UNIVERSITY OF CALIFORNIA, SAN DIEGO

# Cetacean Population Density in the Eastern Pacific Ocean: Analyzing Patterns with Predictive Spatial Models

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

by

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2005

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This dissertation is dedicated to my family, for teaching me the important things in life.

To Storm, Griffin, and Toby,

**It's a great day to be alive...**
**-Travis Tritt**

To Dad,

**Daddies don't just love their children every now**
**and then. It's a love without end, amen...**
**-George Strait**

To Mom,

**Nothing but blue skies...from now on.**
**-Willie Nelson**

To my hero and big brother, Ryan,

Under an old brass paperweight is my list of things to do today
Go to the bank and the hardware store, put a new lock on the cellar door
I cross 'em off as I get 'em done but when the sun is set
There's still more than a few things I haven't got to yet
Go for a walk, say a little prayer
Take a deep breath of mountain air
Put on my glove and play some catch
It's time that I make time for that
Wade the shore and cast a line
Pick up a long lost friend of mine
Sit on the porch and give my girl a kiss
Start livin', that's the next thing on my list
-Toby Keith

## Acknowledgements

The following people and entities supported me throughout the years. Without them, I would be a very different person and this work would not have been possible.

To begin, I would like to thank my friends for keeping me laughing: E. Ferguson, R. Price, J. Peters, C. Orino, T. Nation, A. Deppe, C. Catton, J. Weinberger, J. Bowles, E. Oleson, J. Laresse, M. Tryon, K. Murray, C. Ridley, S. Mumma, E. LaBrecque, J. Redfern, C. Redfern, J. Goosey, L. Weaver, L. Borick, N. Steward, K. Gardner, S. Mahoney, and J. MacLeod.

I am grateful to L. Conquest, D. DeMaster, M. Dethier, and T. Klinger for pre-SIO inspiration.

My doctoral committee (a.k.a. The Magnificent Seven) provided me with essential guidance, yet gave me a long leash from which to conduct my research. They are J. Barlow, P. Dayton, T. Chereskin, D. Goodman, L. Haff, J. Leichter, and P. Smith. I would especially like to thank J. Barlow for giving me a chance; for his unquestioning and unending confidence in my abilities; for his patience, understanding, and friendship; and for teaching me a thing or two.

I would like to thank the Goodman Lab (past and present) for being wonderful colleagues and friends, for setting a good example of how to navigate through academia in order to achieve a good education, and for providing me with a home away from SIO. Thank you T. Eguchi, D. Gustafson, A. Harting, D. Hennen, G. Himes Boor, L. Schwarz, R. Taylor, S. Taylor, F. Taylor, and E. Ward.

Many people at SWFSC were instrumental in providing me with data, ideas, knowledge, and logistical and computer support throughout graduate school. Thank you for letting me join your team: V. Andreassi, L. Ballance, J. Carretta, S. Chivers, R. Cosgrove, J. Cotton, P. Fiedler, K. Forney, T. Gerrodette, K. Handschuh, R. Holland, A.

Jackson, S. Mesnick, B. Perrin, W. Perryman, R. Pitman, S. Rankin, S. Reilly, B. Taylor, and numerous marine mammal observers.

The following people and entities are in a class of their own. The Utah Public Schools helped get me off to a good start – How else would a Utah girl become an oceanographer? The Friday Harbor Laboratories served as a nursery for my scientific brain. T. Ragen provided me with inspiration to proceed during the dark days of grad school. The NOAA ships *David Starr Jordan*, *McArthur*, and *McArthur II* collected the data that I used in my research. Davey Jones was good to me while I was at sea. The SIO Graduate Student Office and Library always had the answers, and provided them with minimal red tape. Finally, the State of Montana and the State of Solitude are largely responsible for my mental well-being throughout this endeavor.

Funding for my research was provided by the National Science Foundation Graduate Fellowship Program, the Department of Navy, and the Strategic Environmental Research Development Program.

I was the primary researcher and author of all chapters appearing in this dissertation. The co-authors for Chapters Two, Three, Five, and Six directed and supervised the research which forms the basis for those chapters. Chapters Three and Five have been submitted for publication.

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Ferguson, M.C. Quantitative studies of beaked whale habitats: a worldwide review. Dissertation Chapter, University of California, San Diego.

Ferguson, M.C., J. Barlow, S. Reilly, and T. Gerrodette. Predicting Cuvier's (*Ziphius cavirostris*) and *Mesoplodon* beaked whale densities as functions of the environment in the eastern tropical Pacific Ocean. Dissertation Chapter, University of California, San Diego.

Ferguson, M.C. and J. Barlow. Variance estimation for a spatial model of Cuvier's beaked whale density. Dissertation Chapter, University of California, San Diego.

Ferguson, M.C., and J. Barlow. 2003. Addendum: spatial distribution and density of cetaceans in the eastern Pacific Ocean based on summer/fall research vessel surveys in 1986-1996. Southwest Fisheries Science Center Administrative Report LJ-01-04 (Addendum), available from National Marine Fisheries Service, Southwest Fisheries Science Center, NMFS, P.O. Box 271, La Jolla, California 92038. 99 pp.

Ferguson, M.C., and J. Barlow. 2001. Spatial distribution and density of cetaceans in the eastern Pacific Ocean based on summer/fall research vessel surveys in 1986-96. Southwest Fisheries Science Center Administrative Report LJ-01-04, available from National Marine Fisheries Service, Southwest Fisheries Science Center, NMFS, P.O. Box 271, La Jolla, California 92038. 61 pp.

# ABSTRACT OF THE DISSERTATION

## CETACEAN POPULATION DENSITY IN THE EASTERN PACIFIC OCEAN: ANALYZING PATTERNS WITH PREDICTIVE SPATIAL MODELS

BY

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DOCTOR OF PHILOSOPHY IN OCEANOGRAPHY
UNIVERSITY OF CALIFORNIA, SAN DIEGO, 2005
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This dissertation introduces methods to quantitatively analyze data from shipboard line-transect surveys of cetaceans in the eastern Pacific Ocean in order to identify patterns in, and make predictions of, cetacean population density. Chapter One provides an introduction to the research questions, the study area, and the methods used to address the research questions. Chapter Two discusses a stratified line-transect analysis of delphinid (family Delphinidae) and Cuvier's beaked whale (*Ziphius cavirostris*) density based upon data from shipboard surveys conducted during the summer and fall between 1986-1996. Spatial patterns were found in delphinid and Cuvier's beaked whale densities, although the analytical methods limited the spatial resolution of the results to relatively large scales. Chapter Three introduces a method to

predict cetacean density on smaller scales from line-transect survey sighting data by relating delphinid encounter rates (number of groups per unit distance) and group sizes to environmental variables in the eastern tropical Pacific. Areas with the highest predicted delphinid densities were the Gulf of California, the equatorial cold tongue, and coastal waters, including the west coast of the Baja Peninsula and the Costa Rica Dome. Chapter Four is a review of quantitative beaked whale habitat studies conducted worldwide; a common theme pervades all studies: to better understand beaked whale habitat, it is necessary to better understand their prey. In Chapter Five, the methods introduced in Chapter Three are used to predict Cuvier's and *Mesoplodon* beaked whale density in the eastern tropical Pacific Ocean. Results from Chapter Five provide evidence that the standard definition of beaked whale habitat proposed in the past may be too narrow, and that beaked whales may be found from the continental slope to the abyssal plain, in waters ranging from well-mixed to highly stratified. In Chapter Six, variance is estimated for the Cuvier's beaked whale density predictions presented in the previous chapter and the relative importance of the predictor variables that were used to predict encounter rate and group size is examined.

# CHAPTER ONE

# INTRODUCTION

BY

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*"If we could first know* where *we are, and* whither *we are tending,*
*we could better judge* what *to do, and* how *to do it."*
-Abraham Lincoln, 1858

Describing and quantifying patterns in the distribution and abundance of species is a fundamental element in ecology. Pure ecologists seek this information to enhance basic knowledge of ecosystems, addressing the questions of "*where* we are" and "*whither* we are tending." Applied ecologists use basic knowledge to address questions pertaining to the conservation and management of natural resources, creating a context and format that can ultimately inform decision-makers on "*what* to do, and *how* to do it." My research draws from the fields of pure and applied marine ecology, oceanography, mathematics, and statistics. It focuses on cetaceans (whales, dolphins, and porpoises) in the eastern Pacific Ocean, primarily the eastern tropical Pacific (ETP), but with extensions to the California Current and Gulf of California ecosystems. Cetaceans respond to spatial and temporal environmental variability across a range of scales. Therefore, environmental patterns may provide insight into cetacean distribution and abundance, two characteristics of their ecology that must be understood in order to conserve and manage their populations. The goals for my research are threefold: 1.) to examine spatial patterns in cetacean distribution and abundance in the eastern Pacific Ocean; 2.) to use relationships between cetaceans and certain physical and biological components of their environment to derive quantitative spatial predictions of the density of individuals throughout the study area; and 3.) to estimate the variance associated with the density predictions. To begin, this chapter addresses the fundamental question of, Why study spatial patterns in cetacean density? It proceeds to describe the study area, discuss the importance of quantitative models, and present an overview of the remaining chapters in the dissertation.

## Why Study Spatial Patterns in Cetacean Density?

Two factors motivate research into estimating cetacean density in a spatial context. First, understanding how cetacean density varies spatially as a function of the environment provides insight into the characteristics that define cetacean habitat. Second, knowledge of cetacean population densities is critical to decision-makers who must act to reduce, minimize, or eliminate the harmful effects of human activities on these protected species.

Because the ocean is a dynamic environment, spatial patterns referenced to a geographic point on Earth are variable in time. There are numerous examples of environmental variability in the California Current, ETP, and Gulf of California systems across a range of temporal scales that are ecologically relevant to cetaceans. In the California Current, seasonal, interannual, and interdecadal variability are evident in cetacean (Forney and Barlow, 1998) and seabird (Hyrenbach and Veit, 2003) distribution and abundance, copepod community structure (Peterson and Keister, 2003), zooplankton (McGowan *et al.*, 2003; Brinton and Townsend, 2003) and fish (Smith and Moser, 2003) biomass and abundance, kelp demography (Dayton *et al.*, 1999), and in physical circulation patterns (Collins *et al.*, 2003, Bograd and Lynn, 2003), sea surface temperature (McGowan *et al.*, 1998; McGowan *et al.*, 2003), and the existence of red tides (Hayward *et al.*, 1995). There is also evidence of variability due to long-term climate change (Roemmich, 1992; Roemmich and McGowan, 1995). The ETP system is logistically more difficult to study than the California Current system because of its large size and geographic location. Furthermore, most physical and biological time series date back to the late 1970's and therefore do not capture the period before the 1976/77 regime shift (Reilly *et al.*, 2002). Nevertheless, distinct seasonal variability has been detected in the magnitude and location of the Costa Rica Dome (Fiedler, 2002a) and other physical oceanographic phenomena (Fiedler, 1992); and interannual variability is apparent in seabird (Ballance *et al.*, 2002), prey fishes, and squid (Pitman *et al.*, 2002) distributions, and physical oceanographic properties such as sea surface temperature, thermocline depth, and primary productivity (Fiedler and Philbrick, 2002; Fiedler, 2002b). Fiedler (1992) notes that several of the mechanisms for, and manifestations of, seasonal and interannual variability in the ETP are analogous: during March-April or in El Niño years, the South Equatorial Current is weak, the equatorial thermocline slope is flat, and the Equatorial Surface Water is warm, whereas during September-October or in La Niña years, the South Equatorial Current is strong, the equatorial thermocline slope is steep, and the Equatorial Surface Water is cold. The Gulf of California is a distinct ecosystem and will be described separately below. Due to the spatiotemporal variability in pelagic marine ecosystems, it is essential to link spatial variability in cetacean density to the animals' physical and biological environment.

There is no doubt that spatial patterns in cetacean density due to associations with the environment exist, and those associations have been relatively consistent through time. Dolphin habitats in the ETP were described by Au and Perryman (1985). To better understand the effects of environmental variability on dolphin density estimates in the ETP, quantitative studies were conducted by Reilly (1990), Reilly and Fiedler (1990), Reilly and Fiedler (1994), and Reilly *et al.* (2002). In the California Current ecosystem, Forney (1999) and Forney (2000) found quantitative relationships between cetacean sightings and the physical environment. To date, however, no one has created spatial models to quantify cetacean density as a function of the environment. Such a model has bearing on both pure and applied marine ecology because it would help define habitat and it would provide a tool that decision-makers could use to estimate or predict cetacean density in a given location based upon observed environmental characteristics.

## Study Area: Eastern Pacific Ocean

The data that I use to examine spatial patterns in cetacean density were collected across a broad expanse of the eastern Pacific Ocean, bounded by the coasts of North, Central, and South America, extending from the northern border of Washington state, across the open ocean to Hawaii, and angling down to Peru. In total, the study area encompasses approximately 25 million km$^2$, roughly the size of the African continent. The oceanographic diversity within the study area is considerable.

Large (1000+ km) regions in the study area with distinct physical and biological oceanographic signatures may be delineated by the North and South subtropical gyres and the equatorial circulation system (Figure 1.1) (McGowan and Walker, 1993). The North subtropical gyre is driven by the northeast trade winds, which set into motion the westward North Equatorial Current (Figure 1.1). Upon reaching the western boundary of the North Pacific basin, the North Equatorial Current splits, some water returning east along the equator as the North Equatorial Countercurrent, and the remainder continuing the clockwise loop around the North Pacific as the Kuroshio Current, Kuroshio

Extension, North Pacific Current, and the California Current. The California Current closes the loop by joining the waters in the North Equatorial Current. This circulation pattern is mirrored in the southern hemisphere as a counterclockwise loop powered by the southeast trade winds, which fuel the westward South Equatorial Current. The South Equatorial Current feeds the poleward East Australian Current, whose waters mix with the easterly flow of the Antarctic Circumpolar Current, which branches off west of South America and continues towards the equator as the Peru Current. Finally, the Peru Current becomes entrenched in the South Equatorial Current.

The California and Peru Currents are "eastern boundary currents," a type of current known worldwide for creating regions of enhanced productivity due to coastal upwelling. Upwelling is a mechanism in which cold water from depth, which is typically high in nutrients from organic matter sinking down from the euphotic zone (the upper surface of the ocean where sunlight penetrates and fuels photosynthesis for primary production), is forced up to sunlit surface waters, where it becomes available again to primary producers. The increase in primary productivity may be transferred through the food web to cetaceans and other apex predators (Ryther, 1969). Coastal upwelling occurs along coastlines that form eastern boundaries in the ocean as a result of surface waters being pushed offshore by prevailing winds; the void left by the surface waters is filled by water that was originally deeper in the water column.

Upwelling also occurs in the equatorial circulation system as "open ocean upwelling" due to surface waters along the equator diverging towards the poles, allowing water from depth to rise to the surface. Open ocean upwelling is also associated with cyclonic eddies and topographic features such as sea mounts that impede flow of water. In the Gulf of California some upwelling is tidally induced.

The Costa Rica Dome is a prominent region of upwelling in the ETP. The Dome is found off the coast of Central America and is a permanent feature in the region, although its location and magnitude vary predictably throughout the year due to seasonal variability in large-scale wind patterns (Fiedler, 2002a). The Costa Rica Dome is a reliable source of high biological productivity, providing important habitat for large marine predators such as seabirds (Ballance *et al.*, 2002) and cetaceans (Fiedler, 2002a).

The Gulf of California is a narrow (~1100km long by 150km wide), marginal sea located in the northwest of Mexico. A region of large islands (the Midriff Islands, including Angel de la Guarda and Tiburon Island) separate the shallow (~120m deep) northern Gulf from the southern Gulf, where basins deeper than 2000m are found (Guitérrez *et al.*, 2004). Evaporation exceeds precipitation in the Gulf of California, forming waters that are high in salinity (Beron-Vera and Ripa, 2000). The primary forces driving circulation in the Gulf of California are wind stress, air-sea heat exchange, and the Pacific Ocean (via Kelvin waves and tidal forcing) (Beier and Ripa, 1999; Guitérrez *et al.*, 2004; Salas-de-León *et al.*, 2003). The complex bathymetry contributes to complex circulation patterns. Tidal currents and, possibly, breaking internal waves on the sill between the northern and southern basins causes mixing and high biological productivity at the south end of the Midriff Islands (Pegau *et al.*, 2002). Coastal upwelling acts to enhance productivity along the eastern Gulf of California (Lluch-Cota, 2000), and basin-wide eddies located between the Midriff Islands and the mouth of the Gulf act to transport phytoplankton from productive waters into deeper regions of the

Gulf (Pegau *et al.*, 2002). One characteristic oceanographic feature of the Gulf of California is a large-scale seasonally reversing gyre located in the northern Gulf, with cyclonic circulation during the summer months and anticyclonic circulation during the winter months (Beier and Ripa, 1999; Carillo *et al.*, 2002).

In the realm of physical oceanography, regions with similar properties of temperature and salinity are referred to as "water masses" (water masses of the ETP are discussed in Chapters Three and Five). Similarly, biological oceanographers define "biogeographic provinces" as regions with consistent assemblages of species: in a given biogeographic province, certain species tend to occur together. The California Current ecosystem exhibits spatial and temporal variability on much smaller scales, in general, than the ETP. This difference is illustrated by comparing the biogeography of the two systems. McGowan and Walker (1993) refer to the ETP (an area of approximately 20 million $km^2$) as a biogeographic province with a unique assemblage of species. By contrast, species from four different biogeographic provinces inhabit the California Current system, which is a mere $10^6 km^2$ in area, and is described as a region where "There is a strong inflow of cold low-salinity water from the north and of warm salty water from the south, and temperate waters are stirred in along the entire outer periphery in a series of quasi-permanent meanders and mesoscale eddies" (McGowan and Walker, 1993). McGowan and Walker (1993) assert that diversity in the California Current system is maintained by the physics of advective stirring and mixing of species from waters located north, west, and south.

## Quantitative Ecological Models: Utility and Limitations

The goal of an ecological model is to make inferences from a sample to a population, with emphasis on repeatability and precision (Burnham and Anderson, 1998). Recognizing that the "true" state of nature has infinite dimension, we seek an approximation to the real world in an ecological model (Burnham and Anderson, 1998). The utility of an ecological model lies in extracting a signal, or recognizable pattern, from noise (unexplainable variation) in order to better understand certain aspect of the ecosystem. Ecological models can be qualitative or quantitative, mechanistic or predictive. The models that I will introduce in the following chapters are quantitative predictive models of cetacean density.

Pace (2001) provides an insightful discussion about the utility and limitations of predictive and mechanistic models. He divulges that "One criticism of predictive approaches is that predictions can be based on poor understanding and still yield statistically significant correlations. For example, a good prediction of the number of priests in North American cities could probably be obtained by counting the number of painters in phonebooks." Mathematics is particularly good at finding patterns, but the ecologist must ask, "Is this pattern ecologically meaningful?" Pace (2001) acknowledges that predictive models and mechanistic models should ideally act in concert:

> Better understanding can lead to better models facilitating better predictions, but this relationship is not absolute. We cannot define all the mechanisms of aquatic systems and hope to build models based on a complete understanding of all parts. Mechanistic research may not contribute to prediction, even though science is often pursued as if the only way to build valid predictions was through detailed studies. Experience suggests instead that key mechanisms need to be collected into relatively condensed models. This is where prediction and understanding come together. Condensed models work because they capture critical processes that drive aquatic systems.

Because of the propensity for the ETP, California Current, and Gulf of California ecosystems to undergo spatial and temporal variability across a range of scales, it is important to refrain from overextending the reach of the predictive models of cetacean distribution and density presented in subsequent chapters. All were built from data collected in well-defined areas during the summer and fall seasons between 1986-1990 and 1993. Applying the models to other seasons or areas should proceed with extreme caution; nevertheless, they may provide clues about cetacean-environment relationships in unsurveyed seasons or regions. As more data becomes available for these ecosystems in future years, model evaluation undoubtedly will be an interesting and educational endeavor that may lead to better mechanistic understandings of the ecosystems.

## Overview of Chapters Two through Six

Chapter Two, "Geographic Patterns in Density of Dolphins (Family Delphinidae) and Cuvier's Beaked Whales (*Ziphius cavirostris*) in the Eastern Pacific Ocean from a Stratified Line-Transect Analysis," reports on geographically-stratified conventional line-transect analyses (Appendix A) of dolphins and Cuvier's beaked whales, examining large-scale patterns in cetacean distribution and density, and identifying the limits to the spatial resolution of this type of analysis. Chapter Three, "Spatial Models of Delphinid (Family Delphinidae) Encounter Rate and Group Size in the Eastern Tropical Pacific Ocean," focuses on the methods used to build a spatial model for predicting dolphin density as a function of environmental variables, identifying the strengths and weaknesses of the approach. Chapter Four, "Quantitative Studies of Beaked Whale

Habitats: A Worldwide Review," is a review of quantitative beaked whale habitat studies that have been conducted to date throughout the world; it provides a context for Chapter Five, "Predicting Cuvier's (*Ziphius cavirostris*) and *Mesoplodon* Beaked Whale Densities as Functions of the Environment in the Eastern Tropical Pacific Ocean," which describes the results from a generalized additive model used to predict the density of Cuvier's beaked whales and *Mesoplodon* beaked whales in the ETP based on oceanographic and geographic variables. The final chapter, Chapter Six, "Variance Estimation for a Spatial Model of Cuvier's Beaked Whale Density," discusses a parametric bootstrap method for estimating the variance in density predictions derived from the gam-based analysis used for Cuvier's beaked whale in Chapter Five.

## Acknowledgements

Thank you to Erin Oleson, Jay Barlow, and Rebecca, Sunny, and Fred Taylor for reviewing an earlier version of this chapter and providing helpful comments on how I could improve it. I would also like to thank my dad for lending me Carl Sandburg's book "*Abraham Lincoln: The Prairie Years and The War Years*," which is where I first came across the opening quote several years ago. Dad, I might return the book one day; until then, you can see it when you come visit!

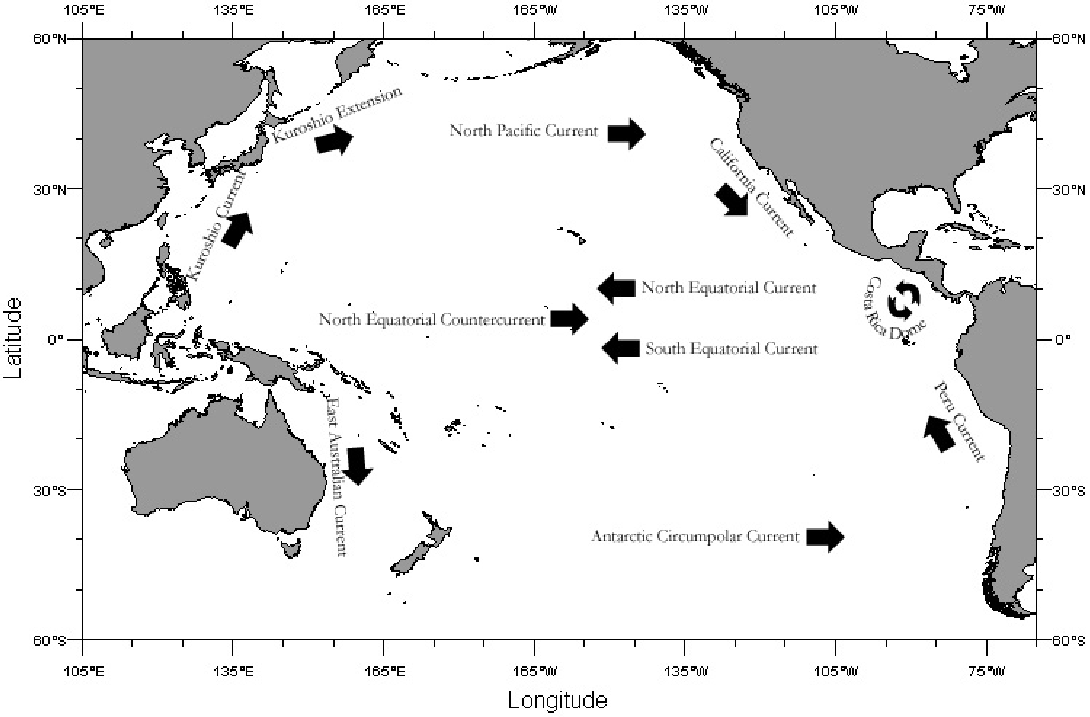

Figure 1.1 Schematic representation of the dominant surface currents comprising the North and South Pacific subtropical gyres.

## Appendix 1A: Line-Transect Methods for Estimating Cetacean Density

The research presented in the following pages relies upon cetacean line-transect data collected during visual shipboard surveys. A standard equation is used to make inferences about cetacean population density or abundance based upon the sample data from the line-transect survey (Buckland *et al.*, 2001). As a new graduate student, I spent a considerable amount of time reading scientific papers describing the line-transect survey methods and the ensuing analytical methods, and I spent even more time trying to get an intuitive understanding for how the inference works. The typical exposition of line-transect methodology in scientific writing is written for someone who does not need to read it, the explanation is often not beginner-friendly. My goal here is to provide an explanation of line-transect methodology that will sharpen the reader's intuition about the inference.

In a shipboard visual line-transect survey, a ship steams along a pre-specified path called a "trackline" while visual observers scan the ocean for cetaceans. When a group or an individual is spotted, data are collected on the taxonomic identification of the cetacean, the number of individuals in the group, the bearing to the group from the ship ($\theta$), and the distance from the horizon to the group (Figure 1A). Using the bearing from the ship and distance from the horizon, the perpendicular distance from the trackline to the group ($x$) can be computed (Lerczak and Hobbs, 1998). The standard line-transect equation for estimating density incorporates the data as follows (Buckland *et al.*, 2001):

$$\hat{D}_i = \frac{n_i \cdot s_i \cdot f_i(0)}{2 \cdot L \cdot g_i(0)}, \qquad (1)$$

where

$i$ = species

$n$ = number of sightings,
$s$ = mean group size,
$f(0)$ = sighting probability density at zero perpendicular distance, or equivalently,
= 1/effective strip width, or $1/ESW$
$L$ = length of transect line completed, and

$g(0)$ = probability of seeing a group located directly on the trackline.

To estimate abundance instead of density, multiply the numerator by the survey area. The sighting parameters $f(0)$ and $g(0)$ are required because not all cetaceans within sighting range are detected. Animals may be missed because they are submerged and therefore not able to be sighted (availability bias) or they may be at the surface but the visual observers did not detect them (perception bias). The parameter $f(0)$ is often the most difficult to intuit, and is perhaps better understood in terms of its reciprocal, $ESW^{-1}$.

The effective strip width is measured from the trackline to the distance $x^*$, where the number of groups detected beyond $x^*$ equals the number of groups *not* detected between the ship and $x^*$ (Figure 2A). Therefore, if observers searched a strip from the trackline to $x^*$ and detected every group in that strip, they would detect the same number of groups as if they had searched from the trackline to the limit of the range of sight ($x_{max}$), yet missed a fraction of the groups in the arena. $ESW$ indicates the proportion of the range of sight that was confidently searched. The raw data on the perpendicular sighting distances $x$ are required to estimate the parameters for the sighting probability density $f(x)$ in order to estimate $f(0)$ or, equivalently, $ESW$. The parameter $g(0)$ may be thought of as a scaling factor to compensate for the proportion of groups that are never seen; the idea is that a group located directly on the trackline is the easiest to see, so, if it is missed, then there exists a constant fraction of groups that are missed, regardless of their distance from the ship. Fitting all of the terms in Eqn 1 together, the product of $n$ and $s$ results in the observed number of individuals, the product of $ESW^{-1}$ (or $f(0)$) and $L$ in the denominator results in an area, and the term $g(0)$ in the denominator corrects for biases due to the constant proportion of animals that are missed at any distance from the trackline.

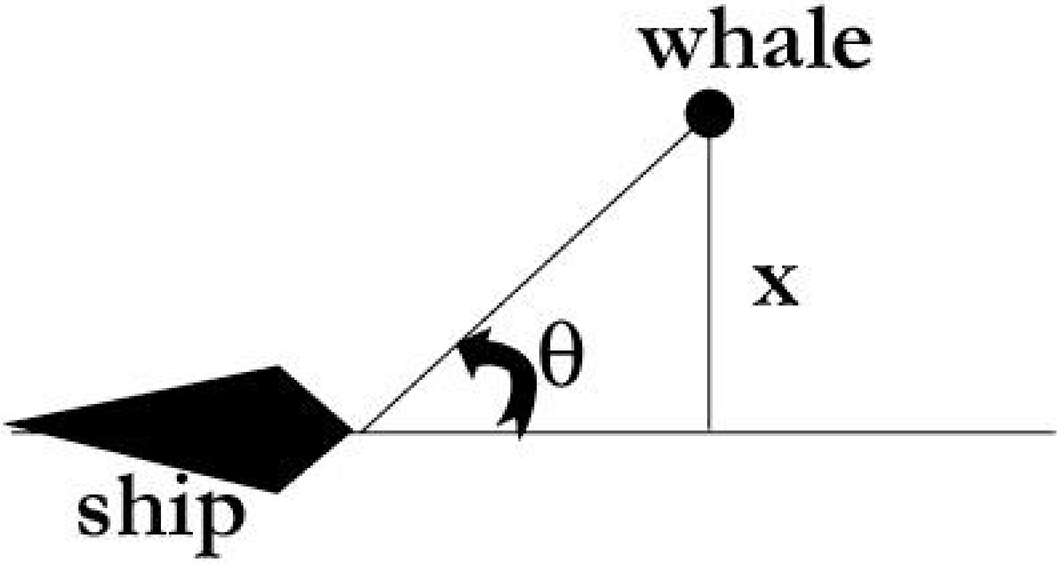

Figure 1A. Data collected during shipboard line-transect surveys for cetaceans include the bearing (θ) from the ship to the sighting and the distance from the horizon to the sighting, from which the perpendicular distance (x) from the sighting to the ship can be computed.

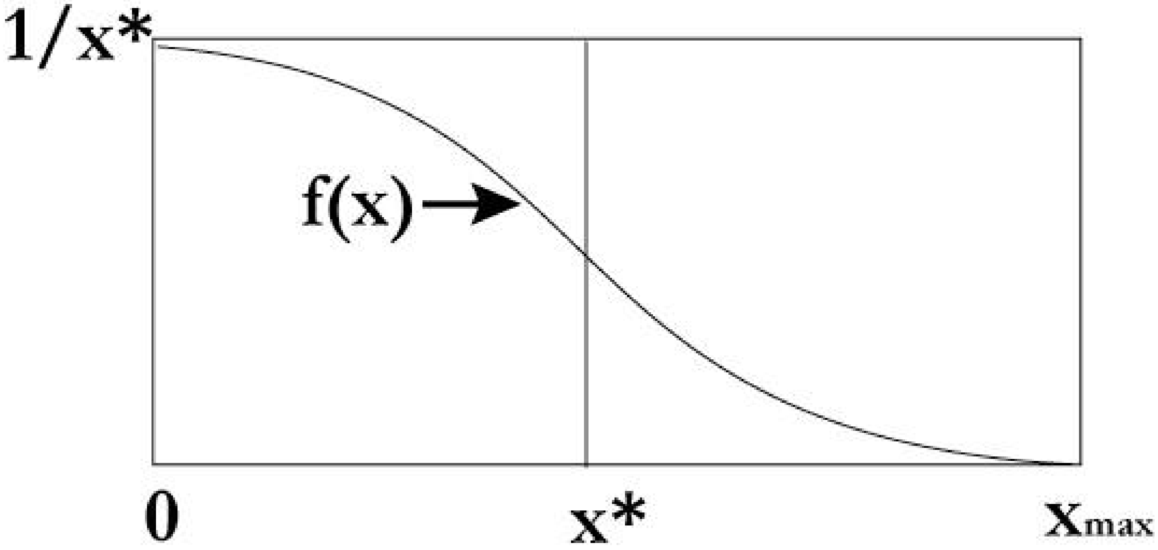

Figure 2A. The shape of the curve represents the number of cetacean sightings at different distances (x) from the trackline. The point $x_{max}$ represents the limit to the range of sight. The effective strip width, x*, is the point at which the number of groups detected beyond x* (represented by the area beneath the curve to the right of x*) equals the number of groups not detected between the ship and x* (the area above the curve to the left of x*). The y-axis is scaled so that the intercept, *f(0)*, equals 1/x*; therefore, the area under the curve equals the area in the rectangle with width x* and height 1/x*, which are both equal to 1.0, making the function *f(x)* a proper probability density function.

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# CHAPTER TWO

# GEOGRAPHIC PATTERNS IN DENSITY OF DOLPHINS (FAMILY DELPHINIDAE) AND CUVIER'S BEAKED WHALES (*ZIPHIUS CAVIROSTRIS*) IN THE EASTERN PACIFIC OCEAN FROM A STRATIFIED LINE-TRANSECT ANALYSIS

BY

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## Abstract

We estimate meso-scale density (number animals/unit area) and abundance of delphinids (dolphins; species from the family Delphinidae) and Cuvier's beaked whale (*Ziphius cavirostris*) in the eastern Pacific Ocean during the summer and fall based on nine research vessel surveys conducted between 1986 and 1996. The study area encompasses over 25 million km$^2$, ranging from the tip of the Olympic Peninsula to the north, the coast of Peru to the south, and the Hawaiian archipelago to the west. We used line-transect methods to analyze the data, relying on published estimates of the line-transect parameters $f(0)$ and $g(0)$. We stratified geographically by 5-degree squares of latitude and longitude, pooling adjacent squares as necessary to achieve adequate samples sizes. Dolphin densities ranged over three orders of magnitude, but the densities in most regions were between 100 and 1000 animals per 1000km$^2$. Densities of Cuvier's beaked whale ranged from 0.3 to 38.0 animals per 1000km$^2$. Our results show that areas of high dolphin and Cuvier's beaked whale density coincide with regions of high productivity in the study area, namely, the waters of the equatorial cold tongue (extending westward from the coast of Peru), the southern Gulf of California, and waters along the west coast of the Americas.

