran amphibians. Animal Behaviour 25:666-693.

Wells, R. S. 1991. The role of long-term study in understanding the social structure of a bottlenose dolphin community. Pages 199-225 *in* K. Pryor and K.S. Norris, eds. Dolphin societies - discoveries and puzzles. University of California Press, Berkeley.

Whitehead, H. and L. Weilgart. 2000. The Sperm Whale. Pages 154-172 *in* J. Mann, R.C. Connor, P.L. Tyack and H. Whitehead, eds. Cetacean societies: Field studies of dolphins and whales. The University of Chicago Press, Chicago.

Whitten, J. L. and J. A. Thomas. 2001. Whistle repertoire of Pacific white-sided dolphins (*Lagenorhynchus obliquidens*) at the John G. Shedd Aquarium. The Journal of the Acoustical Society of America 109:2391.

Wiens, J. J. and C. H. Graham. 2005. Niche conservatism: Integrating evolution, ecology and conservation biology. Annual Review of Ecological and Evolutionary Systems 36:519-539.

Wiggins, S. 2003. Autonomous acoustic recording packages (ARPs) for long-term monitoring of whale sounds. Marine Technology Society Journal 37:13-22.

Wiggins, S. M. and J. A. Hildebrand. 2007. High-frequency Acoustic Recording Package (HARP) for broad-band, long-term marine mammal monitoring. Pages 551-557 International Symposium on Underwater Technology 2007 and International Workshop on Scientific Use of Submarine Cables & Related Technologies 2007. Institute of Electrical and Electronics Engineers, Tokyo, Japan.

Wilke, F., T. Taniwaki and N. Kuroda. 1953. Phocoenoides and Lagenorhynchus in Japan, with Notes on Hunting. Journal of Mammalogy 34:488-497.

Würsig, B., F. Cipriano and M. Würsig. 1991. Dolphin movement patterns: Information from radio and theodolite tracking studies. Pages 79-111 *in* K. Pryor and K.S. Norris, eds. Dolphin Societies: Discoveries and puzzles. University of California Press, Ltd., Berkeley and Los Angeles, California.

Würsig, B., R. R. Reeves and J. G. Ortega-Ortiz. 2002. Global climate change and marine mammals. Pages 589-608 *in* W.E. Evans and J.A. Raga, eds. Marine mammals: biology and conservation. Kluwer Academic/Plenum Publishers.

Würsig, B. and M. Würsig. 1980. Behavior and ecology of the dusky dolphin, *Lagenorhynchus obscurus*, in the south Atlantic. Fishery Bulletin US 77:871-890.

Wyles, J. S., J. G. Kunkel and A. C. Wilson. 1983. Birds, behavior, and anatomical evolution. Proceedings of the National Academy of Sciences of the United States of America Biological Sciences 80:4394-4397.

Yen, P. P. W., W. J. Sydeman, S. J. Bograd and K. D. Hyrenbach. 2006. Spring-time distributions of migratory marine birds in the southern California Current: Oceanic eddy associations and coastal habitiat hotspots over 17 years. Deep-Sea Research II 53:399-418.

Zhang, D. and M. J. McPhaden. 2006. Decadal variability of the shallow Pacific meridional overturning circulation: Relation to tropical sea surface temperatures in observations and climate change models. Ocean Modelling 15:250-273.