## Introduction

Oceanic ecosystems are heterogeneous and dynamic. Physical and biological pattern and diversity in the ocean are evident across a continuum of spatial and temporal scales. Examining marine systems on the appropriate scales is crucial for understanding how they function. Haury *et al.* (1978) wrote:

> It is evident that organisms have aggregated, patchy distributions of abundance on a wide variety of space and time scales….Further,…patchiness strongly affects our efforts to obtain estimates of the abundance of organisms and our ability to detect significant spatial and temporal changes in abundance. It is therefore of great importance that we understand its nature, causes, and effects.

These heterogeneous and variable characteristics are reflected in the patterns of cetacean (whale, dolphin, and porpoise) abundance and distribution. In this study we examine the distribution and abundance of one family (Delphinidae) and one species (Cuvier's beaked whale, *Ziphius cavirostris*) of cetacean in a large section of the eastern Pacific Ocean to identify patterns in their distribution and abundance, and to assess the limitations in the spatial resolution of a stratified line-transect analysis.

Cuvier's beaked whale and several species of pelagic delphinids (dolphins; species from the family Delphinidae), in addition to billfish, oceanic sharks, tunas, and sperm whales, comprise the pelagic marine apex predators who prey primarily on fish and squid (Ryther, 1969; Smith and Casey, 1992). Considerable diversity exists among these large marine predators - the delphinid family alone includes 34 to 36 species from 17 to 19 genera worldwide (LeDuc, 2002), with diverse behaviors, morphologies, vocalizations, prey, geographical distributions, habitats, and life history traits among the species. In addition to sharing food resources, the population densities of many members of this guild are very difficult to measure and have changed markedly due to years of direct (fishing) or indirect (*e.g.*, bycatch in fisheries) exploitation. Furthermore, as endotherms and active predators living where the primary component of the physical environment (seawater) is an efficient conductor of heat, dolphins and Cuvier's beaked whales have relatively high energy requirements. Therefore, it is reasonable to expect greater densities of these cetaceans in productive marine environments such as coastal regions and upwelling zones than in unproductive waters typified by the middle of subtropical gyres (Ryther, 1969).

Taken together, patterns in the estimated densities of delphinids and Cuvier's beaked whale may provide insight into the distributions and relative abundances of other apex predators in the pelagic marine guild. Standing alone, the delphinid analysis lays the foundation for defining habitats of individual delphinid species: knowledge of environmental conditions where a given species is absent but where other delphinids are found is as important to defining habitat as knowledge of the environment where the species is present. Furthermore, from the sampling perspective, the combined species of delphinids is the group with the greatest sample size from the line-transect surveys used in the analysis and, therefore, provides an optimistic test of the spatial resolution of a stratified line-transect analysis. Understanding the distribution and abundance of Cuvier's beaked whale is important in its own right because this species seems to be particularly sensitive to anthropogenic noise in the oceans (Anon., 2001; Peterson, 2003), and the detrimental effects of activities such as seismic surveys and active sonar may be lessened with more information on the ecology of this species. In addition, Cuvier's beaked whales are infrequently sighted, resulting in a relatively small sample size and a challenging test of the spatial resolution of a stratified line-transect analysis.

The data for this study were collected on nine marine mammal survey cruises conducted between 1986 and 1996 by the Southwest Fisheries Science Center (SWFSC), a division of NOAA Fisheries. Cetacean abundance from the 1986-1996 cruises have been estimated previously for large areas within the eastern Pacific (Barlow 1988, Wade and Gerrodette 1993, Barlow 1995, Barlow and Gerrodette 1996, Gerrodette and Palacios 1996, Barlow 1997, and Koski *et al.* 1998). Our investigation considers a broader oceanographic and geographic range than did any of the previous analyses of the SWFSC research vessel survey data, and the spatial resolution of our analysis is comparable to the smallest scale previously explored. We divided a survey area encompassing over 25 million km$^2$ of ocean into approximately 5$^o$ squares. Adjacent squares were pooled, as needed, to achieve an adequate sample size, and the resulting geographic strata varied from 27,250km$^2$ to 927,000km$^2$ in the delphinid analysis and 27,250 to 3,090,000km$^2$ in the Cuvier's beaked whale analysis. For each stratum we estimated dolphin and Cuvier's beaked whale density and abundance. In comparison, Wade and Gerrodette (1993) divided the 19 million km$^2$ of the eastern tropical Pacific study region into four geographic strata for their analysis; Gerrodette and Palacios (1996) divided 3.9 million km$^2$ of EEZ (Exclusive Economic Zone) waters off Central and South America into seven strata; Barlow and Gerrodette (1996) considered all of the waters up to 555km offshore of California to be a single stratum; Barlow's (1997) analysis comprised two strata, the boundaries extending 555km offshore of California and Oregon/Washington; and Koski *et al.* (1998) partitioned approximately 500,000 $km^2$ of waters in and around the Point Mugu Sea Range off California into strata ranging from approximately 3,400 $km^2$ to 209,000 $km^2$.

**Methods**

Data for this analysis were collected by visual observers during nine NMFS cruises over a period of eleven years: five annual Monitoring of Porpoise Stocks (MOPS) cruises from 1986 to 1990; the California Marine Mammal Survey (CAMMS) of 1991; two Population of *Delphinus* Stocks (PODS) cruises, in 1992 and 1993; and the Oregon, California and Washington Line-transect Experiment (ORCAWALE) of 1996. All surveys were conducted between late July and early December of each survey year.

## Study Area

The geographic extent of the combined survey area is vast. It stretches from the tip of the Olympic Peninsula in Washington at $49^{o}N$ to the coastal waters of Peru at $13^{o}S$, and from the west coast of the Americas to the Hawaiian archipelago at $155^{o}W$ (Figure 2.1). Survey effort off the western coast of the United States was limited to the waters within 555km of the continent. The study area covers a wide range of oceanographic diversity. For example, oligotrophic waters in the subtropical gyres have relatively low productivity, whereas the California Current, Peru/Chile Current, and the equatorial cold tongue are highly productive (Ryther, 1969).

## Field Methods

Survey methods remained relatively consistent throughout this 11-year study period (Kinzey *et al.* 2000). Two NOAA ships were used in most years: the 52m David Starr Jordan and the 53m McArthur. On both ships, the observation height from the flying bridge deck was approximately 10m above the sea surface. The primary team consisted of two observers (port and starboard) who searched through 25x150 Fujinon pedestal-mounted binoculars (typically from 10° on the opposite side of the bow to 90° abeam on their respective sides) and one center observer who searched by unaided eyes and (occasionally) with 7x50 hand-held binoculars. The center observer also was responsible for recording search effort and sighting data. Observers rotated among these three observation stations for two hours and then had two hours off-duty. The vessels surveyed pre-determined transect lines at approximately 18.5 km/h during daylight hours (dawn to dusk). Typically when a marine mammal was sighted, the observer team went off-effort and directed the ship towards the animal(s) to obtain species identity and group size estimates. Immediately after making a sighting (and before turning the ship), the bearing angle from the bow to the animal (or the approximate center of a group of animals) was measured using a protractor at the base of the 25x binoculars, and the distance to the animal (or group) was estimated from measurements based on ocular reticles (Lerczak and Hobbs 1998).

Periods of search effort were carefully documented. Conditions that affected search were recorded at the start of effort and whenever conditions changed; these included Beaufort sea state, presence of rain or fog, and (starting in 1991) swell height and air clarity (estimated visibility in nautical miles to a conspicuous cue).

Sightings were classified to the lowest taxonomic level(s) possible based on observable field characteristics (*i.e.*, size, shape, behavior, color). For spotted (*Stenella attenuata*) and spinner (*Stenella longirostris*) dolphins, sightings were often classified into subspecies or stocks. Some sightings could not be identified to species, in which case the sighting was assigned the lowest taxonomic category for which identification was certain (*e.g., Delphinus* sp. or "unidentified dolphin or porpoise"). For groups with multiple species, observers independently estimated the percentage of each species present; we averaged these percentages to estimate the number of each species present in a group. Overall group size also was estimated independently by each observer as "best," "high," and "low" estimates of the numbers present. Species percentages and group sizes were transcribed from individual field notes into the data record at the end of each day by the cruise leader; to maintain independence, observers were not allowed to compare their estimates with each other.

A few changes in protocol were implemented during this time period, but these are not expected to significantly affect the collection of the basic line-transect data. A conditionally independent observer position was used intermittently after 1991 to measure the fraction of animals missed by the primary team; however, the independent observer was instructed not to announce a sighting until the animal(s) had passed abeam and clearly had been missed by the primary observer team. Data from the independent observers were used to derive the correction factors that were used for estimating perception bias (Barlow 1995), but otherwise are not used in this report. In 1991, a computer-based data entry system replaced a system based on paper forms. In 1996, approximately one third of the effort was conducted in passing mode (*i.e.,* not turning towards or approaching cetaceans), and a new data field was recorded to indicate survey mode.

Surveys were designed to cover different geographic areas in each year. The cruises in 1986-90 were designed to estimate the abundance and trends in abundance for all dolphin populations that were affected by tuna fishing in the eastern tropical Pacific. The survey in 1991 was designed to estimate the abundance of all cetaceans in waters offshore of California. The surveys in 1992 and 1993 were designed to estimate the abundance of the central and northern stocks (respectively) of common dolphins *(Delphinus delphis*) in the eastern Pacific. The survey in 1996 was designed to estimate the abundance of all cetaceans in waters offshore of California, Oregon, and Washington. Despite different goals, all sightings of cetaceans were consistently recorded on all cruises. Most groups sighted within 5.6km of the transect lines were approached for species identification and group size estimation.

## Analytical Methods

Data were analyzed using line-transect methods (Buckland *et al.*, 2001). We estimated density ($D_{aij}$) for each species/group size combination in each geographic stratum as:

$$D_{aij} = \frac{n_{aij} S_{aij} f_{ik}(0)}{2 L_a g_{ik}(0)}$$

where $j$ = species

$k$ = species group to which species $j$ belongs (where applicable),

$i$ = group size stratum (where applicable),

$a$ = geographic stratum,

$n$ = number of sightings,

$S$ = mean group size,

$f(0)$ = sighting probability density at zero perpendicular distance, or equivalently,

= 1/effective strip width,

$L$ = length of transect line completed, and

$g(0)$ = probability of seeing a group located directly on the trackline.

We calculated density estimates for each species separately based on estimates for the line-transect parameters $f(0)$ and $g(0)$ given in Tables 2.1 and 2.2. We relied upon published estimates of the line-transect parameters whenever possible. In estimates of species density and abundance in geographic strata for which estimates of $f(0)$ and $g(0)$ were not available, we substituted a published value estimated for another species with similar sighting characteristics and behavior in the same geographic location, or in a region of similar sighting conditions. In most cases, we used the truncation distances and ranges of Beaufort sea state conditions that were used in the original estimates of the line-transect parameters, as reported in the literature; exceptions are noted in Table 2.1. We stratified by group size only those species and regions for which the published line-transect parameters were based on size-stratified data (Tables 2.1 and 2.2). When more than one published *f(0)* estimate existed for a given species (and group size stratum, where applicable) in a particular region, we computed a single *f(0)* value as the weighted average of the available *f(0)* estimates, with weights corresponding to the total number of sightings used to derive the original published estimates of *f(0)*. For those weighted averaged values of *f(0)*, we computed coefficients of variation (CV's) from the weighted average of the variance estimates for the relevant published *f(0)* estimates, with number of sightings used as weights. For all estimates of *g(0)*, and for those cases when only a single *f(0)* estimate was available in the literature for a given species/region/group size stratum, we used the CV estimates reported in the original publication.

For the delphinid analysis, the density estimates for individual species within each geographic stratum were summed to produce an estimate of total dolphin density per stratum. We refer to a "species" as either a biological species or a management stock, depending on how the sightings were initially classified and recorded by visual observers in the field. The following delphinid species were included in the analysis: spotted dolphin (*Stenella attenuata* and *S. attenuata graffmani*), spinner dolphin (*Stenella longirostris, S. longirostris orientalis, S. longirostris centroamericana*), long-beaked or Baja neritic common dolphin (*Delphinus capensis*), short-beaked or offshore common dolphin (*Delphinus delphis*), striped dolphin (*Stenella coeruleoalba*), rough-toothed dolphin (*Steno bredanensis*), bottlenose dolphin (*Tursiops truncatus*), Risso's dolphin (*Grampus griseus*), Pacific white-sided dolphin (*Lagenorhynchus obliquidens*), Fraser's dolphin (*Lagenodelphis hosei*), northern right whale dolphin (*Lissodelphis borealis*), melon-headed whale (*Peponocephala electra*), pygmy killer whale (*Feresa attenuata*), false killer whale (*Pseudorca crassidens*), killer whale (*Orcinus orca*), long-finned pilot whale (*Globicephala melas*), short-finned pilot whale (*Globicephala macrorhynchus*), and the ubiquitous "dolphin, unidentified to species." Spotted dolphin stock boundaries are defined in Dizon *et al.* (1994), and common dolphin (*Delphinus* spp.) stock boundaries are defined in Perrin *et al.* (1985).

Although previous analyses of these line-transect data have been relatively consistent in their methods, one notable difference exists. Visual observers in the field were asked to provide three estimates of group size for each sighting, namely a "low," a "high," and a "best" estimate. When multiple observers recorded group size estimates, the observers' best estimates are typically averaged and used to compute mean group size. Sightings for which only a low estimate of group size was recorded were handled differently by Wade and Gerrodette (1993), Barlow and Gerrodette (1996), and Barlow (1997). To calculate mean group size, Wade and Gerrodette (1993) excluded sightings for which only a low estimate was reported, but they included those sightings in $n_{jk}$ and in their estimation of $f_{jk}(0)$. By contrast, if no best estimates were recorded for a given sighting, Barlow and Gerrodette (1996) and Barlow (1997) used an average of the low estimates to compute mean group size. This difference in methods tends to bias Barlow and Gerrodette's (1996) and Barlow's (1997) estimates of mean group size low compared with those of Wade and Gerrodette (1993). Because smaller groups are more likely to be "lost" and therefore be represented only by a low estimate, the true mean group size is likely to be somewhere in between those estimated as described above. We used Wade and Gerrodette's method of excluding sightings with only a low estimate for estimating mean group size in our analysis of the MOPS, PODS 92, and PODS 93 survey data collected south of 30°N. For consistency with previous analyses, we used Barlow and Gerrodette's (1996) and Barlow's (1997) method of averaging the low size estimates when best estimates were lacking for the CAMMS 91, ORCAWALE 96, and PODS 93 survey data collected north of 30$^{o}$N.

Because analyses of beaked whale abundance are limited to good survey conditions (Beaufort 2 or better) and because there are many more sightings of dolphins than beaked whales, we needed to use larger geographic strata for Cuvier's beaked whales than for dolphins. For delphinids, density estimates were calculated for individual 5$^{o}$ squares, excluding the area covered by land, when at least 700km of transect line had been surveyed in each square. Squares located along the extreme margins of the study area and in which there was less than 100km of survey effort were not included in the analysis. For all other squares with low survey effort, we pooled their data with that of neighboring squares to the east or west until the total length of transect line surveyed in the merged squares was at least 700km (Figures 2.2 and 2.3). Using this criterion, the greatest number of merged 5$^{o}$ squares was three. We chose to pool Beaufort 0-5 squares in an east-west direction because we felt that this reflected the trends in the dominant oceanographic parameters at the relevant scales in the study area. Similarly, for Cuvier's beaked whales, we merged squares so that the habitat within each geographic stratum was likely to be consistent and the total length of transect surveyed was at least 700km (Figures 2.4 and 2.5). The rectangular strata in the southern waters of the study area are consistent with the characteristics of the equatorial currents and the Peru/Chile Current. The Gulf of California was divided into a northern component and a southern component for all analyses, regardless of Beaufort restrictions, because the survey and habitat conditions north of 30$^{o}$N are generally considerably different from those to the south.

To facilitate data analysis, we divided the entire study area into four regions based on overlapping survey grids among the cruises and, presumably, similar sighting conditions and probabilites (Figure 2.6). The "northern region," offshore of Washington and Oregon , is bounded by the 130°W meridian to the west and the 45th and 50th parallels to the south and north, respectively. The northern region was surveyed only during the ORCAWALE cruise in 1996. The "middle region," offshore of southern Oregon, California, and northern Baja California, is bounded by the 135°W and 130°W meridians to the west and the 45th and 30th parallels to the north and south. The middle region contains areas surveyed during the ORCAWALE 96, PODS 93, and CAMMS 91 cruises. The third geographic block comprises the eastern tropical Pacific Ocean (ETP), extending from 30°N to 15°S, and from 160°W to the coastline of Central and South America. It was surveyed during the annual MOPS cruises of 1986-1990 and the PODS cruises of 1992 and 1993. The fourth and smallest region encompasses the waters of the Gulf of California, which were surveyed only once, during the PODS 1993 cruise. To estimate density for a given species, the same *f(0)* and *g(0)* values were used in all of the geographic strata contained within a given geographic region (Tables 2.1 and 2.2).

## Results

The four regions in the study area include all or part of ninety-six 5° squares. More than 200,000km of transect line were surveyed in Beaufort 0 to 5 seas (Figure 2.2) and 30,000km in Beaufort 0 to 2 conditions (Figure 2.4) during the nine cruises included in this analysis. The geographic strata around the western and southern margins of the survey area contained the lowest survey effort, whereas the coastal strata in all regions had the heaviest survey effort. It is important to remember that the results listed below reflect only those sightings that occurred under the specific Beaufort sea state and truncation distance restrictions determined by the use of a given estimate of *f(0)*; some sightings were not included in this analysis because they did not fall within those constraints.

Dolphins were found in every stratum surveyed (Figure 2.7). Dolphin densities ranged over three orders of magnitude, from 10.5 to 2,342 individuals/1000 $km^2$ (Table

2.3). The majority of the study area was covered by densities in the range of 100-1000 individuals per thousand km$^2$. The highest densities were encountered in the southern California bight; off the west coast of the Baja Peninsula; in the Gulf of California; in two strata due south of Guatemala (in the vicinity of the Costa Rica Dome); and in a 5$^o$ band of tropical waters anchored at the coast of Ecuador and continuing out to 100$^o$W. The strata with the lowest densities of dolphins included the coastal waters off Washington and British Columbia, and the subtropical gyre waters around the Hawaiian Islands. The three most abundant species in the northern region were the Risso's dolphin, northern right whale dolphin, and Pacific white-sided dolphin; in the middle region they were the short-beaked common dolphin, Dall's porpoise, and Pacific white-sided dolphin; in the Gulf of California, they were the long-beaked common dolphin, Risso's dolphin, and bottlenose dolphin; and in the ETP they were the short-beaked common dolphin, offshore spotted dolphin, and striped dolphin (see Ferguson and Barlow, 2003, for density estimates of each species of delphinid).

Cuvier's beaked whale sightings covered the map, with the conspicuous exception of the coastal waters off South America, waters west of the Baja Peninsula, and oligotrophic waters of the north subtropical gyre (Figure 2.8, Table 2.4). Cuvier's beaked whale density estimates are greatest for the southern Gulf of California (38 whales/1000 km$^2$) and a band along the equator bounded by 5$^o$N and S (13 whales/1000 km$^2$). The lowest estimate of Cuvier's beaked whale density (0.3 whales/1000 km$^2$) came from the stratum located at the southwestern tip of the Baja Peninsula.

The best test of the results from our stratified analysis was to compare the delphinid abundance estimate for the entire ETP region (computed by summing delphinid abundances over all strata in the region) with the corresponding estimate from Wade and Gerrodette (1993), computed by summing abundance estimates for all species of delphinids in the region. Bias-correction factors were applied to both estimates of total delphinid abundance because they were computed by geographically stratifying the survey region, estimating abundance in each stratum, and then summing the abundances across strata. Using this "additive" method to estimate abundance results in a different value than one computed from an unstratified analysis because the line-transect equation for estimating abundance is a ratio, and the expected value of a ratio is not equivalent to the ratio of expected values (Appendix A in Ferguson and Barlow, 2001). Furthermore, the amount of the bias is not equal between studies because the geographic strata that we used were different from Wade and Gerrodette's (1993). (A similar comparison for Cuvier's beaked whales in the ETP was not conducted because Wade and Gerrodette (1993) assumed that $g(0)$ equaled 1.0 in their analysis, which is much larger than the $g(0)$ value that we used.) We found that our estimate of delphinid abundance was approximately 12% smaller than Wade and Gerrodette's (1993). There are three possible reasons for this difference. First, to compute average group size, Wade and Gerrodette (1993) averaged observer group size estimates for each sighting and then averaged group size estimates for all sightings in each of the four geographic strata in their analysis. Our methods for computing average group size for each sighting are comparable to Wade and Gerrodette's (1993), but the final group size estimates that we used in our analysis were averaged over 76 smaller geographic strata whose combined area approximately equaled the total area in the Wade and Gerrodette (1993) analysis. Using Wade and Gerrodette's (1993) method, the occasional extremely large group size will weigh more heavily in the final estimate, resulting in a relatively higher group size estimate for the line-transect equation. Second, the $f(0)$ values from Ferguson and Barlow (2001) that we incorporated into our analysis correspond to the weighted mean $f(0)$ values from each of the four geographic strata in Wade and Gerrodette (1993). Spatial variation in $f(0)$ could produce a detectable difference between our estimate of total delphinid abundance for the ETP and that of Wade and Gerrodette (1993). Third, we incorporated two additional years of data (1991 and 1993) into our ETP analysis, and that could affect the resulting abundance estimates.

## Discussion

Our analyses clearly show that both delphinds and Cuvier's beaked whale densities vary geographically by at least two orders of magnitude. These patterns appear to have some features that are consistent between groups, and the features seem to be correlated with the oceanography in the study area. Some of the greatest dolphin densities were found close to shore, with a gradual decline in density offshore. This density gradient is likely tied to physical processes that affect the biological productivity in the marine ecosystems. For example, nearshore environments receive nutrient inputs from the continents due to river runoff and winds. In low- to mid-latitude ecosystems where sunlight is plentiful and nutrients limit photosynthesis, fertilization from the land can boost primary productivity, which may increase the amount of energy (prey) available to dolphins and other upper trophic level predators. In addition, the nearshore waters of our study area comprise the eastern boundary current ecosystems of the California Current to the north and the Peru/Chile Current to the south. The interactions between eastern boundary currents, topography, and prevailing winds induce zones of upwelling along the coast. In upwelling regions, nutrient-rich, cold, deep waters rise to the euphotic zone, where they become available to the photosynthetic organisms at the base of marine food webs (Ryther, 1969). Thus, upwelling is a second method through which coastal waters are fertilized, enhancing primary productivity, and potentially making more energy available to cetaceans and other large predators. The equatorial region and the Gulf of Californa are other areas where upwelling is common. The mechanisms driving upwelling in these waters differ from that which acts along the coast, but the result is the same: nutrients necessary for photosynthesis are introduced into the euphotic zone, increasing the rate of primary production, which may result in more prey for the upper trophic level predators. It is likely that the latitudinal band of high delphinid and Cuvier's beaked whale density are linked to the highly productive equatorial ecosystem. Advection of waters into the study area by the California and Peru Currents is yet another source of nutrient input that is concentrated along the continental margins. Waters further offshore and outside of the influence of the equatorial currents are typically limited by nutrient availability. Unlike the coastal and equatorial regions, these oligotrophic waters do not have a reliable outside source of nutrients, and therefore cannot sustain the quantity or diversity of organisms found in nearshore and upwelling regions. The relatively impoverished state of these waters is reflected in the low densities of delphinids and Cuvier's beaked whales in the western half of our study area. In contrast, low observed delphinid densities off the coast of Oregon and Washington coincide with a shift in the composition of marine ecosystems: in northern waters, porpoises fill the niches that dolphins occupy in the tropics and subtropics. The reasons for this taxonomic shift is unknown.

One caveat to applying methods of stratification to examine cetacean distribution and density on small spatial scales is that sample sizes become very small when areas are stratified. For this reason, it is important not to interpret the low abundance or absence of animals in a particular stratum as evidence that they do not occur there. Some common sense must be applied in interpreting patterns on this scale, and particular attention should be paid to the estimates of precision for each abundance estimate. Pooling some of the $5^{o}$ squares, sacrificing spatial resolution for greater precision, was warranted for some strata in the delphinid analysis and for all strata in the Cuvier's analysis. In the delphinid case, this was especially appropriate near the margins of the study areas, where sampling effort was least. We pooled squares to combine areas that tend to be most similar in oceanography. We anticipate that our understanding of meso-scale patterns of cetacean density can be greatly improved by modeling species distributions as functions of oceanographic and geographic variables.

In examining the geographic patterns in delphinid densities, it is important to keep in mind that the current abundance of many populations probably does not represent their historic carrying capacities, primarily due to their incidental catch in tuna purse seine and artisanal gillnet fisheries in the region (Palacios and Gerrodette, 1996). The tuna purse seine fishery originated near the coast of Mexico and expanded southward and offshore, particularly around 10ºN latitude. The artisanal gillnet fishery is largely coastal. Depletion of delphinid stocks by these fisheries is therefore likely to be greatest in coastal areas. The patterns that we see now, with higher densities in coastal areas, may have once been even more pronounced.

## Acknowledgements

We would like to thank the visual observers, cruise leaders, crew, and officers who have devoted many days, months, or years at sea to collecting the wealth of data that we used in this study. Tim Gerrodette was chief scientist on many of these cruises, and we thank him for providing access to and help analyzing these data. Furthermore, we are grateful to Frank Stone, Ernie Young, the Department of Navy, and the National Science Foundation Graduate Fellowship Program for providing financial support for this study. We would also like to thank J. Carretta for introducing us to Surfer, T. Norris, and S. Reilly for their helpful comments on earlier drafts of this paper, and Summer Martin for providing the software to plot the tracklines and sightings.

The dissertation author was the primary researcher and author of Chapter Two, and the co-author listed directed and supervised the research which forms the basis for this chapter.

Table 2.1. Beaufort ranges, group size strata, and *g(0)* values used to estimate cetacean density.

| | All Regions | | | |
|---|---|---|---|---|
| **Species or classification** | **Beaufort** | **g(0)** | **CV( g(0))** | **Reference** |
| *Stenella attenuata* (offshore) | | | | |
| Northeastern spotted | 0-5 | 1 | 0 | 1, 2 |
| Western/southern spotted | 0-5 | 1 | 0 | 1, 2 |
| *Stenella attenuata graffmani* | 0-5 | 1 | 0 | 1, 2 |
| *Stenella attenuata* (unid. Subsp.) | | | | |
| NE, < 100 n mi from shore | 0-5 | 1 | 0 | 1, 2 |
| NE, > 100 n mi from shore | 0-5 | 1 | 0 | 1, 2 |
| W/S, < 100 n mi from shore | 0-5 | 1 | 0 | 1, 2 |
| W/S, > 100 n mi from shore | 0-5 | 1 | 0 | 1, 2 |
| *Stenella longirostris orientalis* | 0-5 | 1 | 0 | 1, 2 |
| *Stenella longirostris* hybrid | 0-5 | 1 | 0 | 1, 2 |
| *Stenella longirostris centroamericana* | 0-5 | 1 | 0 | 1, 2 |
| *Stenella longirostris* (unid. Subsp.) | 0-5 | 1 | 0 | 1, 2 |
| *Delphinus capensis* (long-beak) | | | | |
| group size 1-20 | 0-5 | 0.77 | 0.14 | 1, 2 |
| group size 21-100 | 0-5 | 1 | 0 | 1, 2 |
| group size 100+ | 0-5 | 1 | 0 | 1, 2 |
| *Delphinus delphis* (short-beak) | | | | |
| group size 1-20 | 0-5 | 0.77 | 0.14 | 1, 2 |
| group size 21-100 | 0-5 | 1 | 0 | 1, 2 |
| group size 100+ | 0-5 | 1 | 0 | 1, 2 |
| Northern common dolphin (ETP only) | 0-5 | 1 | 0 | 1, 2 |
| Central common dolphin (ETP only) | 0-5 | 1 | 0 | 1, 2 |
| Southern common dolphin (ETP only) | 0-5 | 1 | 0 | 1, 2 |
| *Delphinus delphis* (unid. Subsp.) | | | | |
| group size 1-20 | 0-5 | 0.77 | 0.14 | 1, 2 |
| group size 21-100 | 0-5 | 1 | 0 | 1, 2 |
| group size 100+ | 0-5 | 1 | 0 | 1, 2 |
| within northern stock boundaries | 0-5 | 1 | 0 | 1, 2 |
| within central stock boundaries | 0-5 | 1 | 0 | 1, 2 |
| within southern stock boundaries | 0-5 | 1 | 0 | 1, 2 |

1. Barlow 1995
2. Barlow 1997

Table 2.1, continued. Beaufort ranges, group size strata, and *g(0)* values used to estimate cetacean density.

| | **All Regions** | | | |
|---|---|---|---|---|
| **Species or classification** | **Beaufort** | **g(0)** | **CV( g(0))** | **Reference** |
| *Stenella coeruleoalba* | | | | |
| group size 1-20 | 0-5 | 0.77 | 0.14 | 1, 2 |
| group size 21-100 | 0-5 | 1 | 0 | 1, 2 |
| group size 100+ | 0-5 | 1 | 0 | 1, 2 |
| *Steno bredanensis* | 0-5 | 1 | 0 | 1, 2 |
| *Tursiops truncatus* | | | | |
| group size 1-20 | 0-5 | 0.74 | 0.39 | 1, 2 |
| group size 20+ | 0-5 | 1 | 0 | 1, 2 |
| *Grampus griseus* | | | | |
| group size 1-20 | 0-5 | 0.74 | 0.39 | 1, 2 |
| group size 20+ | 0-5 | 1 | 0 | 1, 2 |
| *Lagenorhynchus obliquidens* | | | | |
| group size 1-20 | 0-5 | 0.77 | 0.14 | 1, 2 |
| group size 21-100 | 0-5 | 1 | 0 | 1, 2 |
| group size 100+ | 0-5 | 1 | 0 | 1, 2 |
| *Lagenodelphis hosei* | 0-5 | 1 | 0 | 1, 2 |
| *Lissodelphis borealis* | | | | |
| group size 1-20 | 0-5 | 0.77 | 0.14 | 1, 2 |
| group size 21-100 | 0-5 | 1 | 0 | 1, 2 |
| group size 100+ | 0-5 | 1 | 0 | 1, 2 |
| *Peponocephala electra* | 0-5 | 1 | 0 | 1, 2 |
| *Feresa attenuata* | 0-5 | 1 | 0 | 1, 2 |
| *Pseudorca crassidens* | 0-5 | 1 | 0 | 1, 2 |
| *Orcinus orca* | | | | |
| group size 1-20 | 0-5 | 0.74 | 0.39 | 1, 2 |
| group size 20+ | 0-5 | 1 | 0 | 1, 2 |

1. Barlow 1995
2. Barlow 1997

Table 2.1, continued. Beaufort ranges, group size strata, and *g(0)* values used to estimate cetacean density.

| **Species or classification** | **All Regions** | | | |
|---|---|---|---|---|
| | **Beaufort** | **g(0)** | **CV( g(0))** | **Reference** |
| *Globicephala* spp. | | | | |
| group size 1-20 | 0-5 | 0.74 | 0.39 | 1, 2 |
| group size 20+ | 0-5 | 1 | 0 | 1, 2 |
| *Globicephala macrorhynchus* | | | | |
| group size 1-20 | 0-5 | 0.74 | 0.39 | 1, 2 |
| group size 20+ | 0-5 | 1 | 0 | 1, 2 |
| unid. Dolphin | | | | |
| group size 1-20 | 0-5 | 0.77 | 0.14 | 1, 2 |
| group size 21-100 | 0-5 | 1 | 0 | 1, 2 |
| group size 100+ | 0-5 | 1 | 0 | 1, 2 |
| *Ziphius cavirostris* | 0-2 | 0.23 | 0.35 | 3 |

1. Barlow 1995
2. Barlow 1997
3. Barlow 1999

Table 2.2. Truncation distances, group size strata, and *f(0)* values used to estimate cetacean density.

| | **Northern Region** | | | |
|---|---|---|---|---|
| **Species or classification** | **f(0) (1/km)** | **CV( f(0))** | **Truncation Distance (km)** | **Reference** |
| *Stenella attenuata* (offshore) | | | | |
| Northeastern spotted | | | | |
| Western/southern spotted | | | | |
| *Stenella attenuata graffmani* | | | | |
| *Stenella attenuata* (unid. Subsp.) | | | | |
| NE, < 100 n mi from shore | | | | |
| NE, > 100 n mi from shore | | | | |
| W/S, < 100 n mi from shore | | | | |
| W/S, > 100 n mi from shore | | | | |
| *Stenella longirostris orientalis* | | | | |
| *Stenella longirostris* hybrid | | | | |
| *Stenella longirostris centroamericana* | | | | |
| *Stenella longirostris* (unid. Subsp.) | | | | |
| *Delphinus capensis* (long-beak) | | | | |
| group size 1-20 | 1.567 | 0.348 | 3.7 | 1 |
| group size 21-100 | 0.519 | 0.186 | 3.7 | 1 |
| group size 100+ | 0.503 | 0.193 | 3.7 | 1 |
| *Delphinus delphis* (short-beak) | | | | |
| group size 1-20 | 1.567 | 0.348 | 3.7 | 1 |
| group size 21-100 | 0.519 | 0.186 | 3.7 | 1 |
| group size 100+ | 0.503 | 0.193 | 3.7 | 1 |
| Northern common dolphin (ETP only) | | | | |
| Central common dolphin (ETP only) | | | | |
| Southern common dolphin (ETP only) | | | | |
| *Delphinus delphis* (unid. Subsp.) | | | | |
| group size 1-20 | 1.567 | 0.348 | 3.7 | 1 |
| group size 21-100 | 0.519 | 0.186 | 3.7 | 1 |
| group size 100+ | 0.503 | 0.193 | 3.7 | 1 |
| within northern stock boundaries | | | | |
| within central stock boundaries | | | | |
| within southern stock boundaries | | | | |

1. Barlow 1997

Table 2.2, continued. Truncation distances, group size strata, and *f(0)* values used to estimate cetacean density.

| | **Middle Region** | | | |
|---|---|---|---|---|
| **Species or classification** | **f(0) (1/km)** | **CV( f(0))** | **Truncation Distance (km)** | **Reference** |
| *Stenella attenuata* (offshore) | | | | |
| Northeastern spotted | | | | |
| Western/southern spotted | | | | |
| *Stenella attenuata graffmani* | | | | |
| *Stenella attenuata* (unid. Subsp.) | | | | |
| NE, < 100 n mi from shore | | | | |
| NE, > 100 n mi from shore | | | | |
| W/S, < 100 n mi from shore | | | | |
| W/S, > 100 n mi from shore | | | | |
| *Stenella longirostris orientalis* | | | | |
| *Stenella longirostris* hybrid | | | | |
| *Stenella longirostris centroamericana* | | | | |
| *Stenella longirostris* (unid. Subsp.) | | | | |
| *Delphinus capensis* (long-beak) | | | | |
| group size 1-20 | 1.667 | 0.289 | 3.7 | 1 |
| group size 21-100 | 0.783 | 0.24 | 3.7 | 1 |
| group size 100+ | 0.518 | 0.222 | 3.7 | 1 |
| *Delphinus delphis* (short-beak) | | | | |
| group size 1-20 | 1.667 | 0.289 | 3.7 | 1 |
| group size 21-100 | 0.783 | 0.24 | 3.7 | 1 |
| group size 100+ | 0.518 | 0.222 | 3.7 | 1 |
| Northern common dolphin (ETP only) | | | | |
| Central common dolphin (ETP only) | | | | |
| Southern common dolphin (ETP only) | | | | |
| *Delphinus delphis* (unid. Subsp.) | | | | |
| group size 1-20 | 1.667 | 0.289 | 3.7 | 1 |
| group size 21-100 | 0.783 | 0.24 | 3.7 | 1 |
| group size 100+ | 0.518 | 0.222 | 3.7 | 1 |
| within northern stock boundaries | | | | |
| within central stock boundaries | | | | |
| within southern stock boundaries | | | | |

1. Weighted average of values from Barlow and Gerrodette (1996) and Barlow (1997)

Table 2.2, continued. Truncation distances, group size strata, and *f(0)* values used to estimate cetacean density.

| **Species or classification** | **Gulf of California** | | | |
|---|---|---|---|---|
| | **f(0) (1/km)** | **CV( f(0))** | **Truncation Distance (km)** | **Reference** |
| *Stenella attenuata* (offshore) | 0.31 | 0.09 | 7.71 | 3 |
| Northeastern spotted | | | | |
| Western/southern spotted | | | | |
| *Stenella attenuata graffmani* | 0.31 | 0.09 | 7.71 | 3 |
| *Stenella attenuata* (unid. Subsp.) | 0.31 | 0.09 | 7.71 | 3 |
| NE, < 100 n mi from shore | | | | |
| NE, > 100 n mi from shore | | | | |
| W/S, < 100 n mi from shore | | | | |
| W/S, > 100 n mi from shore | | | | |
| *Stenella longirostris orientalis* | 0.28 | 0.09 | 7.71 | 3 |
| *Stenella longirostris* hybrid | | | | |
| *Stenella longirostris centroamericana* | | | | |
| *Stenella longirostris* (unid. Subsp.) | | | | |
| *Delphinus capensis* (long-beak) | | | | |
| group size 1-20 | 0.45 | 0.184 | 6.09 | 2 |
| group size 21-100 | 0.45 | 0.184 | 6.09 | 2 |
| group size 100+ | 0.45 | 0.184 | 6.09 | 2 |
| *Delphinus delphis* (short-beak) | | | | |
| group size 1-20 | 0.41 | 0.121 | 5.54 | 2 |
| group size 21-100 | 0.41 | 0.121 | 5.54 | 2 |
| group size 100+ | 0.41 | 0.121 | 5.54 | 2 |
| Northern common dolphin (ETP only) | | | | |
| Central common dolphin (ETP only) | | | | |
| Southern common dolphin (ETP only) | | | | |
| *Delphinus delphis* (unid. Subsp.) | | | | |
| group size 1-20 | 0.426 | 0.15 | 5.76 | 1 |
| group size 21-100 | 0.426 | 0.15 | 5.76 | 1 |
| group size 100+ | 0.426 | 0.15 | 5.76 | 1 |
| within northern stock boundaries | | | | |
| within central stock boundaries | | | | |
| within southern stock boundaries | | | | |

1. Weighted average of values in Gerrodette and Palacios 1996
2. Gerrodette and Palacios 1996. CV's and truncation distances came from Gerrodette's original output files.
3. Gerrodette and Palacios 1996. CV's and truncation distances are approximate because the original data were unavailable.

Table 2.2, continued. Truncation distances, group size strata, and *f(0)* values used to estimate cetacean density.

| | ETP Region | | | |
|---|---|---|---|---|
| **Species or classification** | **f(0) (1/km)** | **CV( f(0))** | **Truncation Distance (km)** | **Reference** |
| *Stenella attenuata* (offshore) | | | | |
| Northeastern spotted | 0.287 | 0.11 | 5.5 | 1 |
| Western/southern spotted | 0.468 | 0.13 | 5.5 | 1 |
| *Stenella attenuata graffmani* | 0.397 | 0.24 | 5.5 | 1 |
| *Stenella attenuata* (unid. Subsp.) | | | | |
| NE, < 100 n mi from shore | 0.291 | 0.125 | 5.5 | 2 |
| NE, > 100 n mi from shore | 0.287 | 0.11 | 5.5 | 1 |
| W/S, < 100 n mi from shore | 0.463 | 0.138 | 5.5 | 2 |
| W/S, > 100 n mi from shore | 0.468 | 0.13 | 5.5 | 1 |
| *Stenella longirostris orientalis* | 0.387 | 0.17 | 5.5 | 1 |
| *Stenella longirostris* hybrid | 0.541 | 0.13 | 5.5 | 1 |
| *Stenella longirostris centroamericana* | 0.387 | 0.17 | 5.5 | 1 |
| *Stenella longirostris* (unid. Subsp.) | 0.448 | 0.151 | 5.5 | 2 |
| *Delphinus capensis* (long-beak) | | | | |
| group size 1-20 | 0.447 | 0.37 | 5.5 | 1 |
| group size 21-100 | 0.447 | 0.37 | 5.5 | 1 |
| group size 100+ | 0.447 | 0.37 | 5.5 | 1 |
| *Delphinus delphis* (short-beak) | | | | |
| group size 1-20 | | | | |
| group size 21-100 | | | | |
| group size 100+ | | | | |
| Northern common dolphin (ETP only) | 0.447 | 0.37 | 5.5 | 1 |
| Central common dolphin (ETP only) | 0.351 | 0.36 | 5.5 | 1 |
| Southern common dolphin (ETP only) | 0.669 | 0.21 | 5.5 | 1 |
| *Delphinus delphis* (unid. Subsp.) | | | | |
| group size 1-20 | | | | |
| group size 21-100 | | | | |
| group size 100+ | | | | |
| within northern stock boundaries | 0.447 | 0.37 | 5.5 | 1 |
| within central stock boundaries | 0.351 | 0.36 | 5.5 | 1 |
| within southern stock boundaries | 0.669 | 0.21 | 5.5 | 1 |

1. Wade and Gerrodette 1993
2. Weighted average of values from Wade and Gerrodette 1993

Table 2.2, continued. Truncation distances, group size strata, and *f(0)* values used to estimate cetacean density.

| | **Northern Region** | | | |
|---|---|---|---|---|
| **Species or classification** | **f(0) (1/km)** | **CV( f(0))** | **Truncation Distance (km)** | **Reference** |
| *Stenella coeruleoalba* | | | | |
| group size 1-20 | 1.567 | 0.348 | 3.7 | 1 |
| group size 21-100 | 0.519 | 0.186 | 3.7 | 1 |
| group size 100+ | 0.503 | 0.193 | 3.7 | 1 |
| *Steno bredanensis* | | | | |
| *Tursiops truncatus* | | | | |
| group size 1-20 | | | | |
| group size 20+ | | | | |
| *Grampus griseus* | | | | |
| group size 1-20 | 0.366 | 0.167 | 3.7 | 1 |
| group size 20+ | 0.366 | 0.167 | 3.7 | 1 |
| *Lagenorhynchus obliquidens* | | | | |
| group size 1-20 | 1.567 | 0.348 | 3.7 | 1 |
| group size 21-100 | 0.519 | 0.186 | 3.7 | 1 |
| group size 100+ | 0.503 | 0.193 | 3.7 | 1 |
| *Lagenodelphis hosei* | | | | |
| *Lissodelphis borealis* | | | | |
| group size 1-20 | 1.567 | 0.348 | 3.7 | 1 |
| group size 21-100 | 0.519 | 0.186 | 3.7 | 1 |
| group size 100+ | 0.503 | 0.193 | 3.7 | 1 |
| *Peponocephala electra* | | | | |
| *Feresa attenuata* | | | | |
| *Pseudorca crassidens* | | | | |
| *Orcinus orca* | | | | |
| group size 1-20 | 0.366 | 0.167 | 3.7 | 1 |
| group size 20+ | 0.366 | 0.167 | 3.7 | 1 |

1. Barlow 1997

Table 2.2, continued. Truncation distances, group size strata, and *f(0)* values used to estimate cetacean density.

| | **Middle Region** | | | |
|---|---|---|---|---|
| **Species or classification** | **f(0) (1/km)** | **CV( f(0))** | **Truncation Distance (km)** | **Reference** |
| *Stenella coeruleoalba* | | | | |
| group size 1-20 | 1.667 | 0.289 | 3.7 | 1 |
| group size 21-100 | 0.783 | 0.24 | 3.7 | 1 |
| group size 100+ | 0.518 | 0.222 | 3.7 | 1 |
| *Steno bredanensis* | | | | |
| *Tursiops truncatus* | | | | |
| group size 1-20 | 0.661 | 0.405 | 3.7 | 1 |
| group size 20+ | 0.373 | 0.199 | 3.7 | 1 |
| *Grampus griseus* | | | | |
| group size 1-20 | 0.661 | 0.405 | 3.7 | 1 |
| group size 20+ | 0.373 | 0.199 | 3.7 | 1 |
| *Lagenorhynchus obliquidens* | | | | |
| group size 1-20 | 1.667 | 0.289 | 3.7 | 1 |
| group size 21-100 | 0.783 | 0.24 | 3.7 | 1 |
| group size 100+ | 0.518 | 0.222 | 3.7 | 1 |
| *Lagenodelphis hosei* | | | | |
| *Lissodelphis borealis* | | | | |
| group size 1-20 | 1.667 | 0.289 | 3.7 | 1 |
| group size 21-100 | 0.783 | 0.24 | 3.7 | 1 |
| group size 100+ | 0.518 | 0.222 | 3.7 | 1 |
| *Peponocephala electra* | | | | |
| *Feresa attenuata* | | | | |
| *Pseudorca crassidens* | | | | |
| *Orcinus orca* | | | | |
| group size 1-20 | 0.661 | 0.405 | 3.7 | 1 |
| group size 20+ | 0.373 | 0.199 | 3.7 | 1 |

1. Weighted average of values from Barlow and Gerrodette (1996) and Barlow (1997)

Table 2.2, continued. Truncation distances, group size strata, and *f(0)* values used to estimate cetacean density.

| | Gulf of California | | | |
|---|---|---|---|---|
| **Species or classification** | **f(0) (1/km)** | **CV( f(0))** | **Truncation Distance (km)** | **Reference** |
| *Stenella coeruleoalba* | | | | |
| group size 1-20 | | | | |
| group size 21-100 | | | | |
| group size 100+ | | | | |
| *Steno bredanensis* | 1.69 | 0.255 | 3.89 | 1 |
| *Tursiops truncatus* | | | | |
| group size 1-20 | 1.15 | 0.154 | 4.22 | 1 |
| group size 20+ | 1.15 | 0.154 | 4.22 | 1 |
| *Grampus griseus* | | | | |
| group size 1-20 | 1.31 | 0.21 | 3.52 | 1 |
| group size 20+ | 1.31 | 0.21 | 3.52 | 1 |
| *Lagenorhynchus obliquidens* | | | | |
| group size 1-20 | | | | |
| group size 21-100 | | | | |
| group size 100+ | | | | |
| *Lagenodelphis hosei* | | | | |
| *Lissodelphis borealis* | | | | |
| group size 1-20 | | | | |
| group size 21-100 | | | | |
| group size 100+ | | | | |
| *Peponocephala electra* | | | | |
| *Feresa attenuata* | | | | |
| *Pseudorca crassidens* | | | | |
| *Orcinus orca* | | | | |
| group size 1-20 | 0.379 | 0.31 | 5.5 | 2 |
| group size 20+ | 0.379 | 0.31 | 5.5 | 2 |

1. Gerrodette and Palacios 1996. CV's and truncation distances came from Gerrodette's original output files.
2. Wade and Gerrodette 1993

Table 2.2, continued. Truncation distances, group size strata, and *f(0)* values used to estimate cetacean density.

| | ETP Region | | | |
|---|---|---|---|---|
| **Species or classification** | **f(0) (1/km)** | **CV( f(0))** | **Truncation Distance (km)** | **Reference** |
| *Stenella coeruleoalba* | | | | |
| group size 1-20 | 0.588 | 0.09 | 5.5 | 2 |
| group size 21-100 | 0.588 | 0.09 | 5.5 | 2 |
| group size 100+ | 0.588 | 0.09 | 5.5 | 2 |
| *Steno bredanensis* | 1.124 | 0.19 | 5.5 | 2 |
| *Tursiops truncatus* | | | | |
| group size 1-20 | 0.519 | 0.22 | 5.5 | 2 |
| group size 20+ | 0.519 | 0.22 | 5.5 | 2 |
| *Grampus griseus* | | | | |
| group size 1-20 | 1.058 | 0.38 | 5.5 | 2 |
| group size 20+ | 1.058 | 0.38 | 5.5 | 2 |
| *Lagenorhynchus obliquidens* | | | | |
| group size 1-20 | 1.724 | 0.255 | 3.7 | 1 |
| group size 21-100 | 0.905 | 0.24 | 3.7 | 1 |
| group size 100+ | 0.528 | 0.239 | 3.7 | 1 |
| *Lagenodelphis hosei* | 0.33 | 0.32 | 5.5 | 2 |
| *Lissodelphis borealis* | | | | |
| group size 1-20 | | | | |
| group size 21-100 | | | | |
| group size 100+ | | | | |
| *Peponocephala electra* | 0.242 | 0.36 | 5.5 | 2 |
| *Feresa attenuata* | 0.707 | 0.2 | 5.5 | 2 |
| *Pseudorca crassidens* | 1.163 | 0.75 | 5.5 | 2 |
| *Orcinus orca* | | | | |
| group size 1-20 | 0.379 | 0.31 | 5.5 | 2 |
| group size 20+ | 0.379 | 0.31 | 5.5 | 2 |

1. Barlow and Gerrodette 1996
2. Wade and Gerrodette 1993

Table 2.2, continued. Truncation distances, group size strata, and *f(0)* values used to estimate cetacean density.

| | Northern Region | | | |
|---|---|---|---|---|
| **Species or classification** | **f(0) (1/km)** | **CV( f(0))** | **Truncation Distance (km)** | **Reference** |
| *Globicephala* spp. | | | | |
| group size 1-20 | 0.366 | 0.167 | 3.7 | 1 |
| group size 20+ | 0.366 | 0.167 | 3.7 | 1 |
| *Globicephala macrorhynchus* | | | | |
| group size 1-20 | 0.366 | 0.167 | 3.7 | 1 |
| group size 20+ | 0.366 | 0.167 | 3.7 | 1 |
| unid. Dolphin | | | | |
| group size 1-20 | 1.567 | 0.348 | 3.7 | 1 |
| group size 21-100 | 0.519 | 0.186 | 3.7 | 1 |
| group size 100+ | 0.503 | 0.193 | 3.7 | 1 |
| *Ziphius cavirostris* | 0.362 | 0.197 | 3.7 | 1 |

1. Barlow 1997

Table 2.2, continued. Truncation distances, group size strata, and *f(0)* values used to estimate cetacean density.

| | **Middle Region** | | | |
|---|---|---|---|---|
| **Species or classification** | **f(0) (1/km)** | **CV( f(0))** | **Truncation Distance (km)** | **Reference** |
| *Globicephala* spp. | | | | |
| group size 1-20 | 0.661 | 0.405 | 3.7 | 1 |
| group size 20+ | 0.373 | 0.199 | 3.7 | 1 |
| *Globicephala macrorhynchus* | | | | |
| group size 1-20 | 0.661 | 0.405 | 3.7 | 1 |
| group size 20+ | 0.373 | 0.199 | 3.7 | 1 |
| unid. Dolphin | | | | |
| group size 1-20 | 1.667 | 0.289 | 3.7 | 1 |
| group size 21-100 | 0.783 | 0.24 | 3.7 | 1 |
| group size 100+ | 0.518 | 0.222 | 3.7 | 1 |
| *Ziphius cavirostris* | 0.366 | 0.17 | 3.7 | 1 |

1. Weighted average of values from Barlow and Gerrodette (1996) and Barlow (1997)

Table 2.2, continued. Truncation distances, group size strata, and *f(0)* values used to estimate cetacean density.

| | Gulf of California | | | |
|---|---|---|---|---|
| **Species or classification** | **f(0) (1/km)** | **CV( f(0))** | **Truncation Distance (km)** | **Reference** |
| *Globicephala* spp. | | | | |
| group size 1-20 | | | | |
| group size 20+ | | | | |
| *Globicephala macrorhynchus* | | | | |
| group size 1-20 | 0.63 | 0.32 | 4.53 | 1 |
| group size 20+ | 0.63 | 0.32 | 4.53 | 1 |
| unid. Dolphin | | | | |
| group size 1-20 | 0.4 | 0.091 | 7.71 | 2 |
| group size 21-100 | 0.4 | 0.091 | 7.71 | 2 |
| group size 100+ | 0.4 | 0.091 | 7.71 | 2 |
| *Ziphius cavirostris* | 0.91 | 0.19 | 3.57 | 2 |

1. Gerrodette and Palacios 1996. CV's and truncation distances are approximate because the original data were unavailable.

2. Gerrodette and Palacios 1996. CV's and truncation distances came from Gerrodette's original output files.

Table 2.2, continued. Truncation distances, group size strata, and *f(0)* values used to estimate cetacean density.

| | ETP Region | | | |
|---|---|---|---|---|
| **Species or classification** | **f(0) (1/km)** | **CV( f(0))** | **Truncation Distance (km)** | **Reference** |
| *Globicephala* spp. | | | | |
| group size 1-20 | 0.541 | 0.13 | 5.5 | 1 |
| group size 20+ | 0.541 | 0.13 | 5.5 | 1 |
| *Globicephala macrorhynchus* | | | | |
| group size 1-20 | 0.541 | 0.13 | 5.5 | 1 |
| group size 20+ | 0.541 | 0.13 | 5.5 | 1 |
| unid. Dolphin | | | | |
| group size 1-20 | 0.559 | 0.248 | 3.7 | 1 |
| group size 21-100 | 0.559 | 0.248 | 3.7 | 1 |
| group size 100+ | 0.559 | 0.248 | 3.7 | 1 |
| *Ziphius cavirostris* | 0.369 | 0.16 | 3.71 | 2 |

1. Wade and Gerrodette 1993
2. Barlow and Gerrodette 1996

Table 2.3. Estimated density (# individuals per 1000 km$^2$), abundance, and CV of dolphins (family Delphinidae) in the eastern Pacific Ocean based on 1986-1996 summer/fall research vessel surveys.

| geographic stratum | estimated density | estimated abundance | CV |
|---|---:|---:|---|
| 22 & 23 | 71.57 | 17,697.00 | 0.45 |
| 34 | 81.78 | 3,172.00 | 0.48 |
| 35 & 36 | 157.18 | 71,619.00 | 0.43 |
| 46 | 712.48 | 89,802.00 | 0.32 |
| 47 & 48 | 607.15 | 297,737.00 | 0.26 |
| 58 | 1,617.33 | 215,974.00 | 0.25 |
| 59 | 549.43 | 140,808.00 | 0.22 |
| 60 | 143.69 | 37,460.00 | 0.36 |
| 71 | 1,645.58 | 112,490.00 | 0.62 |
| 72 | 191.67 | 51,458.00 | 0.36 |
| 73 | 157.30 | 43,135.00 | 0.36 |
| 85 | 1,093.29 | 231,217.00 | 0.18 |
| 86 | 798.00 | 208,341.00 | 0.45 |
| 87 | 309.34 | 88,364.00 | 0.26 |
| 88 | 143.02 | 40,854.00 | 0.34 |
| 101 & 102 | 761.94 | 187,483.00 | 0.21 |
| 103 | 484.05 | 142,751.00 | 0.17 |
| 104 | 218.91 | 64,559.00 | 0.17 |
| 105 | 153.42 | 45,246.00 | 0.28 |
| 106 | 295.05 | 87,014.00 | 0.41 |
| 111 & 112 | 10.51 | 6,163.00 | 0.61 |
| 118 | 827.84 | 116,841.00 | 0.41 |
| 119 | 1,258.73 | 344,030.00 | 0.26 |
| 120 | 721.56 | 217,853.00 | 0.18 |
| 121 | 780.61 | 235,682.00 | 0.16 |
| 122 | 417.24 | 125,972.00 | 0.25 |

Table 2.3, continued. Estimated density (# individuals per 1000 km$^2$), abundance, and CV of dolphins (family Delphinidae) in the eastern Pacific Ocean based on 1986-1996 summer/fall research vessel surveys. (The southern Gulf of California (SGoC) stratum listed below corresponds to strata 179, 180, and 181 in Ferguson and Barlow, 2001 and Ferguson and Barlow, 2003.)

| **geographic stratum** | **estimated density** | **estimated abundance** | **CV** |
|---|---|---|---|
| 123 | 468.46 | 141,438.00 | 0.22 |
| 124 | 400.17 | 120,820.00 | 0.45 |
| 125 | 112.47 | 33,957.00 | 0.34 |
| 126 | 512.44 | 154,715.00 | 0.35 |
| 127 | 456.18 | 137,729.00 | 0.29 |
| 128 & 129 | 148.81 | 89,857.00 | 0.31 |
| 130 & 131 | 335.34 | 202,493.00 | 0.57 |
| 137 | 391.81 | 40,938.00 | 0.27 |
| 138 | 604.49 | 125,987.00 | 0.38 |
| 139 | 553.40 | 169,609.00 | 0.26 |
| 140 | 1,003.39 | 307,661.00 | 0.27 |
| 141 | 670.92 | 205,717.00 | 0.18 |
| 142 | 411.50 | 126,175.00 | 0.25 |
| 143 | 525.40 | 161,092.00 | 1.42 |
| 144 | 303.15 | 92,952.00 | 0.45 |
| 145 | 184.16 | 56,468.00 | 0.31 |
| 146 | 296.47 | 90,905.00 | 0.26 |
| 147 | 276.56 | 84,798.00 | 0.36 |
| 148 | 456.25 | 139,895.00 | 0.40 |
| 149 | 154.23 | 47,291.00 | 0.61 |
| 150 & 151 | 281.11 | 172,391.00 | 0.47 |
| 158 | 334.90 | 34,667.00 | 0.27 |
| 159 | 218.10 | 67,254.00 | 0.15 |
| 160 | 269.68 | 83,326.00 | 0.22 |
| 161 | 526.93 | 162,811.00 | 0.75 |
| 162 | 444.56 | 137,361.00 | 0.20 |
| 163 | 832.99 | 257,377.00 | 0.25 |
| 164 | 355.99 | 109,995.00 | 0.30 |
| 165 | 325.37 | 100,534.00 | 0.22 |
| 166 | 111.06 | 34,315.00 | 0.23 |
| 167 | 544.72 | 168,309.00 | 0.36 |
| 168, 169, 170 | 216.06 | 200,276.00 | 0.39 |
| SGoC | 1,627.94 | 171,610.00 | 0.27 |

Table 2.3, continued. Estimated density (# individuals per 1000 km$^2$), abundance, and CV of dolphins (family Delphinidae) in the eastern Pacific Ocean based on 1986-1996 summer/fall research vessel surveys.

| **geographic stratum** | **estimated density** | **estimated abundance** | **CV** |
|---|---|---|---|
| 182 | 338.51 | 9,225.00 | 0.59 |
| 200 | 1,706.57 | 460,530.00 | 0.34 |
| 201 | 1,614.69 | 498,909.00 | 0.32 |
| 202 | 2,342.49 | 723,787.00 | 0.42 |
| 203 | 1,015.95 | 313,909.00 | 0.58 |
| 204 | 663.35 | 204,962.00 | 0.30 |
| 205 | 505.75 | 105,692.00 | 0.21 |
| 206 | 266.39 | 55,671.00 | 0.28 |
| 207 | 585.81 | 181,005.00 | 0.35 |
| 208 | 491.96 | 152,007.00 | 0.27 |
| 209 | 466.11 | 144,020.00 | 0.31 |
| 211 | 442.96 | 128,410.00 | 0.48 |
| 212 | 751.62 | 230,462.00 | 0.30 |
| 213 | 421.52 | 129,247.00 | 0.42 |
| 214 | 240.00 | 73,589.00 | 0.49 |
| 215 & 216 | 192.39 | 117,980.00 | 0.30 |
| 218, 219, 220 | 485.76 | 382,858.00 | 0.67 |

Table 2.4. Estimated density (# individuals per 1000 km$^2$), abundance, and CV of Cuvier's beaked whales (*Ziphius cavirostris* ) in the eastern Pacific Ocean based on 1986-1996 summer/fall research vessel surveys. For strata in which there was only one sighting, CV=1.0 is a minimum estimate of variance, assuming that the sightings follow a Poisson distribution.

| **geographic stratum** | **estimated density** | **estimated abundance** | **CV** |
|---|---|---|---|
| A | 3.10 | 1,991.00 | 0.54 |
| B | 5.40 | 4,299.00 | 0.55 |
| E | 0.30 | 365.00 | 1.00 |
| F | 2.50 | 1,906.00 | 0.62 |
| G | 5.40 | 6,540.00 | 0.58 |
| J | 2.20 | 2,624.00 | 0.71 |
| K | 3.00 | 3,638.00 | 0.82 |
| L | 3.50 | 4,142.00 | 0.52 |
| M | 3.70 | 2,816.00 | 0.60 |
| N | 13.00 | 40,306.00 | 1.00 |
| O | 7.30 | 18,094.00 | 0.71 |
| Southern Gulf of California | 38.00 | 4,004.00 | 0.73 |

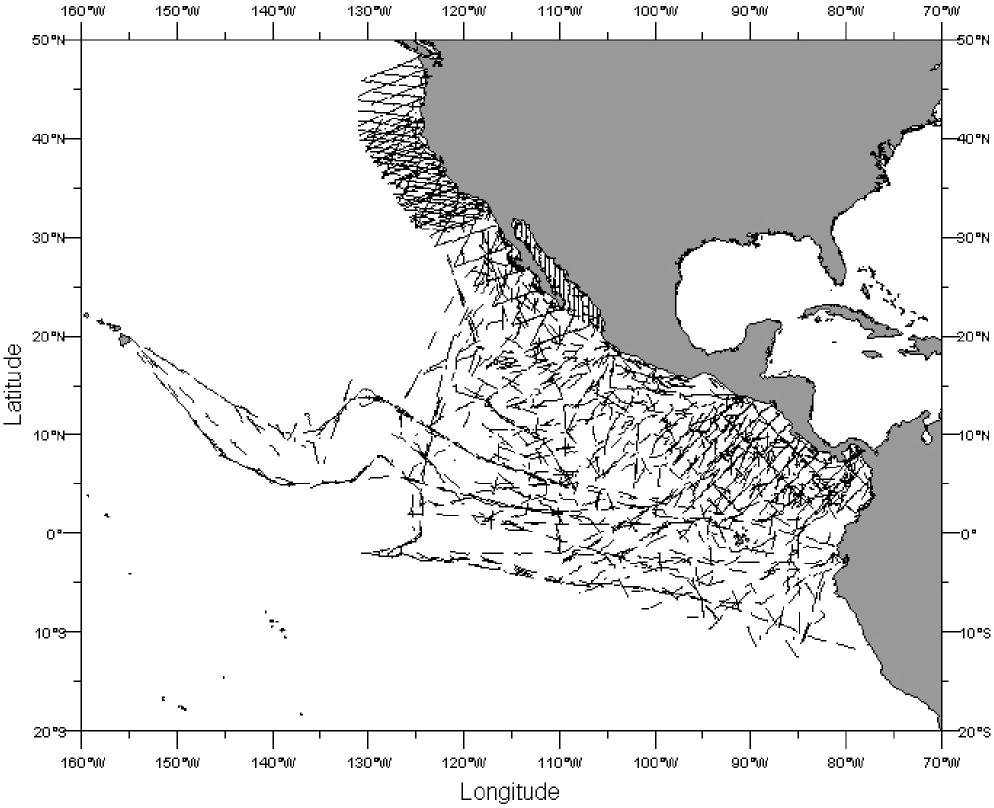

Figure 2.1a. Transect lines covered during the 1986-1996 SWFSC line-transect surveys in the eastern Pacific Ocean.

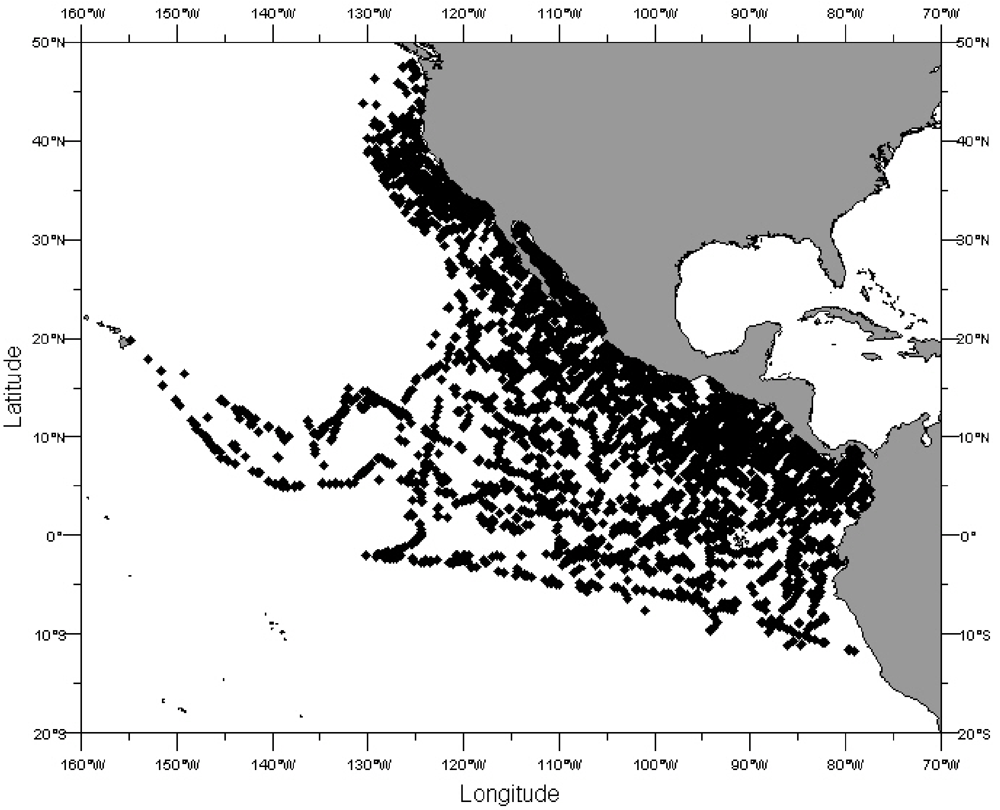

Figure 2.1b. Locations of all delphinid sightings made in Beaufort 0-5 seas during 1986-1996 SWFSC line-transect surveys in the eastern Pacific Ocean.

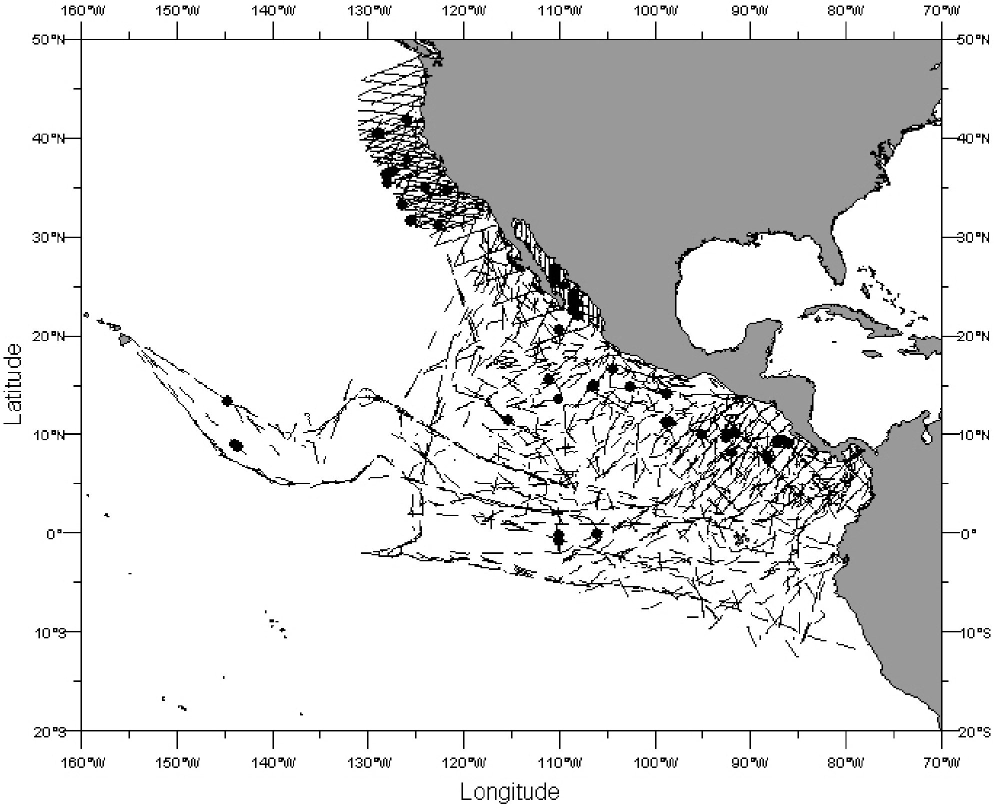

Figure 2.1c. Tracklines and locations of all Cuvier's beaked whale (*Ziphius cavirostris*) sightings made during Beaufort 0-2 conditions during 1986-1996 SWFSC line-transect surveys in the eastern Pacific Ocean.

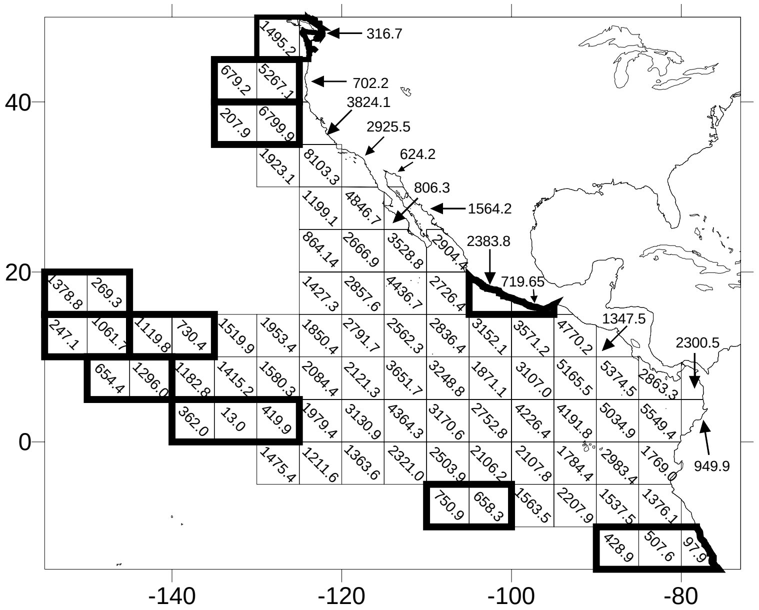

Figure 2.2. Length of transect line surveyed (km) within 5-degree squares in Beaufort 0-5 conditions during 1986-1996 SWFSC line-transect surveys. Heavy lines indicate boundaries of squares that were merged to increase sample size per stratum.

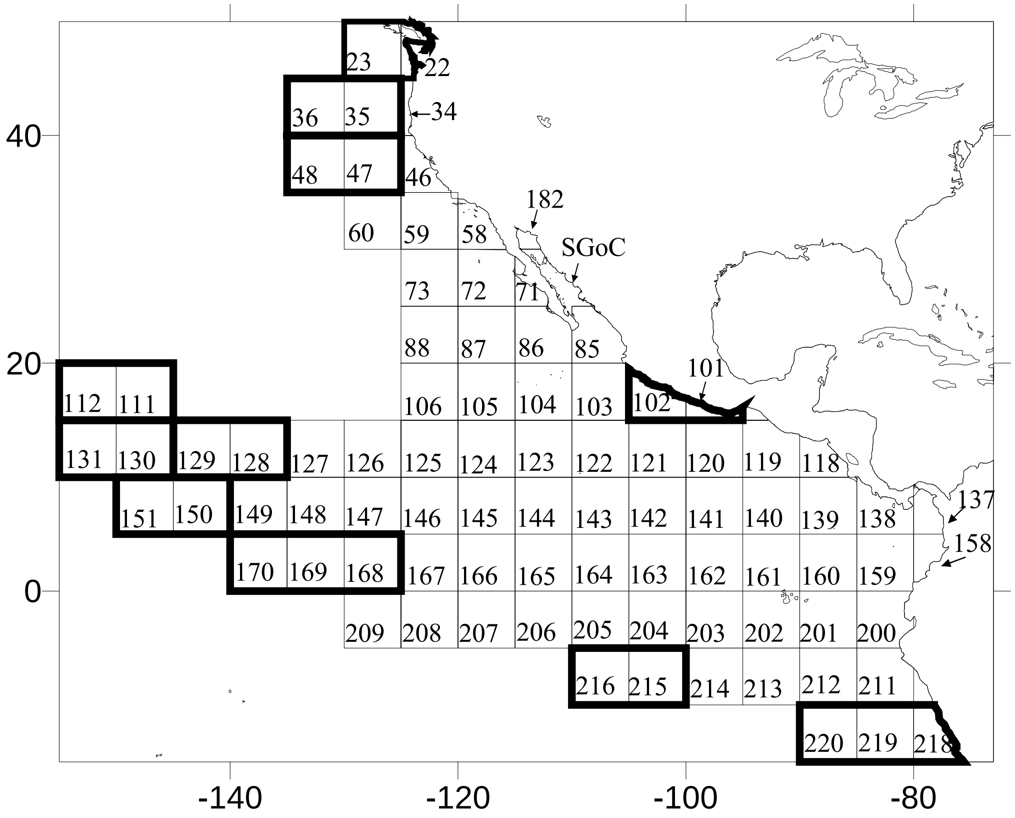

Figure 2.3. Geographic strata names used in the delphinid analysis. The area “SGoC” includes strata 179, 180, and 181 from Ferguson and Barlow (2001 and 2003).

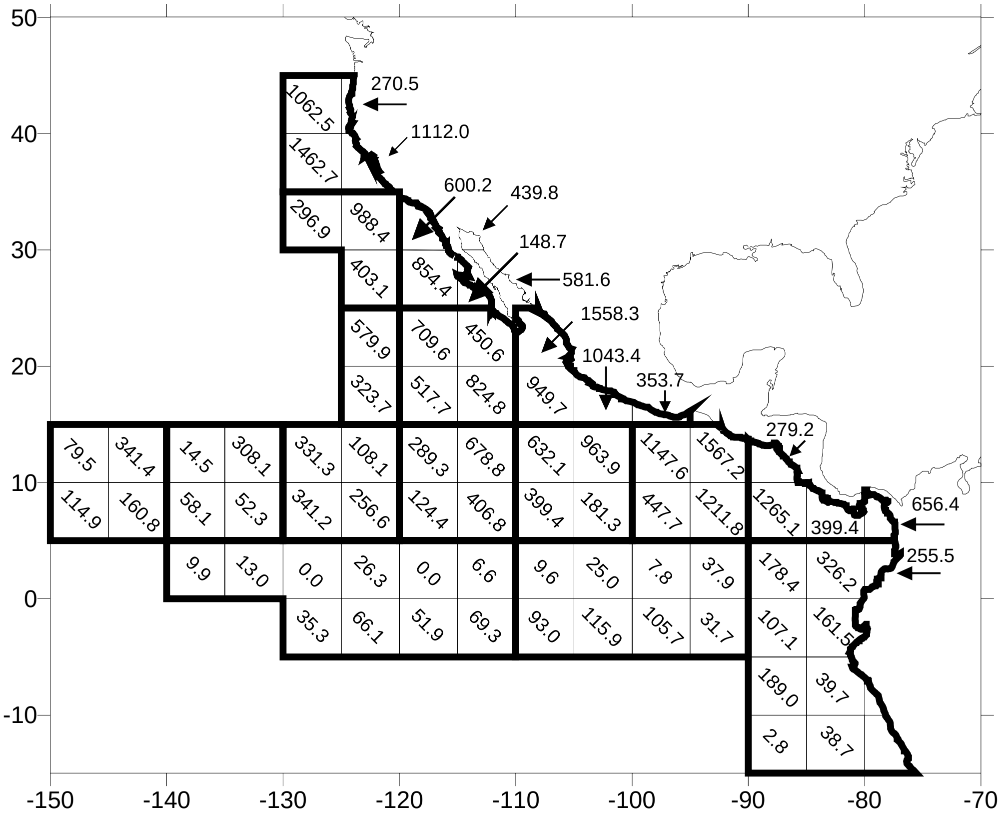

Figure 2.4. Length of transect line surveyed (km) within 5-degree squares in Beaufort 0-2 conditions during 1986-1996 SWFSC line-transect surveys. Heavy lines indicate boundaries of squares that were merged to increase sample size per stratum.

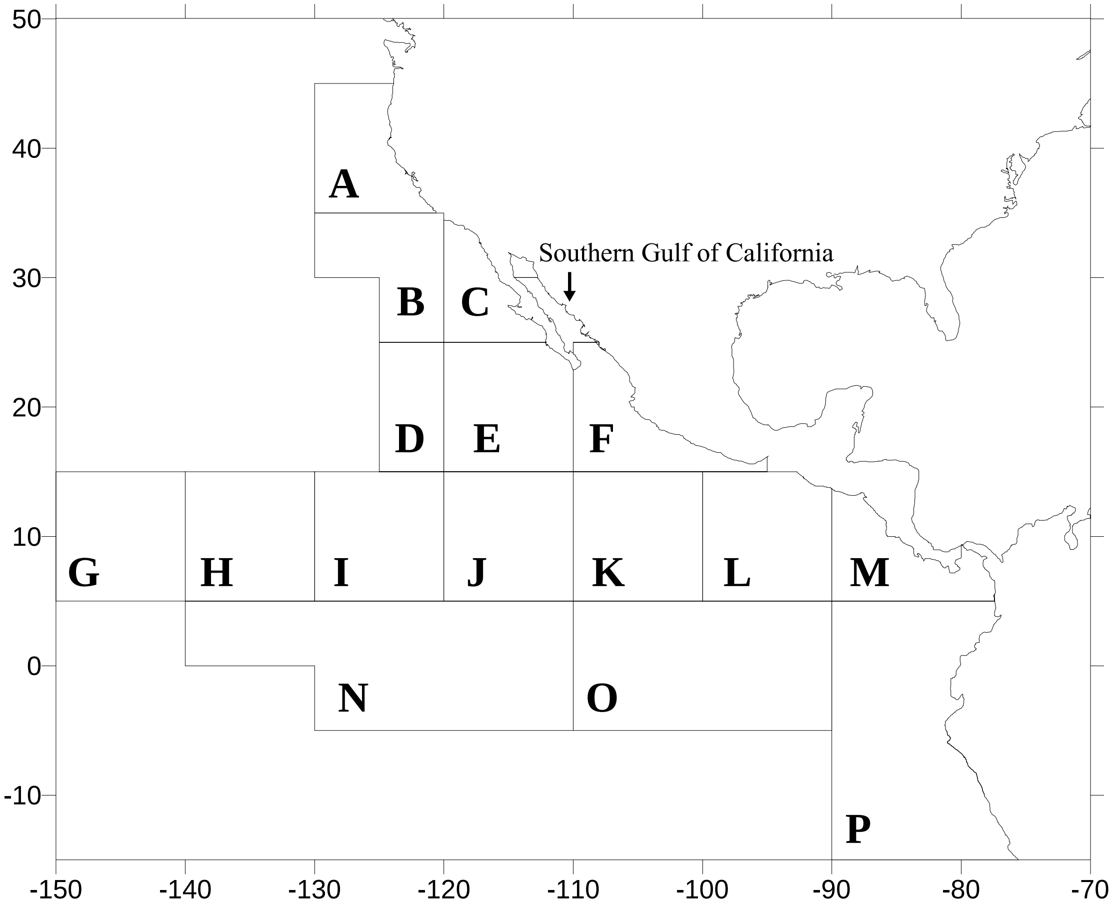

Figure 2.5. Geographic strata names used in the Cuvier's beaked whale (*Ziphius cavirostris*) analysis.

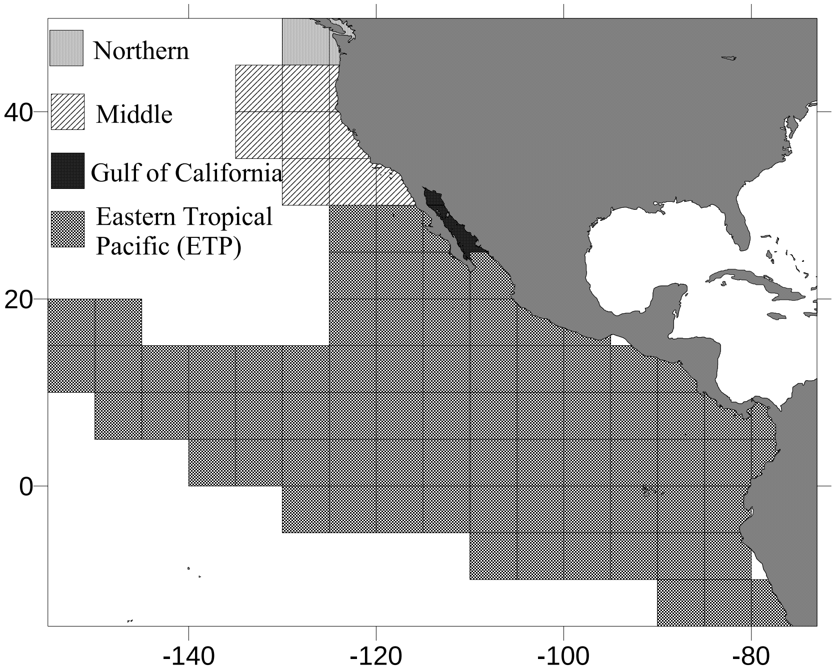

Figure 2.6. Survey regions in the eastern Pacific Ocean referred to in the text.

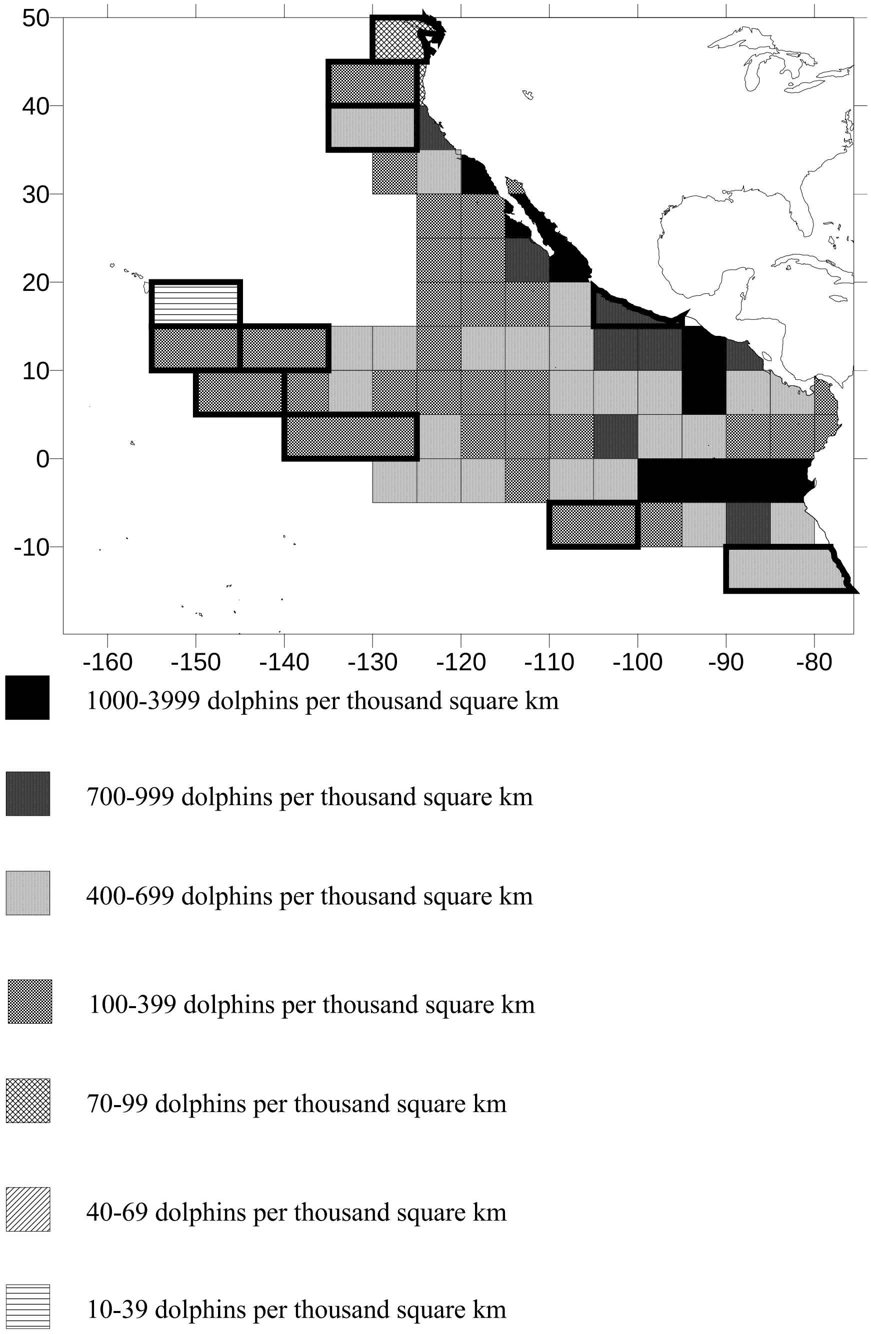

Figure 2.7. Dolphin (family Delphinidae) density in the eastern Pacific Ocean based on 1986-1996 SWFSC line-transect surveys. Heavy lines indicate boundaries of squares merged to increase sample size in the stratum.

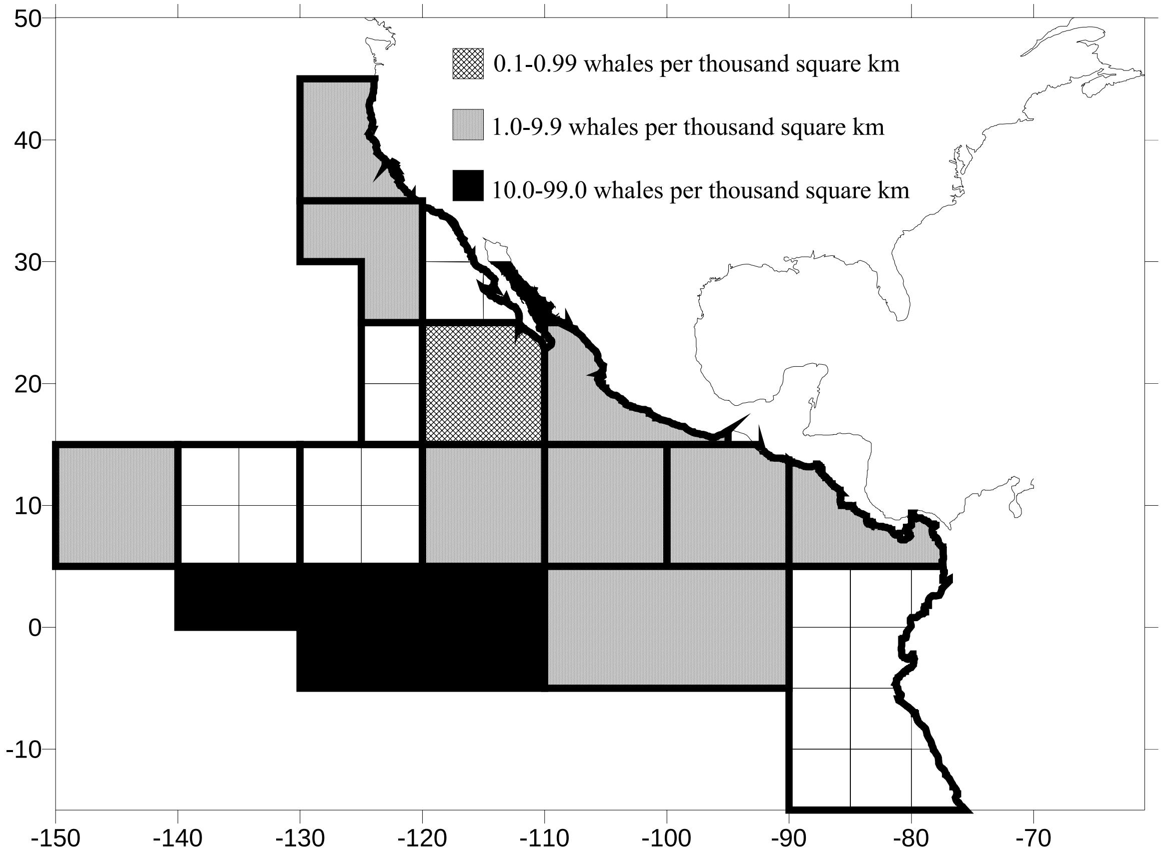

Figure 2.8. Cuvier's beaked whale (*Ziphius cavirostris*) density in the eastern Pacific Ocean based on 1986-1996 SWFSC line-transect surveys. Heavy lines indicate boundaries of squares merged to increase sample size in the stratum.

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# CHAPTER THREE

# SPATIAL MODELS OF DELPHINID (FAMILY DELPHINIDAE) ENCOUNTER RATE AND GROUP SIZE IN THE EASTERN TROPICAL PACIFIC OCEAN

BY

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## Abstract

We use temporally dynamic environmental variables and fixed geographic variables to construct generalized additive models to predict delphinid (Family Delphinidae) encounter rates (number of groups per unit survey effort) and group sizes in the eastern tropical Pacific Ocean. The delphinid sighting data and environmental data were collected simultaneously during the Southwest Fisheries Science Center’s cetacean line-transect surveys conducted during the summer and fall of 1986-90 and 1993. Predictions from the encounter rate and group size models were combined with previously published estimates of line-transect sighting parameters to describe patterns in the density (number of individuals per unit area) of delphinids throughout the study area. Areas with the highest predicted densities were the Gulf of California, the equatorial cold tongue, and coastal waters, including the west coast of the Baja Peninsula and the Costa Rica Dome. Offshore waters in the northern and southern subtropical gyres had the lowest predicted densities. For both encounter rate and group size models, there was no geographic pattern evident in the residuals as measured by the ratio of pooled predicted to pooled observed values within geographic strata.

## Introduction

Dolphin populations in the eastern tropical Pacific Ocean (ETP) gained the international attention of scientists, public policymakers, and conservationists in the late 1960’s when it became evident that large numbers of dolphins were being killed incidental to purse seine fishing operations for tuna (Perrin, 1969). In the mid-1970’s, the National Marine Fisheries Service (NMFS) initiated research to determine the status of the affected ETP dolphin populations, and NMFS has continued this effort to the present. A key component of the NMFS strategy has been to conduct large-scale shipboard surveys to further understanding of the ETP dolphin populations and the ecosystem in which they are embedded. Since 1979, Southwest Fisheries Science Center (SWFSC) surveys have followed line-transect protocols to estimate the abundance of cetaceans in the region; beginning in 1986 SWFSC research surveys expanded to study the ETP ecosystem, collecting data on the physical and biological oceanography of the region to provide a context in which to interpret the results from the cetacean studies.

The ETP study area (Figure 3.1) spans approximately 20 million km$^2$ of the Pacific Ocean; therefore, the scale of the SWFSC research vessel surveys is relatively large. Nevertheless, this ETP study area does not encompass the entire range of any cetacean species (other than the vaquita, *Phocoena sinus*, which is not considered here) and interannual variability in abundance estimates for many species has been attributed to movement of animals in and out of the region (*e.g.*, Gerrodette and Forcada, 2002a). Understanding how movements can affect abundance estimates requires a fine scale understanding of how density changes geographically. Previous methods of density estimation do not provide the needed level of geographic resolution and do not provide any deeper understanding of the factors that might be causing changes in distribution. Furthermore, since the late 1960's, the number and type of human activities that can potentially have adverse effects on marine ecosystems has increased along with public awareness thereof. Policymakers have responded by requiring that those who wish to engage in activities that may be detrimental to the marine environment formally assess the potential impact of their activities. In the U.S., the legal mandates dictating the rules and procedures that must be followed during the planning and implementation of high risk activities are the Endangered Species Act of 1973 (ESA) and the Marine Mammal Protection Act of 1972 (MMPA), as amended in 1994. A critical piece of information necessary to complete an Environmental Impact Statement (required by the ESA) and a take permit (required by the MMPA) is an estimate of the number of individuals of protected species, including threatened or endangered species, or any species of marine mammal, that may be affected by the proposed activity. A large proportion of the high risk activities that fall under the jurisdiction of the ESA and MMPA occur on a relatively small spatial scale; therefore, a conventional line-transect estimate of abundance for a region as large as the ETP cannot address the question of how many animals are likely to be affected by such small-scale activities. As a result, new questions about the ETP ecosystem must be addressed. For example, in addition estimating the total abundance of ETP dolphins, it is now important to understand the spatial patterns in dolphin population density to determine whether patches of high densities of threatened, endangered, or particularly vulnerable species exist within the ETP. Cetacean sighting data from past line-transect surveys such as those conducted by SWFSC contain information on the small-scale distribution of individuals and this, in association with information about the marine environment from relevant oceanographic studies, may be used to estimate dolphin densities on smaller spatial scales.

Considerable work has been done to investigate the distribution and, more specifically, habitat of ETP dolphins in relation to encounter rate (number of groups of animals observed per unit survey effort). Au and Perryman (1985) defined habitat characteristics of common (*Delphinus delphis*), striped (*Stenella coeruleoalba*), spotted (*Stenella attenuata*) and spinner (*Stenella lognirostris*) dolphins in the ETP. They qualitatively identified two contrasting patterns in the distribution of dolphin sightings and postulated that the patterns were linked to the physical oceanography in the region.

In particular, Au and Perryman (1985) noted that common and striped dolphins tended to occur in upwelling-modified conditions typical of waters along the equator and in the eastern boundary currents, whereas spotted and spinner dolphins were found in warm, low salinity surface waters over a strong, shallow thermocline in tropical waters off Mexico. The results from Reilly's (1990) statistical analyses on the ETP dolphin data supported Au and Perryman's hypotheses about spinner, spotted, and common dolphin habitat, but suggested that striped dolphin habitat could not be distinguished from the upwelling-modified or tropical habitats based on the variables used in the analysis, which included thermocline depth and $\sigma_t$ (a measure of seawater density). Furthermore, Reilly (1990) found that spotted, spinner, and striped dolphin distributions move offshore in the summer, when the countercurrent thermocline ridge at $10^{o}$N shoals. Reilly and Fiedler (1994) used canonical correspondence analysis (CCA) to study how encounter rates of ETP dolphins related to the physical oceanography of the region during the period from 1986 to 1990. Their results were in agreement with Reilly's (1990), identifying cool upwelling areas as common dolphin habitat, warm tropical areas as spotted and spinner dolphin habitat, and finding that the amount of variance explained by the environmental data was the least for striped dolphins. Reilly and Fiedler (1994) noted that the interannual variability in the species data was largely accounted for by the interannual variation in the environment. They suggested that dolphin abundance estimates might be improved by using the results of the CCA either 1.) to post-stratify the sighting data before using standard line-transect methods to estimate abundance or 2.) to quantify the amount of good habitat, and extrapolate to the proportion of each population, in the study area at the time of the survey. Reilly *et al.* (2002) investigated dolphin encounter rate data from 1998 to 2000 with CCA and found that, in comparison to Reilly and Fiedler (1994), there was no substantial change in patterns of dolphin habitat use between the late 1980's and the late 1990's.

This paper investigates the use of generalized additive models (GAMs) for predicting delphinid (species in the Family Delphinidae) density (number of individuals per unit area) as a function of environmental variables, thereby increasing the resolution of ecological research in the ETP using the wealth of existing information on the delphinids and oceanography of the region. The following delphinid species were included in the analysis: spotted dolphin (*Stenella attenuata* and *S. attenuata graffmani*), eastern spinner dolphin (*Stenella longirostris orientalis*), whitebelly spinner dolphin (*Stenella longirostris*), long-beaked or Baja neritic common dolphin (*Delphinus capensis*), short-beaked or offshore common dolphin (*Delphinus delphis*), striped dolphin (*Stenella coeruleoalba*), rough-toothed dolphin (*Steno bredanensis*), bottlenose dolphin (*Tursiops truncatus*), Risso's dolphin (*Grampus griseus*), Pacific white-sided dolphin (*Lagenorhynchus obliquidens*), Fraser's dolphin (*Lagenodelphis hosei*), northern right whale dolphin (*Lissodelphis borealis*), melon-headed whale (*Peponocephala electra*), pygmy killer whale (*Feresa attenuata*), false killer whale (*Pseudorca crassidens*), killer whale (*Orcinus orca*), long-finned pilot whale (*Globicephala melas*), short-finned pilot whale (*Globicephala macrorhynchus*), and "dolphin, unidentified to species." We pooled the dolphins of the ETP in this analysis for two reasons. First, dolphins, oceanic sharks, tunas, sperm whales, pilot whales, and ziphiid (beaked) whales comprise a guild of apex predators that prey upon fish and squid in the pelagic marine environment, and obtaining more information about the guild is valuable to ecologists and public policymakers

(Smith and Casey, 1992). Second, this analysis can provide a baseline with which to compare dolphin species-specific habitat analyses because examining why a given species is absent where other delphinids are present may provide further insights into the ecology of the individual species.

We use GAMs to mathematically identify the patterns between the cetacean sighting data from SWFSC line-transect surveys conducted in 1986-1990 and 1993 and *in situ* oceanographic data that were collected simultaneously. Forney (1999 and 2000) and Hedley *et al.* (1999) used GAMs to relate cetacean encounter rates to environmental and geographic variables, but the extrapolation from expected number of groups to the expected number of individuals is not straightforward if group size varies spatially. Spatial variation in group size is indeed evident in the delphinid populations in the ETP. Hedley and Buckland (2004) described, but did not implement, analytical methods for creating spatial models of cetacean group size. We build on these previous studies to produce the first geo-spatial line-transect density estimates for cetaceans from separate encounter rate and group size GAMs for delphinids in the ETP. In addition, our method results in density predictions on a smaller scale than previous analyses.

## Methods

### Study Area

The study area encompasses 19.6 million km$^2$ of the eastern tropical Pacific Ocean (Figure 3.1). Circulation patterns in the surface waters of the region are dominated by the zonal equatorial current system between the anticyclonic North and South Pacific subtropical gyres (Kessler, 2005). The California Current and the Peru Current form the eastern boundaries of the North and South Pacific gyres, respectively

(Figure 3.2). The California Current flows into the North Equatorial Current, and the Peru Current flows into the South Equatorial Current. The North Equatorial Countercurrent flows towards the east in the latitudes between the North and South Equatorial Current. Three primary surface water masses exist in the ETP: the warm, low-salinity Tropical Surface Water, which includes the eastern Pacific warm pool and underlies the Intertropical Convergence Zone (ITCZ), a zonal band between $5^o$ and $10^o$N where rainfall is high as a result of the north and south trade winds converging; the higher-salinity Equatorial Surface Water (the coldest surface water mass) with the equatorial cold tongue projecting from its eastern boundary; and the cool, Subtropical Surface Waters located towards the poleward edges of the ETP, where the highest salinities are found (Fiedler and Talley, 2005) (Figure 3.2). The thermocline is strongest beneath the Tropical Surface Water and weakest beneath the Subtropical Surface Water (Fiedler and Talley, 2005). Although not considered part of the ETP, but included in the analysis nonetheless, the Gulf of California is a region in which evaporation largely exceeds precipitation, resulting in highly saline surface waters. The physical and biological oceanography in the study area interact to produce highly productive waters in the upwelling regions of the California Current, Peru Current, equatorial cold tongue, and Costa Rica Dome, in contrast to the low productivity of the oligotrophic Subtropical Surface Waters (Ryther, 1969; Fiedler and Philbrick, 2002; Fiedler, 2000) (Figure 3.2). In general, both coastal and oceanic upwelling regions are characterized by relatively weak and shallow thermoclines and high levels of chlorophyll. In comparison, the oligotrophic regions have stronger and deeper thermoclines, and lower levels of chlorophyll.

## Field Methods

Cetacean sighting data and *in situ* oceanographic data were collected on SWFSC research cruises conducted during the summer and fall of each year from 1986 to 1990, and in 1993. Two National Oceanic and Atmospheric Administration (NOAA) research vessels, the *David Starr Jordan* and the *McArthur*, followed standard line-transect protocols (Buckland *et al.* 2001) to survey cetaceans in the eastern tropical Pacific Ocean, while concurrently collecting a suite of oceanographic data over the length of the trackline.

Kinzey *et al.* (2000) provide a complete description of the SWFSC cetacean data collection procedures followed during the ship-based line-transect surveys. In brief, two teams of three visual observers rotated through three positions located on the flying bridge of the ship. Starboard and port observers used 25x150 "bigeye" binoculars, scanning an arc of approximately $100^{o}$ extending from the starboard and port beams, respectively, to $10^{o}$ on the opposite side of the trackline. A third observer, the designated data recorder, searched with naked eye and, occasionally, 7x50 binoculars across the entire $180^{o}$ arc in front of the ship. All cetaceans sighted were identified to the lowest taxonomic level possible. Group size estimates were recorded independently by each observer.

The *in situ* oceanographic data collected during the line-transect surveys, and considered as potential predictor variables in the encounter rate and group size models, were: sea surface temperature (SST), sea surface salinity, thermocline depth, thermocline strength, and the natural logarithm of surface chlorophyll concentration (hereinafter simply referred to as surface chlorophyll concentration). Details of the oceanographic data collection methods for each ship and each year between 1986 and 1990 are available in Thayer *et al.* (1988a, 1988b, 1988c, 1988d), Lierheimer *et al.* (1989a, 1989b, 1990a, 1990b), and Philbrick *et al.* (1991a, 1991b). Oceanographic methods and results from the

1993 cruise have not yet been published. The temperature and salinity of the sea surface were recorded continuously using a thermosalinograph and then summarized into hourly means, resulting in a spatial resolution of approximately 18.5km (Table 3.1). Thermocline depth and strength were derived from CTD (conductivity temperature depth) stations and XBT (expendable bathythermograph) probes, having a spatial resolution of approximately 70 to 140km (Table 3.1). Surface chlorophyll concentrations were measured from water samples collected when the CTD was at the surface and have a spatial resolution of approximately 220km (Table 3.1). Beaufort sea state was recorded while the marine mammal observers were on-effort and was updated whenever conditions changed. Beaufort sea state is a dominant factor affecting the visibility of cetaceans; therefore, Beaufort was included in all models to account for potential biases due to visibility. Although it might be possible to account for the sea state visibility bias elsewhere in the density analysis, including Beaufort as a predictor variable in the generalized additive model automatically accounts for correlations among other predictor variables, thereby providing a better assessment of each predictor variable's individual effects on the response variable (Hastie and Tibshirani, 1990).

Additional environmental data that were considered in the models include distance from shore, depth and slope of the ocean bottom, latitude and longitude. Offshore distance was calculated as the shortest distance between a given point on the trackline and the closest point on the North, Central, or South American mainland. Depth data were obtained from the National Geophysical Data Center's TerrainBase data set, which had a spatial resolution of 5 x 5 minutes (approximately 9 x 9km). Slope was derived from the depth data in the two-step process described below.

## Analytical Methods

In preparation for building the models, the delphinid sighting data and oceanographic data were summarized into 9km segments of on-effort trackline, corresponding roughly to the finest resolution of environmental data. The 9km distance for each segment was measured directly along the trackline; therefore, the start and end points of a given segment may be less than 9km apart as measured by straight-line distance if the trackline in the segment followed bends or curves. Conversely, the straight-line distance between segment start and end points could be greater than 9km if off-effort sections of trackline intervened between contiguous on-effort sections in a given segment. In those instances when off-effort sections separated contiguous on-effort sections, data from the discontinuous sections of on-effort trackline were summarized together if the distance between sequential sections of on-effort trackline was less than 9km; otherwise, the on-effort section before observers went off effort was omitted and the start point for the new segment was located at the beginning of the on-effort section following the lag in effort. Due to the relatively small scale of the analysis, autocorrelation undoubtedly exists in the sighting and oceanographic data on neighboring 9km segments. Nevertheless, our primary goal was prediction rather than explaining ecological relationships or hypothesis testing; therefore, the problems associated with inflated sample size and autocorrelation are largely irrelevant because they do not add appreciable bias to the parameter estimates required for prediction (Neter *et al.*, 1990; Hamazaki, 2004).

Oceanography values for each segment were calculated as weighted averages of the data from the oceanography stations immediately before and after each segment midpoint, where the midpoint was defined as the point at which 4.5km of on-effort trackline had been covered. Inverse distance weighting (distance$^{-1}$) was used for thermocline depth, thermocline strength, and surface chlorophyll, whereas time$^{-1}$ weighting was used for sea surface temperature and sea surface salinity. This difference in weighting methods was necessary because the latter oceanography data were recorded with only a time stamp. Nevertheless, the ships traveled at approximately a constant speed, so the inverse distance and inverse time weighting methods are roughly comparable. Depth values for each segment were calculated as the inverse distance weighted average depth of the four closest nodes in the TerrainBase 5 x 5 minute grid to the segment midpoint. Assigning slope values to each segment required two steps. First, slope values were calculated for each node on the 5 x 5 minute grid as the magnitude of the gradient in depth:

$$Slope = \sqrt{\left(\frac{\partial z}{\partial x}\right)^2 + \left(\frac{\partial z}{\partial y}\right)^2} . \qquad (1)$$

Using compass-based grid notation and representing the slope angle in degrees yields the following equation:

$$Slope = \left(\frac{360.0}{2\pi}\right) * \arctan\left[\sqrt{\left(\frac{Z_E - Z_W}{2\Delta x}\right)^2 + \left(\frac{Z_N - Z_s}{2\Delta y}\right)^2}\right], \qquad (2)$$

where $Z_E$, $Z_W$, $Z_N$, and $Z_s$ refer to the grid nodes to the east, west, north, and south of the desired node. Second, the slope for the segment midpoint was assigned the value of the slope of the node closest to the segment midpoint.

Delphinid sighting data for each segment were summarized as the total number of groups sighted and the average group size in the segment. Prior research has shown that individual observers' estimates of group size can be biased compared to counts made from aerial photographs and that group size estimates can be improved by applying individual-specific calibrations to correct this bias (Gerrodette *et al.*, 2002). Computing the average group size for each segment required three steps: 1.) calculate the bias-corrected group size estimate for each observer for each sighting in the segment based on individual calibration coefficients; 2.) calculate the mean group size estimate, averaged over all observers, for each sighting in the segment; and 3.) calculate the mean group size estimate, averaged over all sightings, for each segment. For the first step, calculating individual observers' calibrated group size estimates, one of three methods was used; all methods were derived by comparing the observers' uncalibrated group size estimates with group size estimates obtained from photographs of cetacean groups taken during the surveys. Direct calibration with quasi-maximum likelihood bias correction was the preferred method and was used if the group size estimates and Beaufort sea state data necessary for the observer's calibration were available (Gerrodette *et al.,* 2002). Directly calibrated observers have two types of direct calibrations, one that is year-specific and one that is a general calibration to be used in any year (Gerrodette *et al.*, 2002). If data were not available to use the direct calibration model that was specific to a given year, the next option was to use the general direct calibration model for the observer. If neither direct calibration model could be used due to lack of data, indirect calibration with quasi-maximum likelihood bias correction was considered (Barlow *et al.,* 1998). The indirect calibration method could be used only if an observer's best estimate of group size was available and if an indirect calibration model existed for the observer. At this stage in the selection of a method for calibrating an individual observer's group size estimate, if a best estimate was not available, that observer's data was not included in the mean group size estimate for the sighting. If the indirect calibration method could not be used but a best estimate was available for the observer, then the ratio method was used:

$$\hat{s} = \frac{s_b}{\frac{1}{\sum_{i=1}^{n} m_i}\left[\sum_{i=1}^{n}\sum_{j=1}^{m_i}\left(\frac{s_{b_{i,j}}}{s_{p_i}}\right)\right]} \qquad (3)$$

where $\hat{s}$ = observer's calibrated group size estimate, $s_{b_{i,j}}$ = observer *j*'s best estimate of size for group *i*, and $s_{p_i}$ = size of group *i* estimated from photographs of group *i* (Gerrodette *et al.,* 2002). Thus, in the ratio method, the observer's best estimate ($s_b$) was corrected by the ratio of observer best estimates to photographic counts, averaged over all *n* photographic calibration groups, each having *m* observer estimates. Once each observer's group size estimate was calibrated, a mean group size was calculated for each sighting as the weighted mean of the natural logarithm of the calibrated group size estimates, resulting in a weighted geometric mean group size. The calibrated group size estimates were weighted by variance$^{-1}$, where the value for the variance for each observer was the MSE (mean square error) reported for directly calibrated observers and observers calibrated with the ratio method (Gerrodette *et al.,* 2002) or the ASPE (average square prediction error) reported for indirectly calibrated observers (Barlow *et al.,* 1998). Finally, the mean group size estimate for each segment was calculated as the arithmetic mean of the weighted geometric mean group size estimates for all sightings in the segment.

GAMs were used to relate delphinid sightings to the summarized fixed geographic variables and temporally dynamic *in situ* oceanographic data described above. A GAM may be represented as

$$g(\mu) = \alpha + \sum_{j=1}^{p} f_j(X_j). \qquad (4)$$

(Hastie and Tibshirani, 1990). As in generalized linear models (GLMs), the function $g(\mu)$ is known as the link function, and it relates the mean of the response variable given the predictor variables, $\mu=E(Y|X_1,\ldots,X_p)$, to the additive predictor $\alpha+\Sigma_j f_j(X_j)$. GAMs are nonparametric extensions of GLMs: the components $f_j(X_j)$ in the additive predictor may include nonparametric smooth functions of the predictor variables, allowing GAMs to be considerably more flexible than GLMs, which are restricted by the constraints of the linear predictor, $\alpha+\Sigma_j\beta_j X_j$. Separate GAMs were built to describe and predict delphinid encounter rates and average group sizes. The encounter rate data were essentially clustered counts; therefore, the number of sightings in each segment was modeled using a quasi-likelihood error distribution with variance proportional to the mean and using a logarithmic link function (approximating an over-dispersed Poisson distribution).

Encounter rate models were built using all 9km segments, regardless of whether they contained sightings. Observed distributions of dolphin group sizes in the ETP region typically have long tails and are restricted to the positive real values. Furthermore, after correcting for bias and averaging group sizes across individuals and sightings in each segment, group size estimates are likely to be non-integer valued. Therefore, GAMs were built using the natural logarithm of group size as the response variable and a Gaussian error distribution with the identity link function. Group size models were built on only the 9km segments that contained delphinid sightings with valid group size estimates.

The encounter rate and group size GAMs were built using S-PLUS 6 for Windows. Forward/backward stepwise selection of variables, with linear terms or smoothing splines having 2 and 3 degrees of freedom (df) in the scope of predictor variables, was implemented using the function *step.gam*. Models built using a maximum of 4 df for each variable in the scope of *step.gam* were considered, but resulting models were qualitatively similar to those limited to 3 df, and the added complexity of the 4 df models appeared to have no ecological justification. Akaike's Information Criterion (AIC) was used to determine the best model at each step. Stepwise selection of variables occurred twice for each model. The first stepwise selection process started with the null model, did not contain terms for latitude or longitude, and linear terms were excluded from the scope. Latitude and longitude were excluded from the first call to try to explain the observed variation in the delphinid data using the more informative environmental data before considering fixed geographic coordinates. Linear functions were excluded from the first call because a few instances were found in which AIC was lower for a linear fit than for a quadratic smoothing spline, but a cubic smoothing spline was better than a linear fit. In those instances, the stepwise fitting algorithm would not go beyond the quadratic and test the AIC value resulting from splines with higher degrees of freedom.

The second call to *step.gam* began with the best model from the first call, and included latitude, longitude, and linear functions of all variables in the scope of predictor variables. It is advantageous to call *step.gam* twice because, by default, the function uses the dispersion parameter of the original gam object (Chambers and Hastie, 1991), and the estimated dispersion parameter associated with the best model from the first call to the function is likely to better represent the underlying process than that associated with the null model.

The above stepwise selection of variables finds the model that provides the best fit to the given data as judged by AIC, but it does not provide any information about the predictive power of the resulting model. To assess the predictive power of a number of models, the stepwise building procedure was performed on all combinations of the years 1986-1990 with one year left out; 1993 was included in all trials because it was a relatively small data set. This modified procedure resulted in five "best" encounter rate models and five "best" group size models. To evaluate which encounter rate and group size models performed best according to predictive power, cross-validation methods were applied, testing each model on the excluded year. The model with the lowest average squared prediction error (ASPE) was selected as the model with the best predictive performance. The model selected by the cross-validation process was re-built using the specified degrees of freedom and all years of data to fine-tune the smoothing splines.

The final delphinid encounter rate model included longitude, and the group size model included both latitude and longitude. To determine the effect that fixed geographic variables had on the predictive performance of the model, the stepwise selection and cross-validation procedures were repeated, excluding latitude and longitude from the scopes of both calls to *step.gam*. The ASPE values of the final models built without geographic variables in the scopes were compared to the final models built with geographic variables; the models with the lowest ASPE values were selected as the best overall encounter rate and group size models.

To estimate delphinid density, the encounter rate (*n/L*) and group size (*S*) model results were incorporated into the standard line-transect equation

$$D = \left(\frac{n}{L}\right) \cdot S \cdot \frac{1}{2 \cdot ESW \cdot g(0)} \qquad (5)$$

where,

*n/L* = encounter rate (number of sightings per unit length of trackline),

*S* = expected (or mean) group size,

*ESW* = effective strip half-width, or 1/*f(0)*, where *f(0)* is the sighting probability density at zero perpendicular distance

*g(0)* = probability of detecting an animal on the trackline.

The values of *f(0)* and *g(0)* were the arithmetic average of those given for the delphinids in the ETP by Ferguson and Barlow (2001). It was necessary to apply a bias-correction factor to the group size predictions from the GAMs because the models were built in log space and then the results were transformed back to arithmetic space, converting the group size estimate to a geometric mean in the process (Finney, 1941; Smith, 1993). The ratio estimator was used to correct for this back-transformation bias (Smith, 1993). Density estimates for each segment were smoothed to give a geographic representation of average density over the study period by using an inverse distance weighting interpolation to the first power with anisotropy ratio set to 1.0 in Surfer software (version 7.0).

To evaluate the models' fit to the observed data, the following error analysis was conducted. Encounter rate models were fit to the observed oceanographic and geographic data for all segments in the study area, and the differences between predicted and observed values for each segment ($\Delta ER_i$) were calculated:

$$\Delta ER_i = ER_{i_{predicted}} - ER_{i_{observed}} \qquad (6)$$

for segment *i* in the study area. In addition, the ratio ($R_{ER}$) between pooled predicted values and pooled observed values was calculated:

$$R_{ER} = \frac{\left( \sum_{i=1}^{n} ER_{i_{predicted}} \right)}{\left( \sum_{i=1}^{n} ER_{i_{observed}} \right)}, \ (7)$$

where the summation is over the total number of segments used to build the models or the number of segments in a given geographic stratum, as described below. Group size was predicted from GAMs based on the subset of data comprised of only the segments with delphinid sightings. This subset of predictions was appropriate for testing how well the model predicted group size for each segment ($\Delta SS_i$) and for the study area as a whole ($R_{SS}$) because the group size model was built on the same subset of data upon which the predictions were based. The group size predictions were corrected for the bias due to back-transforming from the log space, and the computations for $\Delta SS_i$ and $R_{SS}$ were analogous to the respective encounter rate statistics (Eqns 6 and 7). To qualitatively determine whether spatial patterns existed in the predictions for encounter rate and group size, a spatially stratified analysis was conducted in which values of $R_{ER}$ and $R_{SS}$ were calculated for geographic strata of approximately 5$^{o}$ latitude x 5$^{o}$ longitude.

## Results

The data extracted from the SWFSC cruises for this analysis contained 2,548 delphinid sightings in 11,802 on-effort segments, covering 106,218km of on-effort trackline. The three most frequently encountered species were striped, offshore spotted, and bottlenose dolphins; Fraser's dolphins and common dolphins had the largest bias-corrected group sizes averaged across all sightings in each segment (Table 3.2). The observed line-transect data showed some spatial structure in delphinid group sizes, with larger groups in the waters around the Baja Peninsula, the Costa Rica Dome, and the equator (Figure 3.3).

The best delphinid encounter rate model contained eight terms: Longitude, Beaufort sea state, offshore distance, depth, SST, sea surface salinity, surface chlorophyll concentration, and thermocline depth (Table 3.3, Figure 3.4). Surface chlorophyll concentration was incorporated into the model as a smoothing spline with two df, whereas the remaining variables were selected as smoothing splines with three df. The decrease in deviance from the null model to the best encounter rate model was 12.12% (Table 3.3). The overall best group size GAM contained six terms: latitude, longitude, offshore distance, depth, slope, and SST (Table 3.3, Figure 3.5). The best group size model built without latitude and longitude resulted in a higher ASPE value in the cross-validation process so it was not considered any further. The variables latitude, offshore distance, depth, and SST were accepted into the model as linear terms; longitude appears as a smoothing spline with two df (although it shows little departure from linearity; Figure 3.5); and seafloor slope was included as a smoothing spline with three df. The decrease in deviance from the null model to the overall best group size model was 4.95% (Table 3.3).

When the selected encounter rate and group size models were applied to *in situ* data from the cruises on which they were built, the resulting density predictions ranged from 26 to 5205 individuals/1000km$^2$ (mean=387, sd=405). Regions with the highest predicted densities were the Gulf of California, the equatorial cold tongue, and coastal waters, including the west coast of the Baja Peninsula and the Costa Rica Dome (Figure 3.6). Offshore waters in the northern and southern subtropical gyres had the lowest predicted densities.

The error analysis showed that the mean differences (averaged across all years and all segments used to build the models) between predicted and observed values of encounter rate and group size were zero. The standard deviation of the differences in predicted and observed encounter rates was 0.5 and the range was –9.0 to 1.15 groups.

For the group size model, the standard deviation of the differences was 134.6 and range was –2412.5 to 288.9 individuals. When pooling all segments used to build the models, the ratio of pooled predicted to pooled observed was 1.0 for both models. The geographically stratified analysis of $R_{ER}$ showed that, in over half of the strata, the ratio of pooled predicted to pooled observed encounter rates is close to 1.0 (±0.25), and there was no apparent geographic pattern in the ratio values (Figure 3.7). The range of $R_{ER}$ values was from 0.5 to 3.4 (50% underestimate to 340% overestimate by the model). The geographically stratified $R_{SS}$ values spanned a broader range (0.4 to 12.6), although, in approximately half of the strata, predicted values were within 25% of observed, and geographic pattern was not evident in the ratio values (Figure 3.8) with the possible exception of a contiguous block of cells south of the Equator between $90^{o}$-$110^{o}$W, which all have higher predicted than observed values .

## Discussion

Our use of generalized additive models in this analysis is unique because we are able to predict the density of individual animals throughout the study area. Previous analyses of cetacean habitat associations in the ETP (Reilly, 1990; Reilly and Fiedler, 1994; Reilly *et al.*, 2002) and elsewhere (Forney, 1999; Hedley *et al.*, 1999; Forney, 2000; Hedley and Buckland, 2004) examined the relationship of group encounter rate to environmental predictors, but understanding the variability in population density in its entirety requires bringing the analysis to the scale of the individual. Although there was some qualitative evidence of increased delphinid group sizes in the waters around the Baja Peninsula, the Costa Rica Dome, and the equator, our models explained relatively little of the variability in the observed data as judged by percent decrease in deviance. This inability to detect patterns could be due to an inappropriate choice for the group size sampling distribution. The gamma distribution was also tested on the group size data and found to perform poorly relative to the lognormal distribution we used. Alternatively (or in conjunction) it is possible that we did not measure the appropriate elements of the ecosystem, such as abundance or density of prey species, in order to identify the existing patterns. Reilly and Fiedler (1994) found that group sizes of spotted, spinner, striped, and common dolphins in the ETP showed no relationship to the environmental variables SST, sea surface salinity, $\sigma_t$, thermocline depth, thermocline strength, and chlorophyll based on a CCA analysis of the same SWFSC 1986 to 1990 data used here. This result may vary by species, location, or time, however, so it would be prudent to examine each case separately. If it is true that the null group size model provides adequate information in a given study area, then it would be possible to multiply the estimated average group size by encounter rate predictions from a model such as the GAM presented here to derive a prediction for the density or abundance of individuals. Nevertheless, we were effectively able to increase the resolution of density predictions by using the information from the SWFSC survey cruises in the ETP more efficiently, relating delphinid density to several environmental predictors in a relatively simple process, and allowing finer resolution of the patterns in delphinid density than is available using a conventional stratified line-transect analysis.

Generalized additive models were chosen for the ETP analysis because of their flexibility, which was manifest in the plots of the smooth functions for the predictor variables that were present in the final delphinid encounter rate and group size GAMs, and in the error analysis for the models. For example, the model fits describing the relationship between slope and group size, and those relating encounter rate to longitude, offshore distance, depth, sea surface salinity, surface chlorophyll concentration, and thermocline depth were all nonlinear. The error analysis showed that differences between observed and predicted values were small and that the ratios of pooled predicted to pooled observed values were close to 1.0. Furthermore, in the geographically stratified analysis comparing model predictions to observed values, encounter rate and group size predictions in the majority of the strata were within 25% of the observed values. The error analysis addressed the question of how well the models fit the data on which they were built, but the predictive performance on completely novel data (*i.e.*, data from a future ETP survey) needs to be addressed further. Most of the predictor variables that we considered were proxies for characteristics of the environment that potentially relate more directly to delphinid density, such as prey concentrations. The predictive performance of these delphinid density models when applied to novel data may be improved if more information about the prey were available.

One drawback to GAM methodology is that estimating variance in predictions is not simple. The sources of uncertainty in the ETP analysis are numerous and not fully understood. Several sources of uncertainty include: 1.) survey design, because changing the spatial or temporal specifications of the shipboard survey tracklines would have produced a different set of delphinid and oceanographic observations; 2.) error in the measurement of environmental variables; 3.) error arising from the stochasticity inherent in the Poisson sampling process generating the encounter rates; 4.) parameter estimation error in the model fitting process; 5.) model selection error associated with choosing the appropriate variables and corresponding degrees of freedom; 6.) errors due to a disassociation between the animals' distribution and the predictor variables used to try to understand the ecology of the system. Hedley *et al.* (1999) and Hedley and Buckland (2004) have addressed the problem of estimating two sources of variance in GAM predictions by applying parametric and nonparametric bootstrap methods to estimate the variance associated with line-transect sampling and model building. Work is ongoing to understand the various sources of uncertainty and to estimate their magnitude.

We consider these GAMs to be a first step in predictive modeling of cetacean densities because our analysis posed more questions than it answered. Three lines of active research involve issues of scale, autocorrelation, and model implementation. The question of scale permeates all aspects of the model-building process: the spatial resolution of raw oceanography data; the unit (*i.e.*, line segment, circle, or sphere) and distance used to define neighborhoods in which the environment influences the habitat of a given point; whether environmental effects are transmitted as a constant function or decay with distance from a point; the appropriate size of the study area, which should be large enough to encompass meaningful contrasts but small enough to thoroughly sample; the taxonomic level (population, species, genus, or family); and the temporal scale (seasonal, annual, multi-year, decadal). We showed that there was no pattern in the residuals on the $5^o$ x $5^o$ scale, but it is unknown whether autocorrelation exists on smaller scales. Assessing whether autocorrelation exists in the model residuals is important for accurately quantifying the variance in the model predictions and, from an ecological perspective, for accurately identifying which environmental variables are associated with observed patterns in animal density. The main issue regarding model implementation is obtaining quality environmental data on which to make predictions. Remotely sensed data and predictions from physical and biological oceanographic models are advantageous because they are synoptic and available for all seasons, but they should be ground-truthed before relied upon as input into predictive models. A further detail related to implementing these encounter rate and group size models to predict densities involves the estimation of *f(0)*. The values of *f(0)* that we used to compute predicted densities were based upon stratified estimates for the survey region. In some situations, it may be more appropriate to incorporate values of *f(0)* that are functions of sighting conditions, location, etc. (*e.g.*, Marques, 2001; Gerrodette and Forcada, 2002a; Gerrodette and Forcada, 2002b).

It is important to keep in mind that predictions from cetacean-habitat models such as ours implicitly assume a particular population size and set of environmental conditions for some specified study area. Just as it would be unwise to use a model built on cetacean and oceanographic data from the ETP to predict cetacean densities in the Gulf of Alaska, it would also be unwise to use a model built on cetacean data gathered when the overall population size was large or climatic conditions were significantly different to predict cetacean densities in the same region when the overall population size is small. Density dependent effects and unknown environmental effects may significantly alter ecosystem, community, or population dynamics, and blind adherence to model predictions could result in significant errors. Therefore, we advocate an iterative approach to predictive modeling where large-scale abundance estimates are used to inform models that predict densities at smaller scales, which, in turn, may be used to fine-tune the large-scale abundance estimates. The same concerns apply when extrapolating from models built from data collected under one set of climatic conditions and applying that model to another climatic regime.

In summary, GAM-based methods have the potential to predict cetacean densities on smaller spatial scales than conventional line-transect analyses. Future work should focus on understanding the ecology of delphinid prey and on addressing questions of variance estimation, scale, autocorrelation, and model implementation. In addition, we can test the performance of our GAMs by evaluating how well they predict delphinid densities observed on future surveys. The model fits from this GAM analysis also provide starting points for testing hypotheses about ecological associations between the cetaceans and their environment, leading to more insight into the mechanisms that structure cetacean distributions. Finally, there is value in comparing predictions from different types of models, and work should continue on developing new and better frameworks for spatial modeling of cetacean density. Even though the truth may never be known, such a comparative analysis may reveal biases associated with each method, increasing our understanding of the ecological system along the way.

## Acknowledgements

We would like to thank the marine mammal observers, cruise leaders, and crew of the *David Starr Jordan* and the *McArthur* who collected the valuable data sets that we used in our analysis. We are also grateful to A. Jackson and V. Andreassi for bringing the data into user-friendly formats. Thanks to J. Carretta, K. Forney, T. Chereskin, P. Dayton, D. Goodman, L. Haff, J. Leichter, and P. Smith for providing intellectual stimulation and guidance through the early days of this analysis. We appreciate S. Hedley's help in answering programming questions. S. Martin helped write the program to plot the survey effort in Figure 3.1. This manuscript was improved by comments from E. Becker. Finally, many thanks to J. Redfern for catching errors before they caught us. Funding for this research came from the Department of Navy through the Office of Naval Research and the Strategic Environmental Research and Development Program and from the National Science Foundation, which supported M. Ferguson under a Graduate Research Fellowship.

The text of Chapter Three has been submitted for publication. The dissertation author was the primary researcher and author, and the co-authors listed directed and supervised the research which forms the basis for this chapter.

Table 3.1. Temporal and spatial resolution of *in situ* oceanographic data collected during SWFSC cetacean line-transect survey cruises.

| Variable Name | Resolution |
|---|---|
| sea surface temperature | recorded every five minutes; summarized into hourly means (approx. 18.5 km) |
| sea surface salinity | recorded every five minutes; summarized into hourly means (approx. 18.5 km) |
| thermocline depth* | 4x/day (approx. every 70-140 km) |
| thermocline strength* | 4x/day (approx. every 70-140 km) |
| surface chlorophyll concentration | 2x/day (approx. every 220 km) |

* These variables were derived from CTD and XBT data.

Table 3.2. Number of sightings and statistics on bias-corrected group size (averaged across all sightings in each segment of effort) for each delphinid species included in encounter rate and group size GAMs. Group size models only used sightings for which valid group size data were available.

| **Common Names** | **Scientific Names** | **encounter rate sample size** | **group size sample size** | **mean group size** |
|---|---|---|---|---|
| dolphin, unidentified to species | | 735 | 398 | 26.11 |
| Striped dolphin | *Stenella coeruleoalba* | 493 | 471 | 55.48 |
| Offshore pantropical spotted dolphin | *Stenella attenuata* (offshore) | 302 | 293 | 131.03 |
| Bottlenose dolphin | *Tursiops truncatus* | 296 | 274 | 24.12 |
| Risso's dolphin | *Grampus griseus* | 206 | 189 | 18.64 |
| Eastern spinner dolphin | *Stenella longirostris orientalis* | 144 | 138 | 108.82 |
| Offshore (short-beaked) common dolphin | *Delphinus delphis* | 131 | 129 | 230.38 |
| Rough-toothed dolphin | *Steno bredanensis* | 123 | 120 | 15.46 |
| Short-finned pilot whale | *Globicephala macrorhynchus* | 122 | 117 | 18.29 |
| Pilot whale, unidentified to species | *Globicephala* sp. | 68 | 62 | 17.18 |
| Whitebelly spinner dolphin | *Stenella longirostris* (whitebelly) | 56 | 56 | 82.54 |
| Killer whale | *Orcinus orca* | 42 | 41 | 5.45 |
| Baja neritic (long-beaked) common dolphin | *Delphinus capensis* | 25 | 23 | 411.69 |
| False killer whale | *Pseudorca crassidens* | 25 | 19 | 11.00 |
| Pygmy killer whale | *Feresa attenuata* | 23 | 23 | 30.12 |
| Pantropical spotted dolphin, unidentified subsp. | *Stenella attenuata* (unidentified subspecies) | 19 | 18 | 186.20 |
| Spinner dolphin, unidentified subsp. | *Stenella longirostris* (unidentified subspecies) | 15 | 13 | 147.74 |
| Coastal spotted dolphin | *Stenella attenuata graffmani* | 15 | 15 | 124.00 |
| Common dolphin, unidentified subsp. | *Delphinus* sp. | 12 | 10 | 311.14 |
| Fraser's dolphin | *Lagenodelphis hosei* | 11 | 11 | 440.05 |
| Melon-headed whale | *Peponocephala electra* | 6 | 5 | 257.70 |
| Pacific white-sided dolphin | *Lagenorhynchus obliquidens* | 3 | 3 | 127.38 |

Table 3.3. Summary of delphinid encounter rate and group size GAMs for the eastern tropical Pacific. Linear fits are represented by "L1," whereas smoothing splines are represented by "S#," where # is the associated degrees of freedom. Final selected model indicated by **bold** font. Percent change in deviance was calculated for final selected model, rebuilt using all years' data, as: ((null deviance - residual deviance)/null deviance)*100%.

| **Model** | **Year Omitted** | **% Change in Deviance** | **Predictor Variables** | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Encounter Rate | | | Lat | Long | Beaufort | Offshore Distance | Depth | Slope | SST | Salinity | ln(Surface Chlorophyll) | Thermocline Depth | Thermocline Strength |
| | 1986 | | | S3 | S3 | S3 | S3 | | S3 | S3 | | S3 | S3 |
| | 1987 | | | S3 | S3 | S3 | S3 | | S2 | S3 | | S3 | S3 |
| | 1988 | | | S3 | S3 | S3 | S3 | | L1 | S3 | | S3 | S3 |
| | 1989 | | S3 | | S3 | S3 | S3 | | S2 | S3 | S2 | S3 | S3 |
| | 1990 | **12.12** | | **S3** | **S3** | **S3** | **S3** | | **S3** | **S3** | **S2** | **S3** | |
| Group Size | | | Lat | Long | Beaufort | Offshore Distance | Depth | Slope | SST | Salinity | ln(Surface Chlorophyll) | Thermocline Depth | Thermocline Strength |
| | 1986 | | S3 | S2 | | L1 | | | L1 | | | | |
| | 1987 | **4.95** | **L1** | **S2** | | **L1** | **L1** | **S3** | **L1** | | | | |
| | 1988 | | S3 | | | | | | L1 | | S2 | S2 | L1 |
| | 1989 | | S3 | | | | L1 | | L1 | | | L1 | S2 |
| | 1990 | | L1 | | | | | | L1 | | S3 | L1 | S2 |

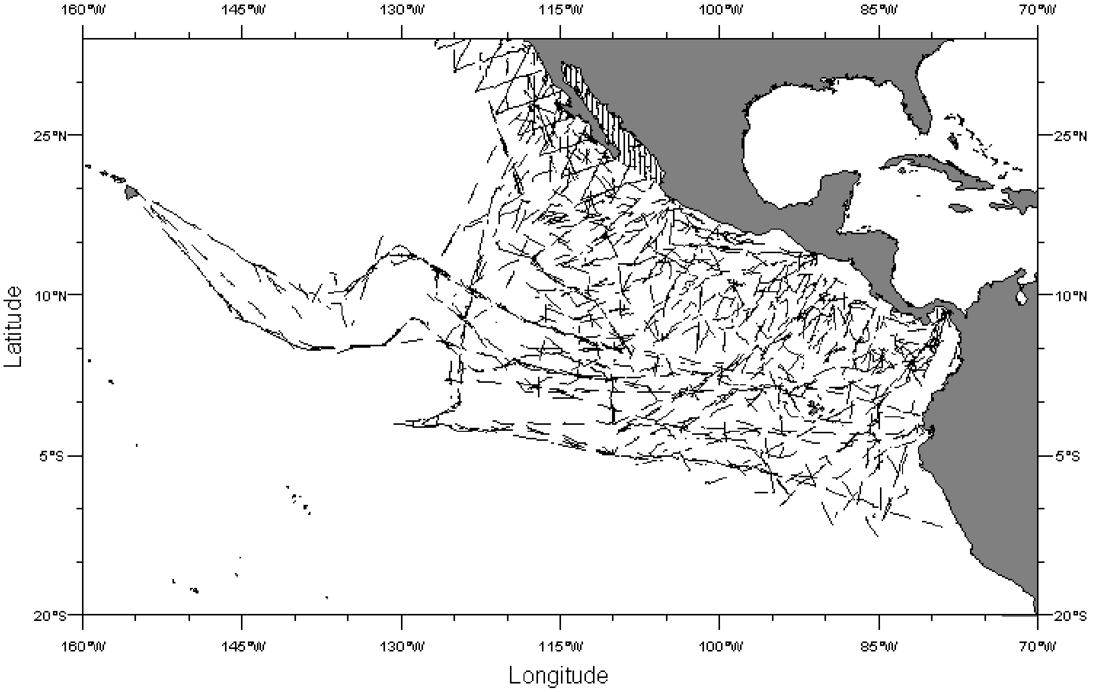

Figure 3.1. Transect lines covered during the 1986-1990 and 1993 line-transect surveys conducted by the Southwest Fisheries Science Center.

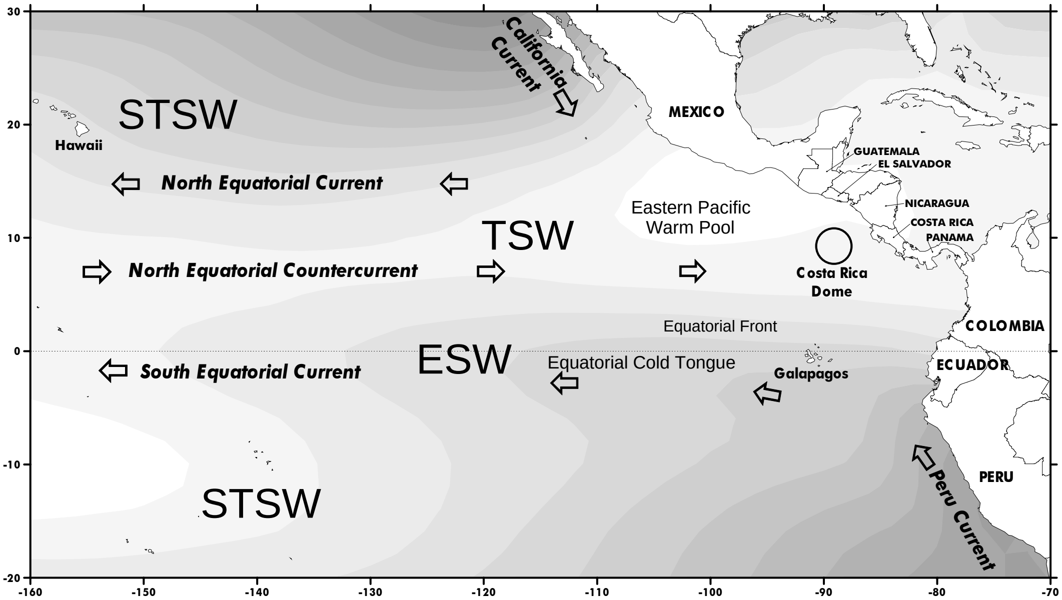

Figure 3.2. Oceanography of the eastern tropical Pacific study area. STSW: Subtropical Surface Water; TSW: Tropical Surface Water; ESW: Equatorial Surface Water. Shading indicates relative sea surface temperatures.

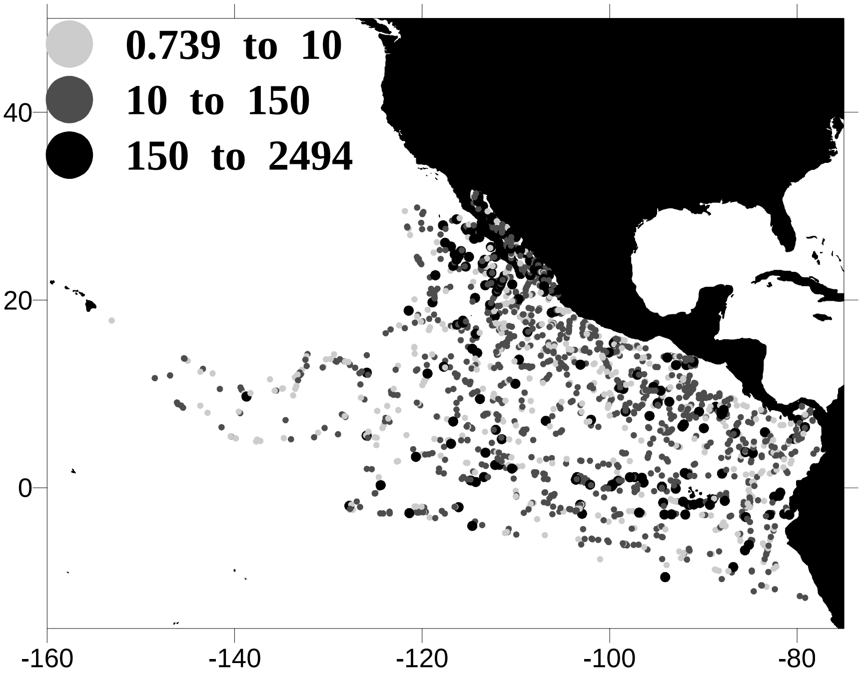

Figure 3.3. Average size of delphinid groups in 9km segments used to build group size GAMs. Data were collected during 1986-1990 and 1993 shipboard cetacean line-transect surveys conducted by the Southwest Fisheries Science Center.

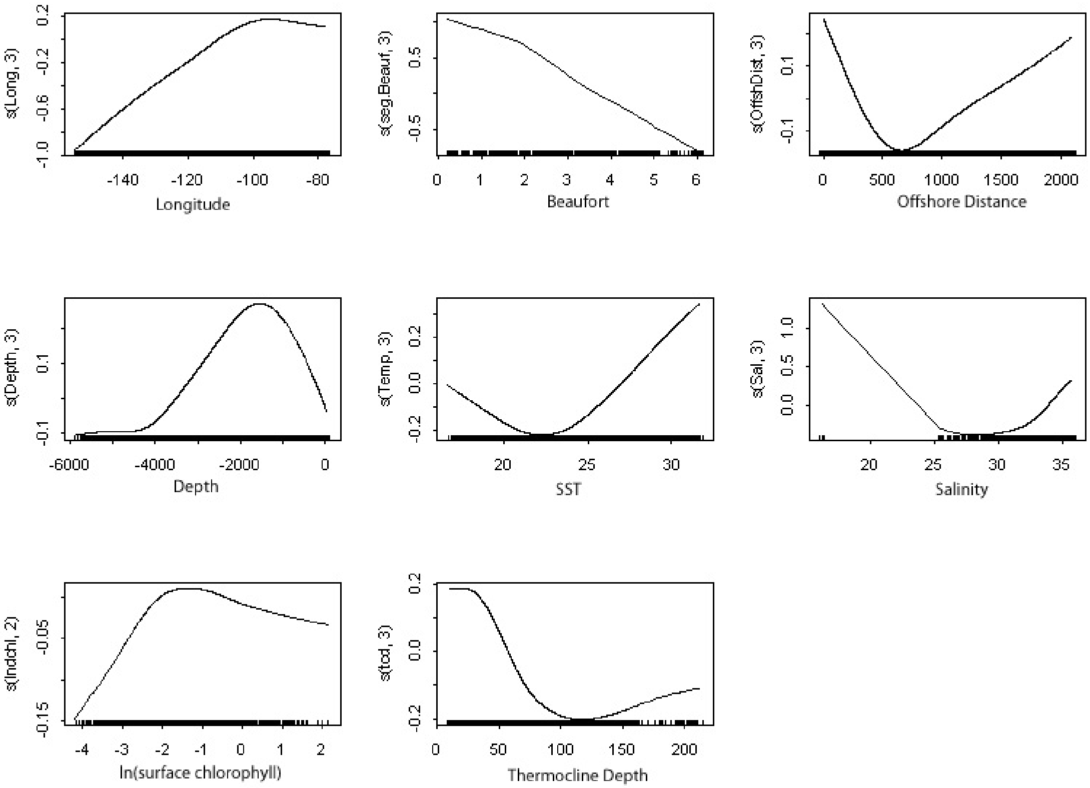

Figure 3.4. Smooth spline functions of the predictor variables incorporated in the final delphinid encounter rate (# sightings/unit survey effort) GAM. Degrees of freedom for non-linear fits are in the parentheses on the y-axis. Tick marks above the x-axis indicate the distribution of observations in all segments (with and without delphinids).

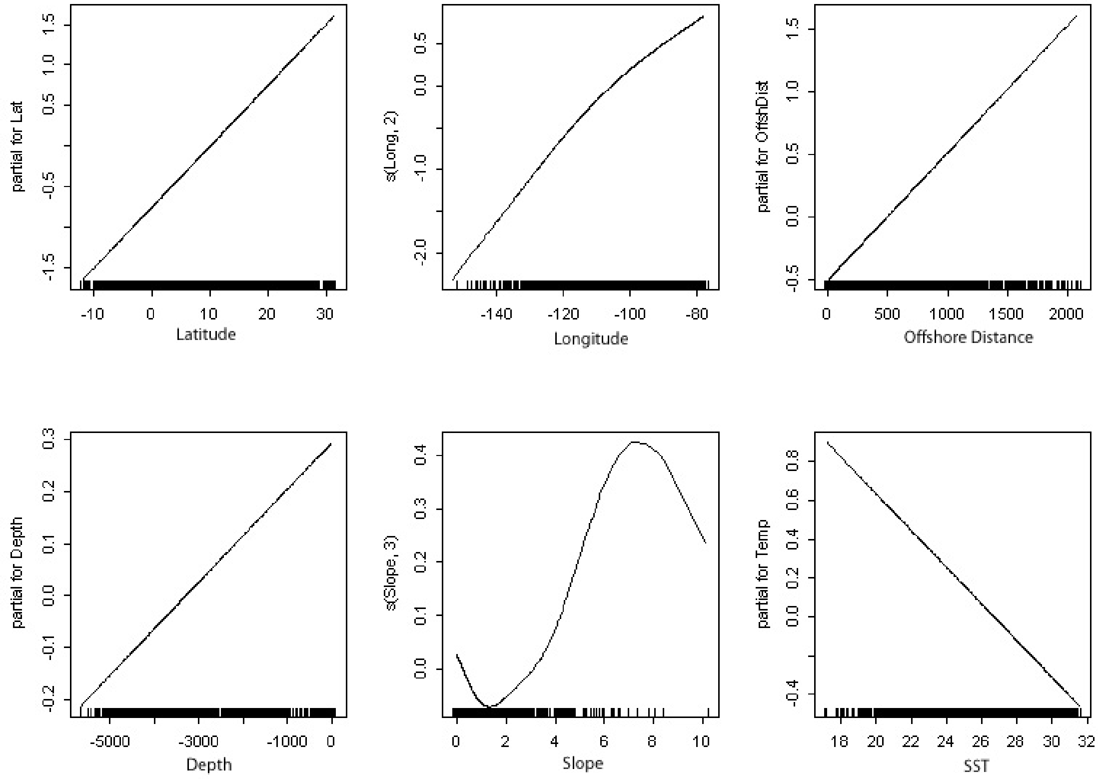

Figure 3.5. Smooth spline functions of the predictor variables incorporated in the final delphinid group size (# sightings/unit survey effort) GAM. Degrees of freedom for non-linear fits are in the parentheses on the y-axis. Tick marks above the x-axis indicate the distribution of observations in all segments with delphinid sightings.

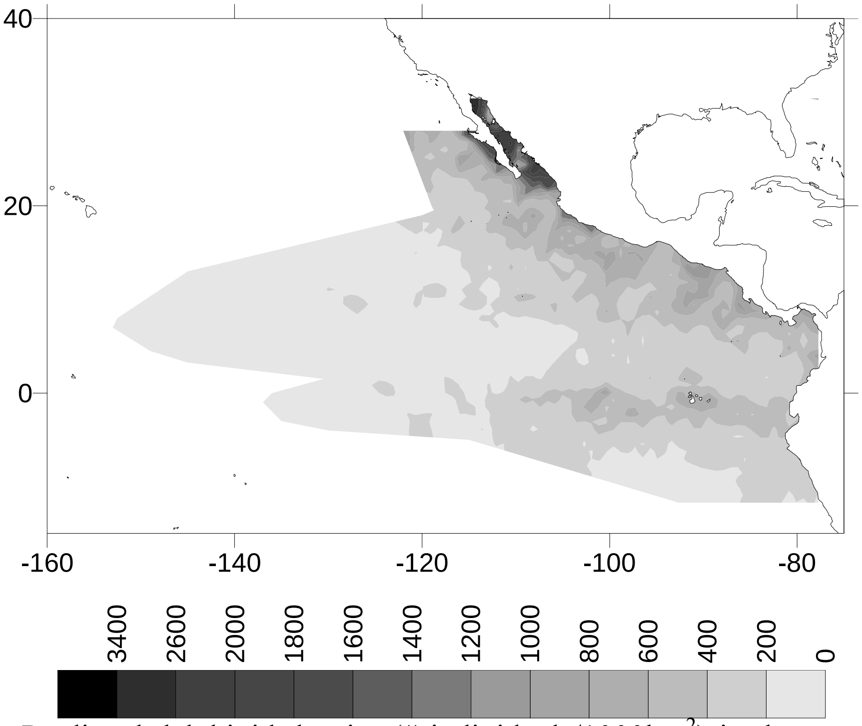

Figure 3.6. Predicted delphinid density (# individuals/1000km$^2$) in the eastern tropical Pacific Ocean. Predictions are based on oceanographic data collected during the 1986-1990 and 1993 cetacean line-transect surveys conducted by the Southwest Fisheries Science center. Predicted values were smoothed in geographic space using an inverse distance weighting.

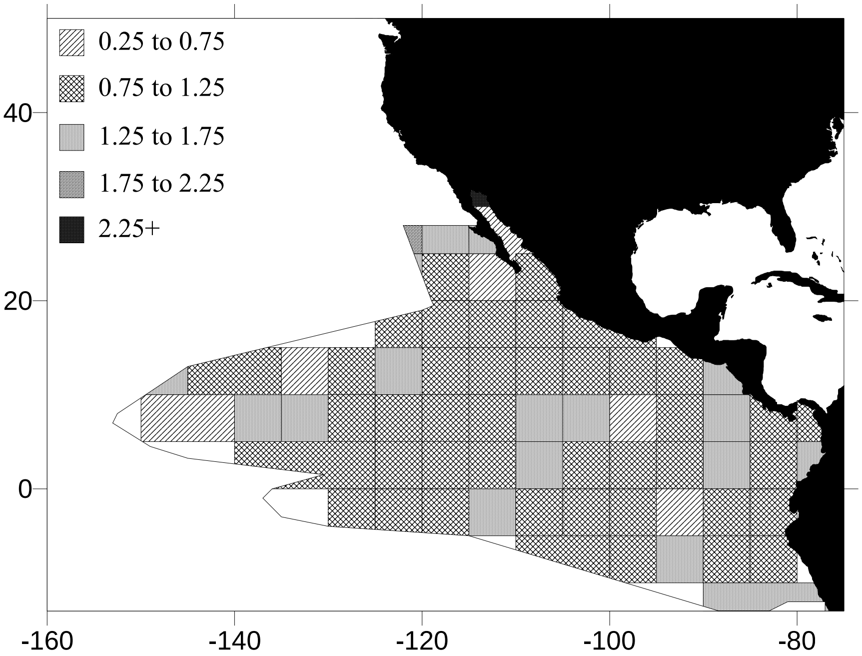

Figure 3.7. Geographic distribution of residuals for delphinid encounter rates measured as the ratio $R_{ER}$=[sum(predicted)/sum(observed)]. Predictions were based on observed oceanography data from Southwest Fisheries Science Center cetacean line-transect survey cruises in 1986-1990 and 1993.

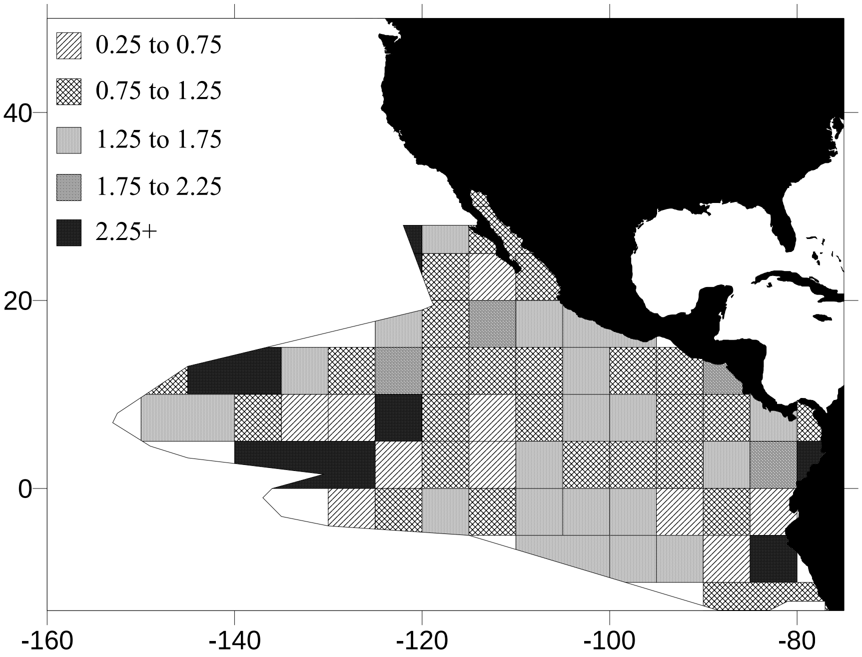

Figure 3.8. Geographic distribution of residuals for delphinid group sizes measured as the ratio $R_{ss}$=*[sum(predicted)/sum(observed)]*. Predictions were based on observed oceanography data from Southwest Fisheries Science Center cetacean line-transect survey cruises in 1986-1990 and 1993.

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# CHAPTER FOUR

# QUANTITATIVE STUDIES OF BEAKED WHALE HABITATS: A WORLDWIDE REVIEW

BY

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## Abstract

Beaked and bottlenose whale (Family Ziphiidae) habitat studies from five regions are reviewed. The review focuses on analyses that were quantitative and investigated a combination of physical oceanographic, biological oceanographic, and geographic variables with potential power to predict ziphiid whale occurrence or density. Included in the review are studies from the following regions: the 1.) North Atlantic Ocean, along the east coast of North America; 2.) Atlantic Frontier, located north and west of Scotland; 3.) Mediterranean Sea; 4.) Bahamas; and 5.) Gulf of Mexico. The studies differed in the scope of environmental variables examined and the analytical methods used to investigate beaked and bottlenose whale habitat preferences. Nevertheless, in all of the studies reviewed, beaked and bottlenose whales were typically found where their prey, deepwater fishes and cephalopods, tend to concentrate. A variety of mechanisms, including stationary features such as the topography of the ocean bottom and dynamic features such as fronts and warm core rings, were identified as being potentially instrumental in concentrating prey.

## Introduction

Beaked whale (family Ziphiidae) mass strandings recently have received international attention (Peterson, 2003). Among the scientific community, it is generally believed that these stranding events were caused by loud anthrophogenic noise, such as seismic surveys and mid-frequency sonar, in the marine environment (Anon., 2001; Peterson, 2003). Beaked whales are infrequently observed because they have long dive intervals (Barlow, 1999) and they are inconspicuous to both visual (Barlow, 1999) and acoustic (Johnson *et al.*, 2004) observers when they are near the surface. As a result, a fundamental obstacle to reducing the negative impacts that human activities have on beaked whales is that relatively little is known about these animals; therefore, understanding beaked whale ecology has become a research priority.

Ostrom (1993) and Ohizumi (2003) used diet analyses to make inferences about the habitat and behavior of Sowerby's beaked whale (*Mesoplodon bidens*) and Baird's beaked whale (*Berardius bairdii*), respectively. With the assumption that the density of individuals in a given region is a function of ecology, examining beaked whale densities in the context of their environment may provide information on habitat. Kasuya and Miyashita (1997) examined the qualitative relationship between Baird's beaked whale sightings, geographic coordinates, and bathymetry off Japan, and Weir *et al.* (2001) reported findings of a similar study on beaked whales in the Atlantic Frontier. D'Amico *et al.* (2003) investigated the qualitative relationships of Cuvier's beaked whale (*Ziphius cavirostris*) sightings in the Mediterranean Sea with physical and biological parameters. Where sufficient data are available, researchers have investigated quantitative relationships between beaked whales and their environment to predict the probability of occurrence or the density of individuals at a given location. The following is a comprehensive review of quantitative studies of beaked whale habitats in five regions: the 1.) North Atlantic Ocean, along the east coast of North America; 2.) Atlantic Frontier, located north and west of Scotland; 3.) Mediterranean Sea; 4.) Bahamas; and 5.) Gulf of Mexico (Figure 4.1) A sixth region, the eastern tropical Pacific ocean, will be discussed in detail in Chapter Five. Representatives of the family Ziphiidae are found in all the world's oceans, from polar to equatorial regions (MacLeod *et al.*, in review). Therefore, the five regions included in this review cover a small fraction of known beaked whale habitat, reflecting our lack of knowledge about these animals.

## 1. North Atlantic Ocean: Northeast Coast of North America

Waring *et al.* (2001) analyzed cetacean sighting data collected during shipboard line-transect surveys conducted during the summers of 1990, 1991, 1993 and 1995 to 1998 in the shelf-edge and deeper waters off the northeastern coast of the US. The purpose of their analysis was to determine if relationships existed between Cuvier's and *Mesoplodon* beaked whale distribution and the environmental variables sea surface temperature (SST), monthly frontal probability (derived from satellite images) and bottom topography, including depth, slope and presence of submarine canyons. They reported that beaked whales were generally sighted along the continental shelf break (200 to 2,000m) and the north wall of the Gulf Stream (a dynamic oceanographic feature), although a few were sighted in proximity to New England seamounts. In addition, results from Wilcoxon signed rank tests suggested that the mean sighting rates of beaked whales were higher in waters above canyons than in non-canyon regions. Predictions from multiple logistic regression models with 4km$^2$ resolution indicated that beaked whales preferred waters along the outer shelf edge. Waring *et al.* (2001) suggested that beaked whales occupy topographically diverse areas such as shelf edges, submarine canyons and seamounts because these features influence the oceanography of the region, thereby concentrating prey. They postulated that beaked whales might also be associated with ephemeral features, such as warm core rings and seasonal frontal boundaries, that tend to concentrate prey. Hamazaki (2002) created a multiple logistic regression model for beaked whales using the same cetacean sighting data, environmental variables and analytical methods as Waring *et al.* (2001), but on a 10-minute grid scale. In spite of the difference in scale, Hamazaki's (2002) model was identical to Waring *et al.*'s (2001) in both the predictor variables and the signs of the coefficients of the predictor variables incorporated into the model.

Hooker *et al.* (2002) studied habitat use and movement patterns of northern bottlenose whales (*Hyperoodon ampullatus*) above a submarine canyon, the Gully, located off eastern Canada during the summer months of 1988 to 1998. They conducted non-systematic surveys and employed photo-identification and radio-tracking methods. The whales were most often found in waters ranging from 500 to 1,500m deep and over steep topography; these relationships were statistically significant based on Kolmogorov-Smirnov (K-S) goodness-of-fit tests. They found that the distribution of the whales differed among survey years and attributed that difference to shifting distributions of prey (their primary prey are adult squid of the genus *Gonatus*).

Wimmer and Whitehead (2004) studied the distribution and movement of northern bottlenose whales on the shelf break off Nova Scotia and in adjacent waters. During the summers of 2001 and 2002, visual, acoustic, and photo identification surveys were conducted. Survey effort in 2001 followed the 1000m contour from 72°W to 54°W (New Jersey to the southern Grand Banks off Newfoundland), whereas in 2002 survey effort was confined to three submarine canyons, the Gully, Shortland Canyon, and Haldimand Canyon. From an extensive review of published and unpublished literature, databases, fisheries observer reports, reports of dedicated surveys and opportunistic sightings, Wimmer and Whitehead (2004) found that the majority of northern bottlenose whale sightings in the region occurred along the edge of the Scotian Shelf. During the 2001 and 2002 surveys, northern bottlenose whales were sighted only in the Gully, and in Shortland and Haldimand Canyons, and were heard more often in canyon areas than on the continental slope (statistical tests were not conducted on acoustic detection rates, but a chi-square test on the number of acoustic detections was not significant). Northern bottlenose whale encounter rates (the ratio of the number of encounters to the number of hours surveyed in good conditions) varied among canyons, ranging from a low of 0.138 in Haldimand canyon to a high of 0.541 in the Gully. A general trend for higher encounter rates in the Gully than in either Shortland or Haldimand Canyon was evident, although not statistically tested. The photo identification data, evaluated using G-tests for goodness of fit, showed that individual northern bottlenose whales exhibited preferences for particular canyons, but that there was no significant preference for particular canyons by different age/sex classes (mature males versus subadult males versus immature males and females). Movement models fit to lagged identification rates (the probability of identifying an animal in the study area after some time lag, given that it was previously identified in the study area) by likelihood methods were used to assess the northern bottlenose whales' pattern of residence within the study area encompassing the three submarine canyons, based upon the photo identification data. Results from the movement models suggested that northern bottlenose whale residence was best described as one of "emigration and re-immigration," with individuals averaging 22 days inside any given canyon; females tended to stay in the study area for 40 days, whereas males remained for only 16 days. Similar methods were used to develop models to investigate northern bottlenose whale movement among the three submarine canyons. The "fully mixed" model of randomly moving relatively quickly among canyons performed approximately as well as the "migration-full interchange" model, which suggested that some individuals move between canyons, staying approximately 1.3 days before moving. This apparent discrepancy was attributed to heterogeneity in movement patterns among individuals in the population. Although the sample size was too small to develop age/sex-based models to describe movement among the canyons, the data suggested that, for northern bottlenose whales, mature males moved more frequently than females and immature males. Likelihood methods were also used to estimate transition probabilities for northern bottlenose whale movement among the three submarine canyons and an unspecified external area. The transition probabilities suggested that individuals were more likely to stay in the same area than to move after one day, rates of movement to new areas was lowest for the Gully, and the whales moved into each of the submarine canyons from the external area with equal probabilities. The home range for northern bottlenose whales in the region was a few hundred kilometres, with individuals moving approximately 50 to 100km over several days.

Wimmer (2003) analyzed the distribution and movement patterns of cetaceans, including northern bottlenose whales and *Mesoplodon* beaked whales, in the same study area and using the same data as Wimmer and Whitehead (2004). Wimmer (2003) found that *Mesoplodon* beaked whales were frequently sighted east of George's Bank off the northeastern US and near the Northeast Channel off southeastern Canada. *Mesoplodon* beaked whales were sighted in canyon and non-canyon slope waters, with higher (but not statistically significant) sighting rates in the latter. K-S goodness of fit tests were used to study whether northern bottlenose whale and *Mesoplodon* beaked whale distributions with respect to five explanatory variables (longitude, month, sea surface temperature, slope, and depth) differed from the general characteristics of the study area. Results from the K-S tests applied to the 2001 survey data implied that *Mesoplodon* beaked whales were typically found early in the summer, in western waters with colder sea surface temperatures, whereas northern bottlenose whales tended to be found later in the summer, in eastern waters, warmer sea surface temperatures, and over topography with steeper slopes. Results from the K-S tests applied to the 2002 survey data suggested that northern bottlenose whales in Shortland canyon were found in warmer, shallower waters with steep slopes. Although not statistically significant, during 2002, *Mesoplodon* beaked whales in Shortland Canyon were found in warmer waters over steeper topography, *Mesoplodon* beaked whales in Haldimand Canyon were found over gently sloping topography, and northern bottlenose whales in Haldimand Canyon were found in deeper waters. Wimmer (2003) warns that the results from the K-S tests might be misleading, however, due to small sample sizes, lack of independence among sightings, and strong relationships between month and sea surface temperature and between month and longitude due to the non-random survey design (west to east, from beginning in early spring and continuing through late summer).

## 2. Atlantic Frontier

The Atlantic Frontier is a region in the North Atlantic Ocean stretching from west of the Hebrides in Scotland to the west and north of Shetland. It covers a range of topographic features, from the continental shelf edge to slope and oceanic waters, including a number of seamounts, ridges and troughs. MacLeod (2005) studied the habitat preferences of northern bottlenose whales and Sowerby's beaked whales in this region, applying ecological niche factor analysis (ENFA) to presence-only datasets collected year-round between 1979 and 1999. MacLeod (2005) considered three oceanographic variables in the analysis: depth, seabed slope and aspect of the seabed. The sighting data for the two beaked whale species were pooled and compared to the oceanographic data on a grid of 1km x 1km cells. The ENFA analysis predicted that beaked whales (both species pooled) may be found in waters characterized by a relatively narrow range of values for the topographic variables compared to the overall study area. In particular, beaked whales tended to occupy deeper waters in areas with higher slopes than average, and southward or westward facing slopes. Based upon these criteria, two areas were identified as key beaked whale habitat: 1) the Faroe-Shetland Channel and waters to the northeast of it, and 2) the open Atlantic waters to the southwest and west of the Faroe Islands. Less suitable for beaked whales in this region were areas over the continental shelf and the deeper waters of the Rockall Trough. MacLeod (2005) hypothesized that beaked whale habitat preferences in this region are related to the distribution of the cephalopods and deepwater fishes that comprise their prey.

### 3. Mediterranean Sea

Cañadas *et al.* (2002) examined the relationships of several cetacean species, including beaked whales, to depth and slope in the Alboran Sea, a highly productive region of the Mediterranean Sea, located South of Spain. They reported that 33 beaked whales were encountered during their ship-based visual surveys conducted during the months of April, June, July, August, September in 1992 and 1995 to 2001. Based on results from a chi-square analysis, Cañadas *et al.* (2002) concluded that beaked whales in the Alboran Sea 'showed a strong preference' for areas greater than 600m depth with slopes of more than $2.3^{o}$. To model beaked whale encounter rates, Cañadas *et al.* (2002) specified a generalized linear model (GLM) with a Poisson distribution and log link function, and used stepwise selection via AIC (Akiake Information Criterion) to identify explanatory variables from a scope that included linear or higher order polynomial functions of depth and slope, and an interaction term between depth and slope. The final beaked whale encounter rate GLM incorporated only depth and a quadratic function of depth. Cañadas *et al.* (2002) noted that the distribution of beaked whales in their surveys 'appears to match' the habitat of their prey, namely deep sea squid.

### 4. The Bahamas: East of Great Abaco

MacLeod *et al.* (in press) describe the cetacean community structure in the waters east of Great Abaco in the northern Bahamas. This region is approximately 35km in length and up to 34km in width, encompassing coral reefs, shallow shelves, steeply sloping shelf edges, the upper reaches of the Little Abaco Canyon and deep oceanic areas. They reported that nine cetacean species were recorded during surveys conducted between May and August each year from 1998 to 2000 and in May of 2001. They divided the cetacean community into two groups, 'permanent species' and 'sporadic species,' based upon relative sighting rates. Blainville's beaked whale (*Mesoplodon* *densirostris*) and Cuvier's beaked whale were the only beaked whales sighted, and they were placed in the permanent species group. To better understand the cetacean community structure in this region, MacLeod *et al.* (in press) divided the study area into a grid of 500 x 500m cells and used chi-square tests to examine patterns in the distribution of each of the four permanent species with respect to water depth and seabed slope. Blainville's beaked whales were most often sighted in waters 200 to 1,000m deep, having slopes between $5.7^o$ and $16.7^o$; and Cuvier's beaked whales were found in waters greater than 1,000m with slopes between $11.3^o$ to $16.7^o$.

MacLeod and Zuur (in press) examined the habitat use by Blainville's beaked whale in the Great Abaco region of the Bahamas in greater detail using multiple logistic regression in a generalized additive model (GAM) framework and classification and regression trees (CART). Data were collected during small boat surveys conducted regularly between May and August of 1998 to 2000. They related Blainville's beaked whale occurrence to the topographic variables water depth, seabed slope and seabed aspect using a grid size of 500 x 500m. MacLeod and Zuur (in press) observed that Blainville's beaked whales selected specific habitats within the study region. The whales were found in depths ranging from 136 to 1,319m, whereas the range for the entire study area spanned from 10 to over 3000m depth. Furthermore, the whales were observed over slopes of $3.9^o$ to $16.5^o$, compared to $0^o$ to $27.7^o$ present in the study area as a whole. Results from the GAM indicated that all three topographic variables were important in describing Blainville's beaked whale occurrence; depth and slope factored into the models as nonlinear functions. Results from the CART analysis implied that aspect was the most important variable examined, followed by slope and depth: Blainville's beaked whales preferred northeast facing slopes, with slopes between $4.7^o$ and $10.1^o$ and depths between 249.5 and 605m. MacLeod and Zuur (in press) suggested that these small-scale patterns in Blainville's beaked whale distribution are a function of their prey distribution, which may accumulate in habitats identified by the characteristics listed above due to interactions between the Deep Western Boundary Current and seabed topography.

## 5. Gulf of Mexico

To characterize cetacean habitats along the continental slope in the north-central and western Gulf of Mexico, Davis *et al.* (1998) related cetacean sighting data from shipboard visual surveys conducted seasonally from April 1992 to May 1994 to simultaneous oceanographic measurements from hydrographic sampling and satellite remote sensing. Included in their analysis were *Mesoplodon* beaked whales, unidentified beaked whales, and eleven other species (bottlenose dolphins (*Tursiops truncatus*), Atlantic spotted dolphins (*Stenella frontalis*), spinner dolphins (*Stenella longirostris*), striped dolphins (*Stenella coeruleoalba*), pantropical spotted dolphins (*Stenella attenuata*), Clymene dolphins (*Stenella clymene*), Risso's dolphins (*Grampus griseus*), short-finned pilot whales (*Globicephala macrorhynchus*), pygmy/dwarf sperm whales (*Kogia* spp.), rough-toothed dolphins (*Steno bredanensis*) and sperm whales (*Physeter macrocephalus*)). To test whether environmental differences were evident among species, they gridded the environmental data into 1.1 x 1.1km cells and used the Kruskall-Wallis one way analysis of variance with a posteriori comparisons. Unidentified beaked whales were sighted in waters with some of the steepest sea surface temperature gradients (mean = 0.12$^{o}$C/1.1km); the mean value for *Mesoplodon* was slightly smaller (0.09$^{o}$C/1.1km). Both categories of beaked whales showed wide ranges in sea surface temperatures (21.5 to 28.8$^{o}$C for unidentified beaked whales and 18.2 to 28.6$^{o}$C for *Mesoplodon* beaked whales), encompassing some of the coolest to the warmest observed in the Gulf of Mexico study. Beaked whales were sighted over moderate slopes (mean = 0.932$^{o}$ for unidentified beaked whales, and 0.771$^{o}$ for *Mesoplodon* whales). The environmental variable exhibiting the greatest range and variability among species was bottom depth. Beaked whales were found in the deepest water (mean = 1,273.7m for unidentified beaked whales, and 1,196.9m for *Mesoplodon* beaked whales). The differences among species in sea surface temperature gradient, sea surface temperature, slope and depth were all significant. In contrast, Davis *et al.* (1998) found no differences among species in the depth of the 15°C isotherm, water temperature at 100 m, or sea surface salinity. They hypothesized that the dynamic oceanography of the Gulf of Mexico and the remarkable mobility and physiological tolerances of the cetaceans studied contributed to the inability to differentiate among species based upon many of the physical oceanographic variables. Davis *et al.* (1998) concluded by saying, 'The distribution of cetaceans is probably better explained by the availability of prey, which may be influenced secondarily by oceanographic features.'

### Summary

A common theme in all of the ziphiid whale habitat studies reviewed was that these cetaceans tend to be found where their prey, deepwater fishes and cephalopods, are concentrated. Furthermore, a variety of mechanisms for concentrating prey were postulated by the different habitat studies, including interactions between topographic features and currents (Waring *et al.*, 2001; Hooker *et al.*, 2002; MacLeod, 2005; MacLeod and Zuur, in press), and ephemeral oceanographic features such as warm core rings and fronts (Waring *et al.*, 2001; Hamazaki *et al.*, 2002). It is important to recognize, however, that results from the habitat studies described above were not directly comparable because they examined different environmental variables, investigated different spatial scales, and utilized different analytical methods. In general, the studies relied upon environmental data that were easy to acquire, such as topographic variables (depth, slope, aspect, presence of canyons), sea surface temperature, sea surface salinity and derivatives thereof (Table 4.1). These variables are surrogates that are correlated with more causal factors, such as the abundance of prey. To better understand the ecology of ziphiid whales, researchers must understand the ecology of their prey.

## Acknowledgements

I would like to thank Jay Barlow, Jessica Redfern, Colin MacLeod, and three anonymous reviewers for their helpful comments on previous drafts. This work was funded by the National Science Foundation Graduate Fellowship Program, the U.S. Navy through the Office of Naval Research (ONR), and the Strategic Environmental Research and Development Program (SERDP).

Table 4.1. Comparison of beaked whale habitat studies.

| Source | Species | Scale of Data Analysis | Variables Examined | Analytical Methods |
|---|---|---|---|---|
| Davis *et al* ., 1998 | *Mesoplodon spp. &* unidentified beaked whales | 1.1 x 1.1 km | Sea Surface Temperature* | Kruskall-Wallis one-way ANOVA with a posteriori comparisons[a] |
| | | | SST gradient* | |
| | | | Depth of 15-degree C isotherm | |
| | | | Water Temperature at 100m | |
| | | | Sea Surface Salinity | |
| | | | Depth* | |
| | | | Slope* | |
| Waring *et al* ., 2001 | *Mesoplodon* spp. & *Ziphius cavirsotris* | 2 x 2 km | Sea Surface Temperature | multiple logistic regression GLM (stepwise selection)[b,c] |
| | | | Monthly Probability of a Front* | |
| | | | Depth * | |
| | | | Slope* | |
| | | | Presence of Submarine Canyon* | Wilcoxin Signed Rank Test |

[a] Used to test differences among species.

[b] Did not elaborate on type of stepwise selection.

[c] Did not state selection criterion.

*Variable found to be important in the analysis.

Table 4.1, continued. Comparison of beaked whale habitat studies.

| Source | Species | Scale of Data Analysis | Variables Examined | Analytical Methods |
|---|---|---|---|---|
| Hamazaki, 2002 | *Mesoplodon* spp. and *Ziphius cavirostris* | 10 x 10 min (approx. 18.5 x 18.5km) | Sea Surface Temperature | multiple logistic regression GLM (forward/backward stepwise selection)[a] |
| | | | Monthly Probability of a Front* | |
| | | | Depth* | |
| | | | Slope* | |
| Hooker *et al.*, 2002 | *Hyperoodon ampullatus* | 500 x 500 m | Depth* | Kolmogorov-Smirnov goodness of fit |
| | | | Slope* | |
| Canadas *et al*., 2002 | Family Ziphiidae | 2 x 2 min | Depth* | Poisson-based GLM (stepwise selection via AIC) and Chi-square |
| | | | Slope | |
| Wimmer, 2003 | *Hyperoodon ampullatus* & *Mesoplodon* spp. | (approx. 1 km to 11 km) | Depth* | Kolmogorov-Smirnov goodness of fit |
| | | | Slope* | |
| | | | Sea Surface Temperature* | |
| | | | Longitude* | |
| | | | Presence of Submarine Canyon* | Chi-square goodness of fit |
| MacLeod, 2005 | *Hyperoodon ampullatus* & *Mesoplodon bidens* | 1 km x 1 km | Depth* | Eclogical Niche Factor Analysis |
| | | | Slope* | |
| | | | Aspect* | |

[a] Did not state selection criterion.

*Variable found to be important in the analysis.

Table 4.1, continued. Comparison of beaked whale habitat studies.

| **Source** | **Species** | **Scale of Data Analysis** | **Variables Examined** | **Analytical Methods** |
|---|---|---|---|---|
| MacLeod *et al* ., in press | *Mesoplodon bidens* & *M. densirostris* | 500 x 500 m | Depth* | Chi-square goodness of fit |
| | | | Slope* | |
| MacLeod & Zuur, in press | *Mesoplodon densirostris* | 500 x 500 m | Depth* | CART & multiple logistic regression GAM (backwards selection via AIC) |
| | | | Slope* | |
| | | | Aspect* | |
| Ferguson *et al* ., Chapter 5 | *Ziphius cavirostris* and *Mesoplodon* spp. | 9 km | Latitude* | Poisson-based and lognormal GAMs (forward/backward stepwise AIC; cross-validation) |
| | | | Longitude | |
| | | | Beaufort Sea State* | |
| | | | Distance Offshore* | |
| | | | Depth* | |
| | | | Slope | |
| | | | Sea Surface Temperature* | |
| | | | Sea Surface Salinity* | |
| | | | Discrete Surface Chlorophyll | |
| | | | Thermocline Strength* | |
| | | | Thermocline Depth* | |

*Variable found to be important in the analysis.

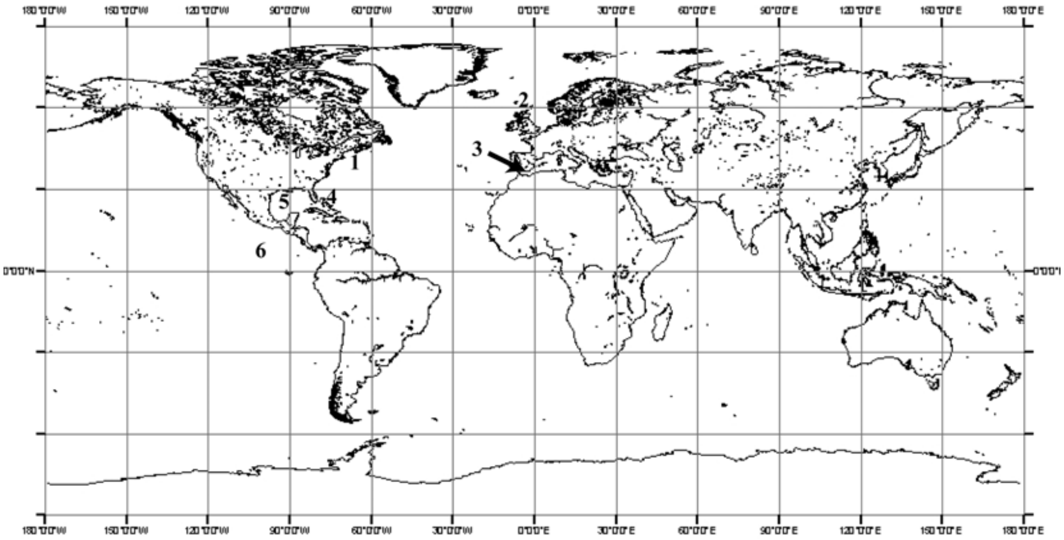

Figure 4.1. Location of beaked whale habitat studies: 1.) North Atlantic Ocean, Northeast coast of North America; 2.) Atlantic Frontier; 3.) Mediterranean Sea; 4.) The Bahamas: East of Great Abaco; 5.) Gulf of Mexico; 6.) eastern tropical Pacific Ocean (Chapter Five).

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# CHAPTER FIVE

# PREDICTING CUVIER'S (*ZIPHIUS CAVIROSTRIS*) AND *MESOPLODON* BEAKED WHALE DENSITIES AS FUNCTIONS OF THE ENVIRONMENT IN THE EASTERN TROPICAL PACIFIC OCEAN

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## Abstract

We use temporally dynamic environmental variables and fixed geographic variables to construct generalized additive models to predict Cuvier's (*Ziphius cavirostris*) and *Mesoplodon* beaked whale encounter rates (number of groups per unit survey effort) and group sizes in the eastern tropical Pacific Ocean. The beaked whale sighting data and environmental data were collected simultaneously during the Southwest Fisheries Science Center's cetacean line-transect surveys conducted during the summer and fall of 1986-90 and 1993. Predictions from the encounter rate and group size models were combined with previously published estimates of line-transect sighting parameters to describe patterns in beaked whale density (number of individuals per unit area) throughout the study area. Results provide evidence that the standard definition of beaked whale habitat proposed in the past may be too narrow, and that beaked whales may be found from the continental slope to the abyssal plain, in waters ranging from well-mixed to highly stratified. Areas with the highest predicted densities were the Gulf of California, the equatorial cold tongue, and coastal waters, including the west coast of the Baja Peninsula and the Costa Rica Dome. Offshore waters in the northern and southern subtropical gyres had the lowest predicted *Mesoplodon* densities, but density predictions were high for Cuvier's beaked whales in the waters southeast of the Hawaiian Islands. For both encounter rate and group size models, there was no geographic pattern evident in the residuals as measured by the ratio of pooled predicted to pooled observed values within geographic strata.

## Introduction

Recent scientific efforts to describe and quantify beaked and bottlenose whale (family Ziphiidae) habitats have been primarily motivated by an interest in mitigating, minimizing, or eliminating harmful effects of human activities on ziphiid whales for conservation or management purposes. Concerns regarding the association of beaked whale mass strandings and loud anthropogenic noise in the marine environment (Anon., 2001; Peterson, 2003) have placed an ecological imperative on the quest for basic knowledge about these cetaceans.

Beaked whales are particularly difficult cetaceans to study because they are infrequently encountered (Houston, 1990a; Ostrom *et al.*, 1993; Weir *et al.*, 2001; Mead, 2002). Furthermore, when human observers are in close proximity to beaked whales, the cetaceans may go unnoticed because they have long dive times, they surface without a visible blow or splash (Barlow 1999, Weir *et al.* 2001) and they are relatively silent when they are within 200m of the surface (Johnson *et al.* 2004). As a result, most knowledge about many beaked whale species comes only from stranded specimens (Palacios, 1996; Houston, 1990a; Houston, 1990b; Dalebout *et al.* 2002). New species recently have been identified and described (Reyes *et al.* 1991; Pitman *et al.*, 1999; Pitman and Lynn, 2001; Dalebout *et al.* 2002). Dalebout *et al.* (2002) note that, 'Of the twelve cetacean species described in the last 100 years, eight have been ziphiids, primarily of the genus *Mesoplodon*.' Nevertheless, progress is ongoing in efforts to understand the ecology of beaked whales.

It is conventionally thought that beaked and bottlenose whales prefer deep-water habitats (Jefferson *et al.* 1993; Reeves *et al.* 2002; Mead 2002). Beyond this basic preference, several authors have described beaked and bottlenose habitat preferences for specific study areas based on qualitative or correlation studies (reviewed by Ferguson 2005, Chapter Four). In the Gulf of Mexico, beaked whales were found in the deepest average water depths of any cetacean species (Davis *et al.*, 1998). Most studies have reported that beaked whales are commonly seen in waters over the continental slope (200-2000m depth) (Waring *et al.*, 2001; Hooker *et al.*, 2002; Wimmer, 2003; MacLeod *et al.*, in press) and submarine canyons (D'Amico *et al.*, 2003; Wimmer, 2003; Wimmer and Whitehead, 2004). MacLeod *et al.* (in press) also found that Cuvier's and *Mesoplodon* beaked whales were most often sighted over seafloors with greater slopes than the remainder of the study area in the Bahamas. Several authors have speculated that the distribution of beaked whales (or cetaceans in general) is likely to be primarily determined by the availability of the prey (Davis *et al.*, 1998; Cañadas *et al.*, 2002; Hooker *et al.*, 2002; MacLeod, 2005).

Various methods have been used to quantitatively model the habitat preferences of beaked whales (reviewed by Ferguson 2005, Chapter Four). The most commonly used method has been logistic regression or generalized linear models (GLMs) with a logistic link function to model number of beaked whales seen per unit of search effort, as a function of habitat variables. Waring *et al.* (2001) and Hamazaki (2002) found that Cuvier's and *Mesoplodon* beaked whales off the northeastern coast of the United States were associated with the outer shelf edge. Cañadas *et al.* (2002) used GLMs to examine beaked whale distributions in the Mediterranean Sea and found that functions of depth were better predictors than functions of seafloor slope. Other quantitative methods applied to beaked whale habitat studies have included ecological niche factor analysis (ENFA, MacLeod, 2005), which showed that beaked whales in the North Atlantic Frontier (from west of the Hebrides in Scotland to the west and north of Shetland) tended to occupy deeper waters in areas with higher slopes than average, and preferred southward and westward facing slopes. MacLeod and Zuur (in press) used generalized additive models (GAMs) and classification and regression trees (CART) to examine beaked whale habitat associations in the Bahamas and found that depth, seabed slope, and seabed aspect were all important factors.

Few of the previous attempts to model beaked whale distribution were based on data collected over broad geographic areas and few included substantial areas of deep-water habitat with low seafloor slope (abyssal plains). None of the previous studies included variation in beaked whale group size with habitat variables. Only the recent studies by MacLeod and Zuur (in press) allowed for non-parametric, non-linear responses to habitat gradients. In this paper, we quantitatively model beaked whale habitat preferences and distributions from ship line-transect surveys conducted in a vast area of the eastern tropical Pacific Ocean that includes continental shelf, slope, and abyssal plain habitats. We quantify geographic variation in density for two species of beaked whales (Cuvier's beaked whales (*Ziphius cavirostris*) and *Mesoplodon* beaked whales (*Mesoplodon densirostris, Mesoplodon peruvianus,* and *Mesoplodon* spp.)) by modelling variation in encounter rates and group sizes using generalized additive models (GAMs). Our results show that some of the previous generalities that have been inferred from more limited studies do not appear valid for these species in our study area.

## Methods

### Study Area

The study area encompasses 19.6 million km$^2$ of the eastern tropical Pacific Ocean (Figure 5.1). Circulation patterns in the surface waters of the region are dominated by the zonal equatorial current system between the anticyclonic North and South Pacific subtropical gyres (Kessler, 2005). The California Current and the Peru Current form the eastern boundaries of the North and South Pacific gyres, respectively (Figure 5.2). The California Current flows into the North Equatorial Current, and the Peru Current flows into the South Equatorial Current. The North Equatorial Countercurrent flows towards the east in the latitudes between the North and South Equatorial Current. Three primary surface water masses exist in the ETP: the warm, low-salinity Tropical Surface Water, which includes the eastern Pacific warm pool and underlies the Intertropical Convergence Zone (ITCZ), a zonal band between 5$^o$ and 10$^o$N where rainfall is high as a result of the north and south trade winds converging; the higher-salinity Equatorial Surface Water (the coldest surface water mass) with the equatorial cold tongue projecting from its eastern boundary; and the cool, Subtropical Surface Waters located towards the poleward edges of the ETP, where the highest salinities are found (Fiedler and Talley, 2005) (Figure 5.2). The thermocline is strongest beneath the Tropical Surface Water and weakest beneath the Subtropical Surface Water (Fiedler and Talley, 2005). Although not considered part of the ETP, but included in the analysis nonetheless, the Gulf of California is a region in which evaporation largely exceeds precipitation, resulting in highly saline surface waters. The physical and biological oceanography in the study area interact to produce highly productive waters in the upwelling regions of the California Current, Peru Current, equatorial cold tongue, and Costa Rica Dome, in contrast to the low productivity of the oligotrophic Subtropical Surface Waters (Ryther, 1969; Fiedler and Philbrick, 2002; Fiedler, 2000) (Figure 5.2). In general, both coastal and oceanic upwelling regions are characterized by relatively weak and shallow thermoclines and high levels of chlorophyll. In comparison, the oligotrophic regions have stronger and deeper thermoclines, and lower levels of chlorophyll.

## Field Methods

Cetacean sighting data and *in situ* oceanographic data were collected on SWFSC research cruises conducted during the summer and fall of each year from 1986 to 1990, and in 1993. Two National Oceanic and Atmospheric Administration (NOAA) research vessels, the *David Starr Jordan* and the *McArthur*, followed standard line-transect protocols (Buckland *et al.* 2001) to survey cetaceans in the eastern tropical Pacific Ocean, while concurrently collecting a suite of oceanographic data over the length of the trackline.

Kinzey *et al.* (2000) provide a complete description of the SWFSC cetacean data collection procedures followed during the ship-based line-transect surveys. In brief, two teams of three visual observers rotated through three positions located on the flying bridge of the ship. Starboard and port observers used 25x150 “bigeye” binoculars, scanning an arc of approximately 100° extending from the starboard and port beams, respectively, to 10° on the opposite side of the trackline. A third observer, the designated data recorder, searched with naked eye and, occasionally, 7x50 binoculars across the entire 180° arc in front of the ship. All cetaceans sighted were identified to the lowest taxonomic level possible. Group size estimates were recorded independently by each observer.

The *in situ* oceanographic data collected during the line-transect surveys, and considered as potential predictor variables in the encounter rate and group size models, were: sea surface temperature (SST), sea surface salinity, thermocline depth, thermocline strength, and the natural logarithm of surface chlorophyll concentration (hereinafter simply referred to as surface chlorophyll concentration). Details of the oceanographic data collection methods for each ship and each year between 1986 and 1990 are available in Thayer *et al.* (1988a, 1988b, 1988c, 1988d), Lierheimer *et al.* (1989a, 1989b, 1990a, 1990b), and Philbrick *et al.* (1991a, 1991b). Oceanographic methods and results from the 1993 cruise have not yet been published. The temperature and salinity of the sea surface were recorded continuously using a thermosalinograph and then summarized into hourly means, resulting in a spatial resolution of approximately 18.5km (Table 5.1). Thermocline depth and strength were derived from CTD (conductivity temperature depth) stations and XBT (expendable bathythermograph) probes, having a spatial resolution of approximately 70 to 140km (Table 5.1). Surface chlorophyll concentrations were measured from water samples collected when the CTD was at the surface and have a spatial resolution of approximately 220km (Table 5.1). Beaufort sea state was recorded while the marine mammal observers were on-effort and was updated whenever conditions changed. Beaufort sea state is a dominant factor affecting the visibility of cetaceans; therefore, Beaufort was included in all models to account for potential biases due to visibility. Although it might be possible to account for the sea state visibility bias elsewhere in the density analysis, including Beaufort as a predictor variable in the generalized additive model automatically accounts for correlations among other predictor variables, thereby providing a better assessment of each predictor variable's individual effects on the response variable (Hastie and Tibshirani, 1990).

Additional environmental data that were considered in the models include distance from shore, depth and slope of the ocean bottom, latitude and longitude. Offshore distance was calculated as the shortest distance between a given point on the trackline and the closest point on the North, Central, or South American mainland. Depth data were obtained from the National Geophysical Data Center's TerrainBase data set, which had a spatial resolution of 5 x 5 minutes (approximately 9 x 9km). Slope was derived from the depth data in the two-step process described below.

## Analytical Methods

In preparation for building the models, the beaked whale sighting data and oceanographic data were summarized into 9km segments of on-effort trackline, corresponding roughly to the finest resolution of environmental data. The 9km distance for each segment was measured directly along the trackline; therefore, the start and end points of a given segment may be less than 9km apart as measured by straight-line distance if the trackline in the segment followed bends or curves. Conversely, the straight-line distance between segment start and end points could be greater than 9km if off-effort sections of trackline intervened between contiguous on-effort sections in a given segment. In those instances when off-effort sections separated contiguous on-effort sections, data from the discontinuous sections of on-effort trackline were summarized together if the distance between sequential sections of on-effort trackline was less than 9km; otherwise, the on-effort section before observers went off effort was omitted and the start point for the new segment was located at the beginning of the on-effort section following the lag in effort. Due to the relatively small scale of the analysis, autocorrelation undoubtedly exists in the sighting and oceanographic data on neighboring 9km segments. Nevertheless, our primary goal was prediction rather than explaining ecological relationships or hypothesis testing; therefore, the problems associated with inflated sample size and autocorrelation are largely irrelevant because they do not add appreciable bias to the parameter estimates required for prediction (Neter *et al.*, 1990; Hamazaki, 2004).

Oceanography values for each segment were calculated as weighted averages of the data from the oceanography stations immediately before and after each segment midpoint, where the midpoint was defined as the point at which 4.5km of on-effort trackline had been covered. Inverse distance weighting (distance$^{-1}$) was used for thermocline depth, thermocline strength, and surface chlorophyll, whereas time$^{-1}$ weighting was used for sea surface temperature and sea surface salinity. This difference in weighting methods was necessary because the latter oceanography data were recorded with only a time stamp. Nevertheless, the ships traveled at approximately a constant speed, so the inverse distance and inverse time weighting methods are roughly comparable. Depth values for each segment were calculated as the inverse distance weighted average depth of the four closest nodes in the TerrainBase 5 x 5 minute grid to the segment midpoint. Assigning slope values to each segment required two steps. First, slope values were calculated for each node on the 5 x 5 minute grid as the magnitude of the gradient in depth:

$$Slope = \sqrt{\left(\frac{\partial z}{\partial x}\right)^2 + \left(\frac{\partial z}{\partial y}\right)^2} \quad . \qquad (1)$$

Using compass-based grid notation and representing the slope angle in degrees yields the following equation:

$$Slope = \left(\frac{360.0}{2\pi}\right) * \arctan\left[\sqrt{\left(\frac{Z_E - Z_W}{2\Delta x}\right)^2 + \left(\frac{Z_N - Z_s}{2\Delta y}\right)^2}\right], \qquad (2)$$

where $Z_E$, $Z_W$, $Z_N$, and $Z_s$ refer to the grid nodes to the east, west, north, and south of the desired node. Second, the slope for the segment midpoint was assigned the value of the slope of the node closest to the segment midpoint.

Beaked whale sighting data for each segment were summarized as the total number of groups sighted and the average group size in the segment. Prior research has shown that individual observers' estimates of group size can be biased compared to counts made from aerial photographs and that group size estimates can be improved by applying individual-specific calibrations to correct this bias (Gerrodette *et al.*, 2002). Computing the average group size for each segment required three steps: 1.) calculate the bias-corrected group size estimate for each observer for each sighting in the segment based on individual calibration coefficients; 2.) calculate the mean group size estimate, averaged over all observers, for each sighting in the segment; and 3.) calculate the mean group size estimate, averaged over all sightings, for each segment. For the first step, calculating individual observers' calibrated group size estimates, one of three methods was used; all methods were derived by comparing the observers' uncalibrated group size estimates with group size estimates obtained from photographs of cetacean groups taken during the surveys. Direct calibration with quasi-maximum likelihood bias correction was the preferred method and was used if the group size estimates and Beaufort sea state data necessary for the observer's calibration were available (Gerrodette *et al.,* 2002). Directly calibrated observers have two types of direct calibrations, one that is year-specific and one that is a general calibration to be used in any year (Gerrodette *et al.*, 2002). If data were not available to use the direct calibration model that was specific to a given year, the next option was to use the general direct calibration model for the observer. If neither direct calibration model could be used due to lack of data, indirect calibration with quasi-maximum likelihood bias correction was considered (Barlow *et al.,* 1998). The indirect calibration method could be used only if an observer's best estimate of group size was available and if an indirect calibration model existed for the observer. At this stage in the selection of a method for calibrating an individual observer's group size estimate, if a best estimate was not available, that observer's data was not included in the mean group size estimate for the sighting. If the indirect calibration method could not be used but a best estimate was available for the observer, then the ratio method was used:

$$\hat{s} = \frac{s_b}{\frac{1}{\sum_{i=1}^{n} m_i}\left[\sum_{i=1}^{n}\sum_{j=1}^{m_i}\left(\frac{s_{b_{i,j}}}{s_{p_i}}\right)\right]} \qquad (3)$$

where $\hat{s}$ = observer's calibrated group size estimate, $s_{b_{i,j}}$ = observer *j*'s best estimate of size for group *i*, and $s_{p_i}$ = size of group *i* estimated from photographs of group *i* (Gerrodette *et al.,* 2002). Thus, in the ratio method, the observer's best estimate ($s_b$) was corrected by the ratio of observer best estimates to photographic counts, averaged over all *n* photographic calibration groups, each having *m* observer estimates. Once each observer's group size estimate was calibrated, a mean group size was calculated for each sighting as the weighted mean of the natural logarithm of the calibrated group size estimates, resulting in a weighted geometric mean group size. The calibrated group size estimates were weighted by variance$^{-1}$, where the value for the variance for each observer was the MSE (mean square error) reported for directly calibrated observers and observers calibrated with the ratio method (Gerrodette *et al.,* 2002) or the ASPE (average square prediction error) reported for indirectly calibrated observers (Barlow *et al.,* 1998). Finally, the mean group size estimate for each segment was calculated as the arithmetic mean of the weighted geometric mean group size estimates for all sightings in the segment.

GAMs were used to relate beaked whale sightings to the summarized fixed geographic variables and temporally dynamic *in situ* oceanographic data described above. A GAM may be represented as

$$g(\mu) = \alpha + \sum_{j=1}^{p} f_j(X_j). \qquad (4)$$

(Hastie and Tibshirani, 1990). As in generalized linear models (GLMs), the function $g(\mu)$ is known as the link function, and it relates the mean of the response variable given the predictor variables, $\mu=E(Y|X_1,\ldots,X_p)$, to the additive predictor $\alpha+\Sigma_j f_j(X_j)$. GAMs are nonparametric extensions of GLMs: the components $f_j(X_j)$ in the additive predictor may include nonparametric smooth functions of the predictor variables, allowing GAMs to be considerably more flexible than GLMs, which are restricted by the constraints of the linear predictor, $\alpha+\Sigma_j\beta_jX_j$. Separate GAMs were built to describe and predict beaked whale encounter rates and average group sizes. The encounter rate data were essentially clustered counts; therefore, the number of sightings in each segment was modeled using a quasi-likelihood error distribution with variance proportional to the mean and using a logarithmic link function (approximating an over-dispersed Poisson distribution). Encounter rate models were built using all 9km segments, regardless of whether they contained sightings. Observed distributions of cetacean group sizes in the ETP region typically have long tails and are restricted to the positive real values. Furthermore, after correcting for bias and averaging group sizes across individuals and sightings in each segment, group size estimates are likely to be non-integer valued. Therefore, GAMs were built using the natural logarithm of group size as the response variable and a Gaussian error distribution with the identity link function. Group size models were built on only the 9km segments that contained Cuvier's or *Mesoplodon* beaked whale sightings with valid group size estimates.

The encounter rate and group size GAMs were built using S-PLUS 6 for Windows. Forward/backward stepwise selection of variables, with linear terms or smoothing splines having 2 and 3 degrees of freedom (df) in the scope of predictor variables, was implemented using the function *step.gam*Models built using a maximum of 4 df for each variable in the scope of *step.gam* were considered, but resulting models were qualitatively similar to those limited to 3 df, and the added complexity of the 4 df models appeared to have no ecological justification. Akaike's Information Criterion (AIC) was used to determine the best model at each step. Stepwise selection of variables occurred twice for each model. The first stepwise selection process started with the null model, did not contain terms for latitude or longitude, and linear terms were excluded from the scope. Latitude and longitude were excluded from the first call to try to explain the observed variation in the beaked whale data using the more informative environmental data before considering fixed geographic coordinates. Linear functions were excluded from the first call because a few instances were found in which AIC was lower for a linear fit than for a quadratic smoothing spline, but a cubic smoothing spline was better than a linear fit. In those instances, the stepwise fitting algorithm would not go beyond the quadratic and test the AIC value resulting from splines with higher degrees of freedom. The second call to *step.gam* began with the best model from the first call, and included latitude, longitude, and linear functions of all variables in the scope of predictor variables. It is advantageous to call *step.gam* twice because, by default, the function uses the dispersion parameter of the original gam object (Chambers and Hastie, 1991), and the estimated dispersion parameter associated with the best model from the first call to the function is likely to better represent the underlying process than that associated with the null model.

The above stepwise selection of variables finds the model that provides the best fit to the given data as judged by AIC, but it does not provide any information about the predictive power of the resulting model. To assess the predictive power of a number of models, the stepwise building procedure was performed on all combinations of the years

1986-1990 with one year left out; 1993 was included in all trials because it was a relatively small data set. This modified procedure resulted in five "best" encounter rate models and five "best" group size models. To evaluate which encounter rate and group size models performed best according to predictive power, cross-validation methods were applied, testing each model on the excluded year. The model with the lowest average squared prediction error (ASPE) was selected as the model with the best predictive performance. The model selected by the cross-validation process was re-built using the specified degrees of freedom and all years of data to fine-tune the smoothing splines.

The final *Mesoplodon* encounter rate model and Cuvier's group size model included latitude. To determine how the fixed geographic variable affected the predictive performance of the models, the stepwise selection and cross-validation procedures were repeated, excluding latitude and longitude from the scopes of both calls to *step.gam*. The ASPE values of the final models built without geographic variables in the scopes were compared to the final models built with geographic variables; the models with the lowest ASPE values were selected as the best overall *Mesoplodon* encounter rate and Cuvier's group size models.

To estimate beaked whale density, the encounter rate (*n/L*) and group size (*S*) model results were incorporated into the standard line-transect equation

$$D = \left(\frac{n}{L}\right) \cdot S \cdot \frac{1}{2 \cdot ESW \cdot g(0)} \qquad (5)$$

where,

*n/L* = encounter rate (number of sightings per unit length of trackline),

*S* = expected (or mean) group size,

*ESW* = effective strip half-width, or 1/*f(0)*, where *f(0)* is the sighting probability density at zero perpendicular distance

*g(0)* = probability of detecting an animal on the trackline.

The values of *f(0)* and *g(0)* were those for Cuvier's and *Mesoplodon* beaked whales in the ETP and Gulf of California in Ferguson and Barlow's (2001) analysis. It was necessary to apply a bias-correction factor to the group size predictions from the GAMs because the models were built in log space and then the results were transformed back to arithmetic space, converting the group size estimate to a geometric mean in the process (Finney, 1941; Smith, 1993). The ratio estimator was used to correct for this back-transformation bias (Smith, 1993). Density estimates for each segment were smoothed to give a geographic representation of average density over the study period by using an inverse distance weighting interpolation to the first power with anisotropy ratio set to 1.0 in Surfer software (version 7.0).

To evaluate the models' fit to the observed data, the following error analysis was conducted. Encounter rate models were fit to the observed oceanographic and geographic data for all segments in the study area, and the differences between predicted and observed values for each segment ($\Delta ER_i$) were calculated:

$$\Delta ER_i = ER_{i_{predicted}} - ER_{i_{observed}} \qquad (6)$$

for segment *i* in the study area. In addition, the ratio ($R_{ER}$) between pooled predicted values and pooled observed values was calculated:

$$R_{ER} = \frac{\left( \sum_{i=1}^{n} ER_{i_{predicted}} \right)}{\left( \sum_{i=1}^{n} ER_{i_{observed}} \right)}, \ (7)$$

where the summation is over the total number of segments used to build the models or the number of segments in a given geographic stratum, as described below. Group size was predicted from GAMs based on the subset of data comprised of only the segments with either Cuvier's or *Mesoplodon* beaked whale sightings, as appropriate. This subset of predictions was used to test how well the model predicted group size for each segment ($\Delta SS_i$) and for the study area as a whole ($R_{SS}$) because the group size model was built on the same subset of data upon which the predictions were based. The group size predictions were corrected for the bias due to back-transforming from the log space, and the computations for $\Delta SS_i$ and $R_{SS}$ were analogous to the respective encounter rate statistics (Eqns 6 and 7). To qualitatively determine whether spatial patterns existed in the predictions for encounter rate, group size, and number of individuals, a spatially stratified analysis was conducted in which values of $R_{ER}$ and $R_{SS}$ were calculated for geographic strata of approximately $5^o$ latitude x $5^o$ longitude.

## Results

In total, 90 Cuvier's beaked whale sightings and 106 *Mesoplodon* sightings were included in the models. Cuvier's and *Mesoplodon* beaked whales were sighted in groups of approximately two individuals, on average, with maximum group sizes of six and five individuals, respectively. The mean water depth where Cuvier's beaked whales were sighted in the eastern tropical Pacific was approximately 3,400m with a maximum depth of over 5,100m; similarly, the mean depth of *Mesoplodon* beaked whale sightings was just over 3,500m and the maximum depth was approximately 5,750m (Table 5.2; standard deviations for all environmental variables and summary statistics for the entire study area are also presented in Table 5.2). Cuvier's was found over seafloors with a mean slope of $0.732^o$ (range: 0.003 to $6.425^o$), and *Mesoplodon* was found over a mean slope of $0.673^o$ (range: 0.006 to $4.935^o$). In addition, beaked whales in the eastern tropical Pacific were found in waters that ranged from well-mixed to stratified, with a continuum of weak to strong thermoclines. Both species were sighted an average of 1000km offshore, with a range of approximately 37 to 3704km. The concentration of chlorophyll at the surface associated with the Cuvier's and *Mesoplodon* sightings ranged from 0.048 to $0.649 mg/m^3$ (mean=$0.203 mg/m^3$) and 0.047 to $2.26 mg/m^3$ (mean=$0.255 mg/m^3$), respectively.

Models for both genera predicted highest densities in the highly productive coastal and equatorial waters (Figures 5.3 and 5.4). The mean predicted Cuvier's beaked whale density resulting from the overall best encounter rate and group size models was 4.55 individuals per 1,000km$^2$ (SD=1.96). The best Cuvier's beaked whale encounter rate and group size models reduced deviance by 7.15% and 15.07%, respectively, compared to the null models (Table 5.3). The Cuvier's beaked whale encounter rate model used only Beaufort sea state and the fixed geographic variables offshore distance and depth (Figure 5.5 and Table 5.3), and the group size model incorporated latitude, Beaufort, thermocline depth, and thermocline strength (Figure 5.6 and Table 5.3). Beaufort sea state entered both Cuvier's models as a linear fit with negative slope, indicating smaller observed encounter rates and group sizes with increasing sea states (Figures 5.5 and 5.6). Offshore distance was included in the encounter rate model as a smoothing spline with two degrees of freedom, showing a minimum around 926km (500 nmi) and the highest rates further offshore (Figure 5.5); the slight increase in encounter rate very close to shore is likely due to the cluster of sightings in the Gulf of California and along the Baja Peninsula (Figure 5.3). In addition, the encounter rate model incorporated depth as a smoothing spline with three degrees of freedom, and implies that Cuvier's beaked whales tended to be sighted most often in waters approximately 2000m deep (Figure 5.5), corresponding to the offshore edge of the continental slope. In the Cuvier's group size model, linear fits for latitude and thermocline strength suggest smaller groups at higher latitudes and in waters with stronger thermoclines (Figure 5.6). Thermocline depth entered the Cuvier's group size model as a smoothing spline with two degrees of freedom, with larger groups observed over shallower thermoclines, although there were few observations at deeper thermoclines and, therefore, the tail of the smooth function should be interpreted with caution (Figure 5.6).

*Mesoplodon* beaked whales were predicted to have a mean density of 2.96 individuals per 1000km$^2$ (SD=2.06). The decrease in deviance between the best *Mesoplodon* encounter rate model and the null encounter rate model was 8.39%, whereas the best group size model resulted in an 11.18% decrease in deviance compared to the null (Table 5.4). The *Mesoplodon* encounter rate model without latitude resulted in a lower ASPE value than the model with latitude (Table 5.4). In total, the *Mesoplodon* encounter rate model included Beaufort sea state, depth, SST, salinity, and thermocline strength, and the group size model contained Beaufort sea state, salinity, and thermocline depth. The effects of Beaufort are similar in both *Mesoplodon* models, suggesting that more animals were observed in calmer waters, as expected (Figures 5.7 and 5.8). *Mesoplodon* encounter rates and group sizes displayed positive associations with sea surface salinity (a smoothing spline with three degrees of freedom in the encounter rate model, and a linear term in the group size model; Figures 5.7 and 5.8, respectively), a trend that is likely due to the sightings in the Gulf of California and stretching out from the coast along 10$^o$S (Figure 5.4), both of which are regions of relatively high salinity waters (Fiedler, 1992). Similar to the Cuvier's encounter rate model, the *Mesoplodon* encounter rate model selected depth as a smoothing spline with three degrees of freedom, showing a peak at approximately 2000m depth, with a secondary increase from about 4000m to the maximum depth at which the genus was observed (Figure 5.7). The smooth fit of sea surface temperature to *Mesoplodon* encounter rate suggests a relative minimum in waters of 25$^o$C (Figure 5.7). The linear fit for thermocline strength in the *Mesoplodon* encounter rate model, showing higher encounter rates with stronger thermoclines (Figure 5.7), is likely produced by the numerous sightings centered near the coast around 10$^o$N, in the Tropical Surface Water (Fiedler, 1992). The *Mesoplodon* group size model fit a smoothing spline with two degrees of freedom to thermocline depth (Figure 5.8), indicating larger groups in waters with 60m deep thermoclines, which is close to the mean value for the study area (Table 5.2).

The error analysis showed that the mean differences (averaged across all years and all segments used to build the models) between predicted and observed values of encounter rate and group size were zero for both Cuvier's and *Mesoplodon* beaked whales. The standard deviations in the differences between predicted and observed values were similar for both genera, with stdev($\Delta ER$)$\cong$0.085 and stdev($\Delta SS$)$\cong$1.00. In addition, for both Cuvier's and *Mesoplodon*, when pooling all segments used to build the models, the ratios between the pooled predicted encounter rates and the pooled observed encounter rates ($R_{ER}$) equalled unity out to at least two decimal places, and ($R_{SS}$) was identically equal to 1.0. The geographically stratified analysis of residuals in the encounter rate for Cuvier's (Figure 5.9) and *Mesoplodon* (Figure 5.10) beaked whales shows that, in approximately half of the strata, the ratio of pooled predicted to observed values, $R_{ER}$, is close to unity (1.0 ± 0.25). Values of $R_{ER}$ did depart considerably from unity in some strata (from 0.38 to 2.06 for Cuvier's beaked whale), but the distribution of residuals did not show much geographic pattern. Residuals in the group size estimates for pooled strata, $R_{SS}$ , were near unity (1.0 ± 0.25) for the majority of strata for both species (Figures 5.11 and 5.12), and again there is little geographic pattern to the residuals.

## Discussion

The beaked whale models presented here are the first to estimate density. In addition, they were based upon the largest study area with a substantial amount of survey effort over the abyssal plain. Although it is clear that some species of ziphiid whales are associated with continental slopes or topographic features such as seamounts, ridges and canyons in some areas, this association pattern may not hold for all species throughout their distributions. The ETP Cuvier's and *Mesoplodon* beaked whale analyses appear to expand the definition of what is considered suitable beaked whale habitat. Beaked whales in the ETP were sighted in considerably deeper waters than in any of the other studies discussed. In addition, beaked whales in the ETP were found in waters that ranged from well-mixed to stratified. High densities were predicted in the southern Gulf of California, in coastal waters, and in the equatorial cold tongue of the ETP study area, but beaked whales did not appear to be narrowly restricted to the highly productive waters typified by those coastal and upwelling systems, and they were not limited to the continental slope and shelf waters, which is where the majority of beaked whale field studies have been conducted.

This analysis has shown that the extent and location of the study area can considerably affect the interpretation of results from beaked whale habitat studies. Two additional aspects of such studies with power to influence the results are the type of analytical method chosen for the analysis and the scale of the analysis. The analytical methods used in previous studies to examine beaked whale habitats ranged from hypothesis tests such as the Kruskall-Wallis one-way ANOVA (Davis *et al.*, 1998), Kolmogorov-Smirnov (Hooker *et al.*, 2000; Wimmer, 2003) and Chi-square (Cañadas *et al*, 2002; Wimmer, 2003; MacLeod *et al.*, in press) goodness of fit tests, and the Wilcoxin signed rank test (Waring *et al.*, 2001), all of which are used to answer the dichotomous question of "reject" or "fail to reject" a null hypothesis (*i.e.*, that a given environmental variable is related to beaked whale distribution patterns) to multivariate tools such as GLMs (Waring *et al.*, 2001; Hamazaki, 2002; Cañadas *et al*, 2002) GAMs (MacLeod and Zuur, in press), ENFA (MacLeod, 2005) and CART (MacLeod and Zuur, in press), which can quantify effect sizes (*i.e.*, address the question, *How much* does a given environmental variable affect beaked whale distribution?). Generalized additive models were chosen for the ETP analysis because of their flexibility. One weakness of GAMs, however, is that they are data-intensive. All species of *Mesoplodon* sighted in the ETP study area were modeled together because small sample sizes of individual species (n=17 *Mesoplodon peruvianus*, n=11 *Mesoplodon densirostris*) prevented building separate models and there was a need to include a large number (n=78) of "unidentified *Mesoplodon*t beaked whales." Lumping of all "*Mesoplodon* spp." undoubtedly obscured the species-specific differences in habitat (Pitman and Lynn, 2001), thereby lowering explanatory or predictive power in the final models; this could potentially account for the low percent explained deviance in the GAMs. Other potential reasons for the relatively small reduction in deviance between the null and best GAMs exist: 1.) the signal-to-noise ratio in the environment might be too high relative to the number of observations in the data set, 2.) the environmental predictors used to build the models might not be strongly associated with beaked whale habitat, or 3.) the error distributions specified for the encounter rate and group size models might be inappropriate. Addressing these questions, and the issue of understanding and enumerating the various sources of uncertainty in the models, are active areas of research. Nevertheless, as noted above, a dominant strength of GAMs is their flexibility, which was manifest in the error analysis for Cuvier's and *Mesoplodon* encounter rate and group size. The error analysis found small differences between observed and predicted values, and found that the ratios of pooled predicted to pooled observed values were close to 1.0. Furthermore, in the geographically stratified residual analysis, predictions in the majority of the strata for both genera and both response variables (encounter rate and group size) were within 25% of the observed values, and there was no evidence of a spatial pattern.

The spatial or temporal scale at which data are analyzed in habitat studies is likely to have profound effects on the results. Ecological mechanisms affecting beaked whale distribution may be scale-specific, and there may be a hierarchy of such mechanisms operating on different scales that influence where beaked whales are found. The slope of the seafloor is one variable that may be especially sensitive to the spatial scale of the analysis. For example, the steep wall of a submarine canyon is a feature that would appear in an analysis conducted on scales of a few hundred meters to a few kilometers, whereas it would almost disappear in a larger scale analysis such as that described for the ETP. Such small-scale features are likely to be important to the success of localized beaked whale foraging. Nevertheless, the animals may incorporate information from larger spatial scales, as exemplified by upwelling regions such as the Costa Rica Dome, California Current, Peru Current and equatorial cold tongue, to guide them to larger regions of enhanced foraging success. In the time domain, small scale patches with high densities of prey are likely to be temporally dynamic; therefore, instantaneous information about the present environment is most relevant to determining foraging success at a specific point and place in time. To arrive in the general vicinity of patches with high densities of prey, however, successful predators might have processed time-lagged information, averaging their foraging experiences in different regions over the past week, month, year, or decade, for example. Time lags are particularly important when proxies such as chlorophyll data are used to indicate beaked whale habitat because it is not the primary producers themselves, but the squid and mesopelageic fishes several trophic levels higher up, that beaked whales eat, and time lapses before energy and nutrients from the primary producers climb the food chain up to cetacean prey species. It is noteworthy that the ETP analysis found no associations between beaked whales and surface chlorophyll concentration, which is a biological variable commonly used as a proxy for cetacean prey. In the end, ecologists are left with a conundrum: to determine which environmental predictors define beaked whale habitat, it is important to know the scale at which to observe the ecology of the system; simultaneously, to determine the scale at which to observe the ecology of the system, it is important to know which environmental predictors define beaked whale habitat. This conundrum suggests that an iterative approach may be the best way to increase ecological understanding of these animals.

Understanding of ziphiid whale habitats may be enhanced by conducting more surveys in a greater diversity of potential habitats, thoughtfully selecting the types of environmental data collected and the scale at which they are collected, investigating the effects of scale on habitat models, and explicitly accounting for detection bias (*e.g.*, by incorporating Beaufort sea state and availability bias correction) in occurrence, density and abundance models.

## Research Recommendations

1) Accurate habitat models for ziphiid whales will not be possible unless surveys cover a broader range of potential habitats, including deep waters over the abyssal plains. Surveys that only cover the suspected habitat, such as slope waters, cannot be used to confirm this habitat preference.

2) Oceanographic data should be collected in conjunction with cetacean surveys to improve the data available for habitat modeling. There is a particular need to identify ziphiid whale prey and to develop methods to measure their abundance.

3) To reconcile apparent differences in results among different habitat studies, the influences of observation scale (including total survey area and the sample size used to partition that area into smaller units), detection bias (the effect of sea state on apparent density), and suite of predictor variables considered must be addressed.

## Acknowledgements

We gratefully acknowledge the vast number of people who collected the cetacean sighting and oceanographic data for the Southwest Fisheries Science Center and made these data available to us. We thank Teri Chereskin, Paul Dayton, Dan Goodman, Len Haff, Jim Leichter, and Paul Smith, the members of Megan Ferguson's doctoral committee who provided stimulating discussion and shared ideas that helped focus the research and identify missing pieces in the analysis. We thank Summer Martin for providing us with the tools to make Figure 5.1. This project was funded by the U.S. Navy through the Office of Naval Research (ONR) and the Strategic Environmental Research and Development Program (SERDP). We wish to thank Frank Stone, Ernie Young, and Bob Gisiner for their continued support. Previous versions of this manuscript were significantly improved by comments from Bill Perrin, Jessica Redfern, Angela D’Amico, John Durban, Bob Pitman, Erin Vos, Colin MacLeod, and two anonymous reviewers.

The text of Chapter Five has been submitted for publication. The dissertation author was the primary researcher and author, and the co-authors listed directed and supervised the research which forms the basis for this chapter.

Table 5.1. Temporal and spatial resolution of *in situ* oceanographic data collected during SWFSC cetacean line-transect survey cruises.

| Variable Name | Resolution |
|---|---|
| sea surface temperature | recorded every five minutes; summarized into hourly means (approx. 18.5 km) |
| sea surface salinity | recorded every five minutes; summarized into hourly means (approx. 18.5 km) |
| thermocline depth* | 4x/day (approx. every 70-140 km) |
| thermocline strength* | 4x/day (approx. every 70-140 km) |
| surface chlorophyll concentration | 2x/day (approx. every 220 km) |

* These variables were derived from CTD and XBT data.

Table 5.2. Summary statistics of environmental variables for the ETP study area and the segments in which *Ziphius* and *Mesoplodon* (*Mesop.*) beaked whale sightings occurred.

| | Minimum | | | Mean | | | Maximum | | | Standard Deviation | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | *Ziphius* | *Mesop.* | Study Area | *Ziphius* | *Mesop.* | Study Area | *Ziphius* | *Mesop.* | Study Area | *Ziphius* | *Mesop.* | Study Area |
| Beaufort* | 0.8 | 0.2 | 0.2 | 2.9 | 2.9 | 3.7 | 5.0 | 5.0 | 6.0 | 1.3 | 1.3 | 1.1 |
| Distance Offshore (km) | 42.5 | 36.0 | 3.8 | 1097.8 | 1052.0 | 1249.7 | 3670.6 | 3844.6 | 3851.8 | 1064.5 | 970.0 | 942.2 |
| Depth (m) | 1167.5 | 717.7 | 46.2 | 3445.8 | 3513.6 | 3573.8 | 5197.6 | 5749.9 | 5873.0 | 902.7 | 878.5 | 917.1 |
| Slope (degrees) | 0.003 | 0.006 | 0.000 | 0.732 | 0.673 | 0.504 | 6.425 | 4.935 | 10.487 | 1.145 | 1.097 | 0.935 |
| Sea Surface Temperature (deg. C) | 19.7 | 18.5 | 16.6 | 26.8 | 26.3 | 26.1 | 30.6 | 31.3 | 31.7 | 3.2 | 3.6 | 2.8 |
| Sea Surface Salinity (psu) | 30.1 | 30.3 | 16.3 | 33.9 | 34.0 | 33.9 | 35.3 | 35.3 | 35.7 | 0.8 | 1.0 | 1.0 |
| Surface Chlorophyll Concentration (mg/m3) | 0.048 | 0.047 | 0.015 | 0.203 | 0.255 | 0.220 | 0.649 | 2.260 | 8.976 | 0.110 | 0.306 | 0.270 |
| Thermocline Depth (m) | 15.0 | 15.0 | 11.0 | 53.9 | 56.2 | 61.4 | 151.0 | 126.0 | 211.7 | 24.0 | 23.9 | 28.0 |
| Thermocline Strength (deg/m) | 0.149 | 0.108 | 0.068 | 0.367 | 0.391 | 0.393 | 0.795 | 0.795 | 0.973 | 0.140 | 0.154 | 0.155 |

*Beaufort sea state was treated as a continuous variable in the analysis.

Table 5.3. Summary of Cuvier's (*Ziphius cavirostris*) beaked whale encounter rate and group size GAMs for the eastern tropical Pacific. Linear fits are represented by "L1," whereas smoothing splines are represented by "S#," where # is the associated degrees of freedom. "NLL" designates model built without latitude or longitude. Final selected model is indicated by **bold** font. Percent change in deviance was calculated for final selected model, rebuilt using all years' data, as: ((null deviance - residual deviance)/null deviance)*100%.

| **Model** | **Year Omitted** | **% Change in Deviance** | **Predictor Variables** | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Cuvier's Encounter Rate | | | Lat | Long | Beaufort | Offshore Distance | Depth | Slope | SST | Salinity | log Surface Chlorophyll | Thermocline Depth | Thermocline Strength |
| | 1986 | | | L1 | L1 | S2 | S3 | | L1 | | S2 | L1 | S3 |
| | 1987 | | | | L1 | | S3 | | | L1 | | L1 | |
| | **1988** | **7.15** | | | **L1** | **S2** | **S3** | | | | | | |
| | 1989 | | | L1 | L1 | S2 | S3 | | S3 | L1 | S3 | L1 | L1 |
| | 1990 | | | L1 | L1 | S2 | S3 | | S3 | L1 | | L1 | L1 |
| Cuvier's Group Size | | | Lat | Long | Beaufort | Offshore Distance | Depth | Slope | SST | Salinity | log Surface Chlorophyll | Thermocline Depth | Thermocline Strength |
| | **1986** | **15.07** | **L1** | | **L1** | | | | | | | **S2** | **L1** |
| | 1987 | | | | | S2 | | | S3 | | | | |
| | 1988 | | | L1 | | | | | | | | S3 | |
| | 1989 | | | | | S3 | | | | S2 | | L1 | L1 |
| | 1990 | | | L1 | | | | | | | | | |

Table 5.4. Summary of *Mesoplodon* beaked whale encounter rate and group size GAMs for the eastern tropical Pacific. Linear fits are represented by "L1," whereas smoothing splines are represented by "S#," where # is the associated degrees of freedom. "NLL" designates model built without latitude or longitude. Final selected model is indicated by **bold** font. Percent change in deviance was calculated for final selected model, rebuilt using all years' data, as: ((null deviance - residual deviance)/null deviance)*100%.

| **Model** | **Year Omitted** | **% Change in Deviance** | **Predictor Variables** | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| *Mesoplodon* Encounter Rate | | | Lat | Long | Beaufort | Offshore Distance | Depth | Slope | SST | Salinity | log Surface Chlorophyll | Thermocline Depth | Thermocline Strength |
| | 1986 | | L1 | | L1 | | S3 | | S3 | S2 | S3 | | |
| | 1987 | | S3 | | L1 | | S3 | | S3 | | | | |
| | 1988 | | | | S3 | | S3 | | | L1 | S3 | | S2 |
| | 1989 | | L1 | | S3 | | S3 | | S3 | S3 | | | |
| | 1990 | | S3 | | L1 | | S3 | | S3 | | S3 | | |
| | **NLL** | **8.39** | | | **L1** | | **S3** | | **S3** | **S3** | | | **L1** |
| *Mesoplodon* Group Size | | | Lat | Long | Beaufort | Offshore Distance | Depth | Slope | SST | Salinity | log Surface Chlorophyll | Thermocline Depth | Thermocline Strength |
| | 1986 | | | | L1 | | | | | S2 | | | |
| | **1987** | **11.18** | | | **L1** | | | | | **L1** | | **S2** | |
| | 1988 | | | | L1 | S3 | | | | | S3 | | |
| | 1989 | | | | L1 | | | S3 | | S2 | | | |
| | 1990 | | | | | | | | | S2 | | | |

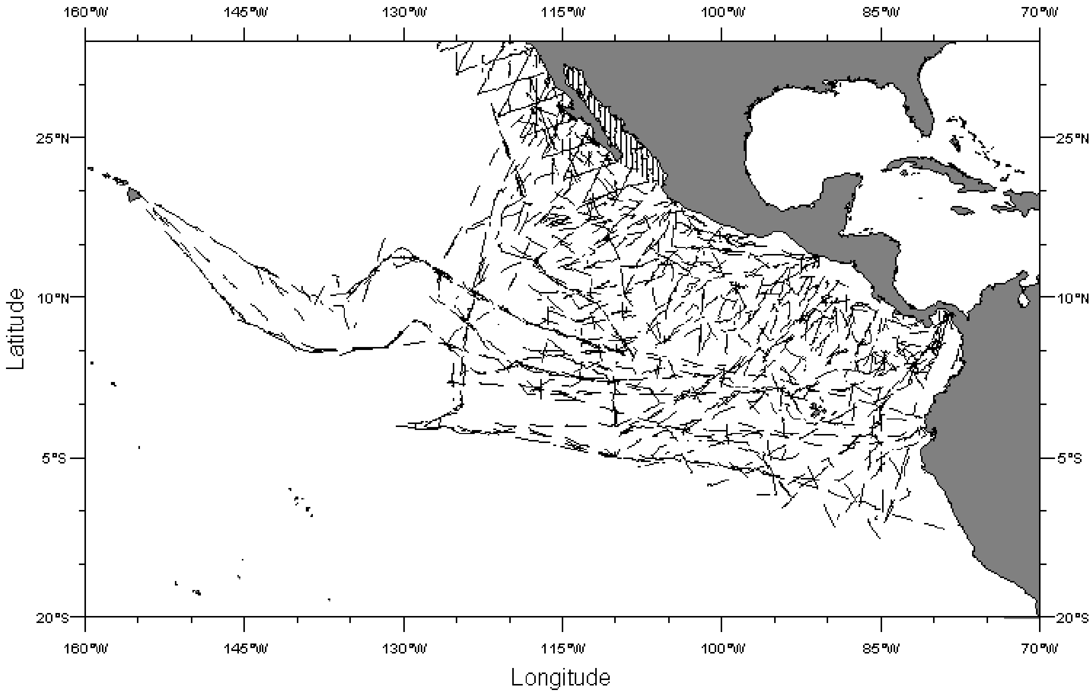

Figure 5.1. Transect lines covered during the 1986-1990, and 1993 shipboard cetacean line-transect surveys conducted by the Southwest Fisheries Science Center in the eastern tropical Pacific Ocean.

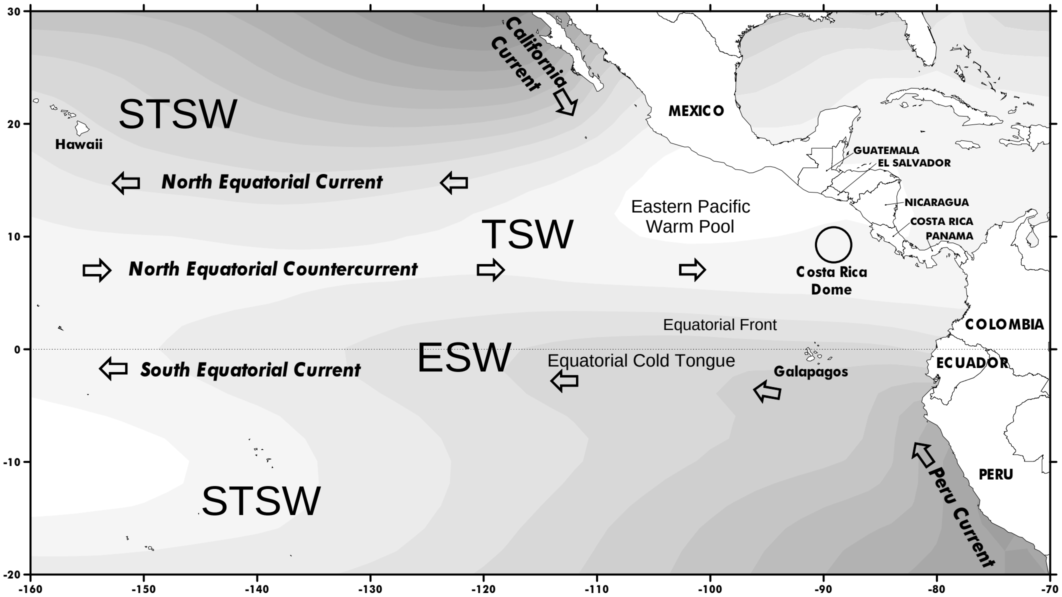

Figure 5.2. Oceanography of the eastern tropical Pacific study area. STSW: Subtropical Surface Water; TSW: Tropical Surface Water; ESW: Equatorial Surface Water.

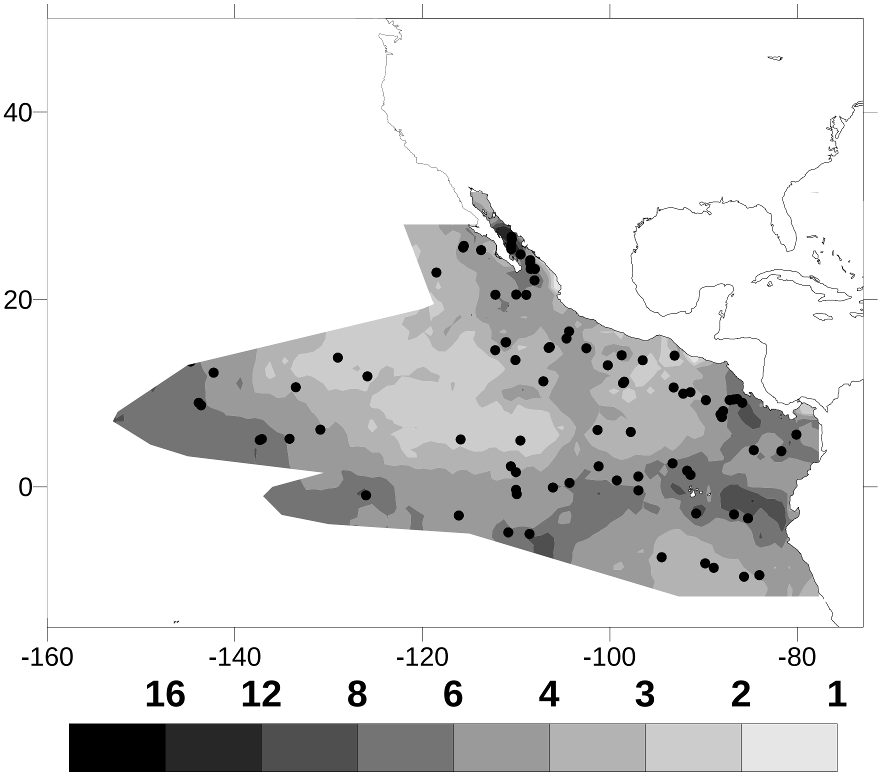

Figure 5.3. Predicted Cuvier's beaked whale (*Ziphius cavirostris*) density (# individuals/1000 km$^2$) in the eastern tropical Pacific Ocean. Predictions are for Beaufort sea state of 1. Black circles mark locations of all transect segments with on-effort Cuvier's sightings and oceanography data from Southwest Fisheries Science Center surveys in 1986 to 1990 and 1993.

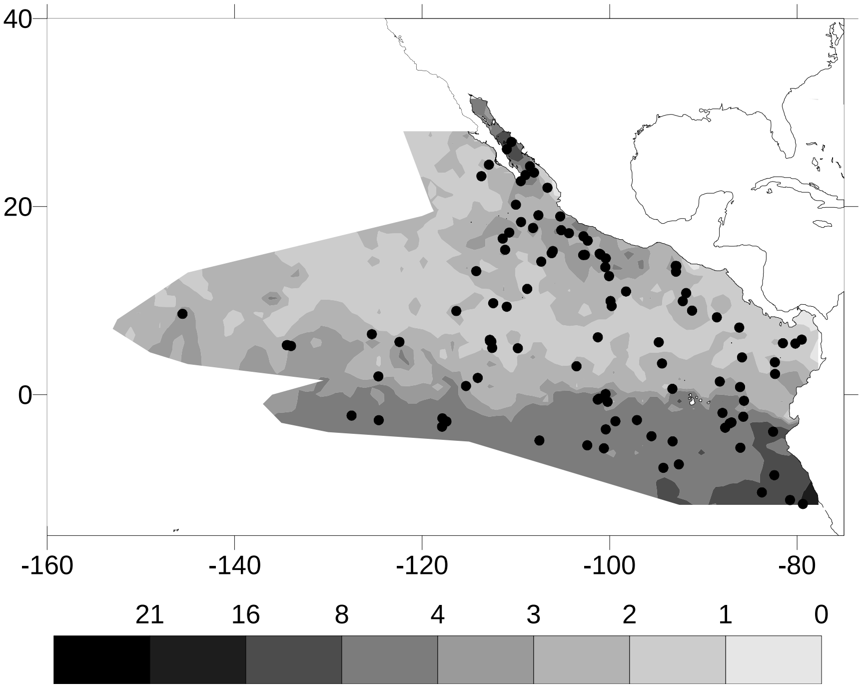

Figure 5.4. Predicted *Mesoplodon* beaked whale (*Mesoplodon* spp.) density (# individuals/1000 km$^2$) in the eastern tropical Pacific Ocean. Predictions are for Beaufort sea state of 1. Black circles mark locations of all on-effort *Mesoplodon* sightings and oceanography data from Southwest Fisheries Science Center surveys in 1986 to 1990 and 1993.

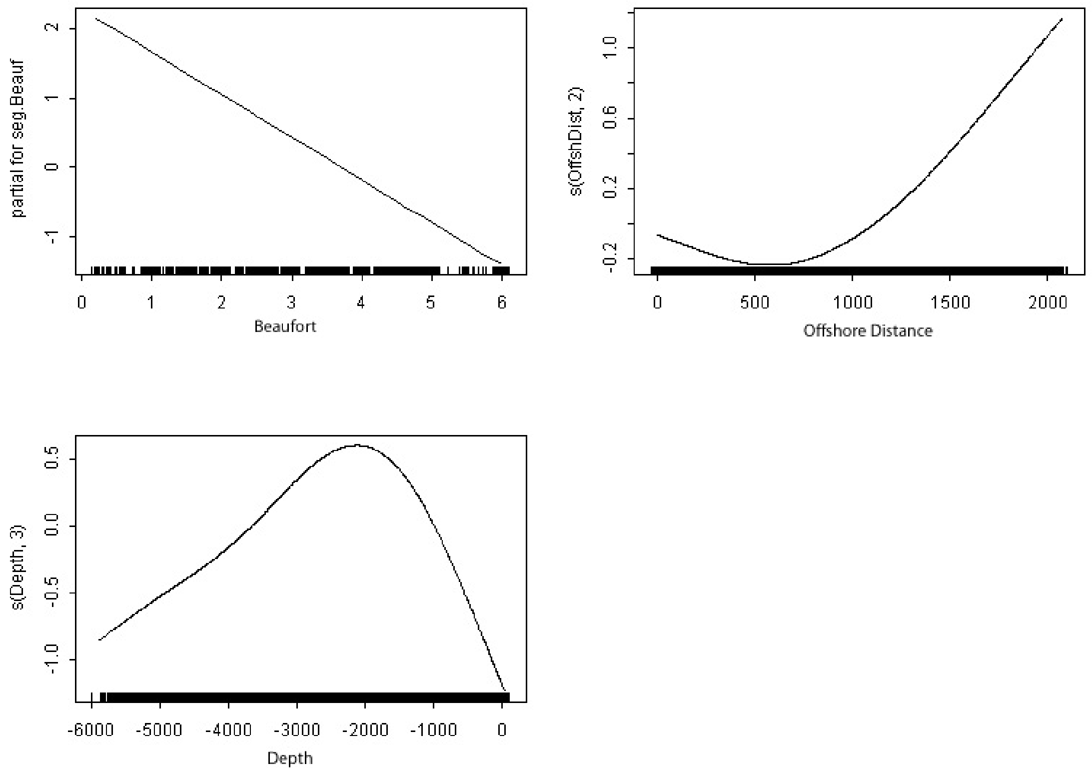

Figure 5.5. Smooth spline functions of the predictor variables incorporated into the final Cuvier's beaked whale (*Ziphius cavirostris*) encounter rate (# sightings/unit survey effort) GAM. Degrees of freedom for non-linear fits are in the parentheses on the y-axis. Tick marks above the x-axis indicate the distribution of observations in all segments (with and without Cuvier's beaked whales).

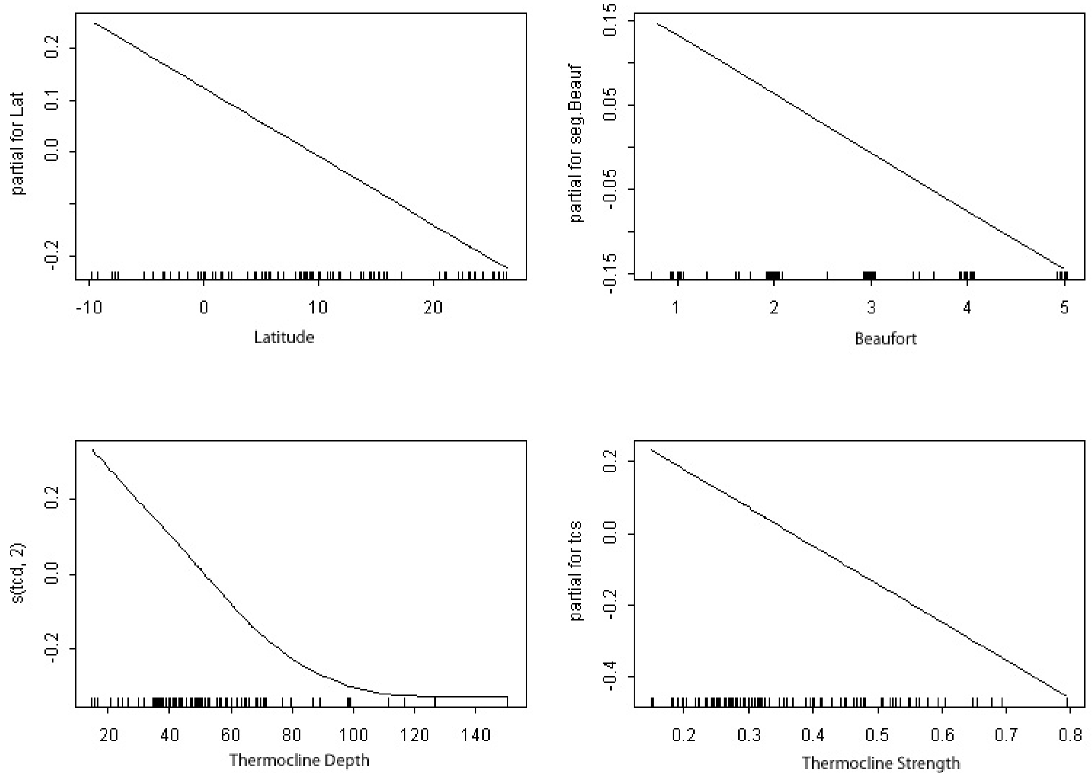

Figure 5.6. Smooth functions of the predictor variables incorporated into the final Cuvier's beaked whale (*Ziphius cavirostris*) group size GAM. Degrees of freedom for non-linear fits are in the parentheses on the y-axis. Tick marks above the x-axis indicate the distribution of observations in all segments with Cuvier's beaked whales.

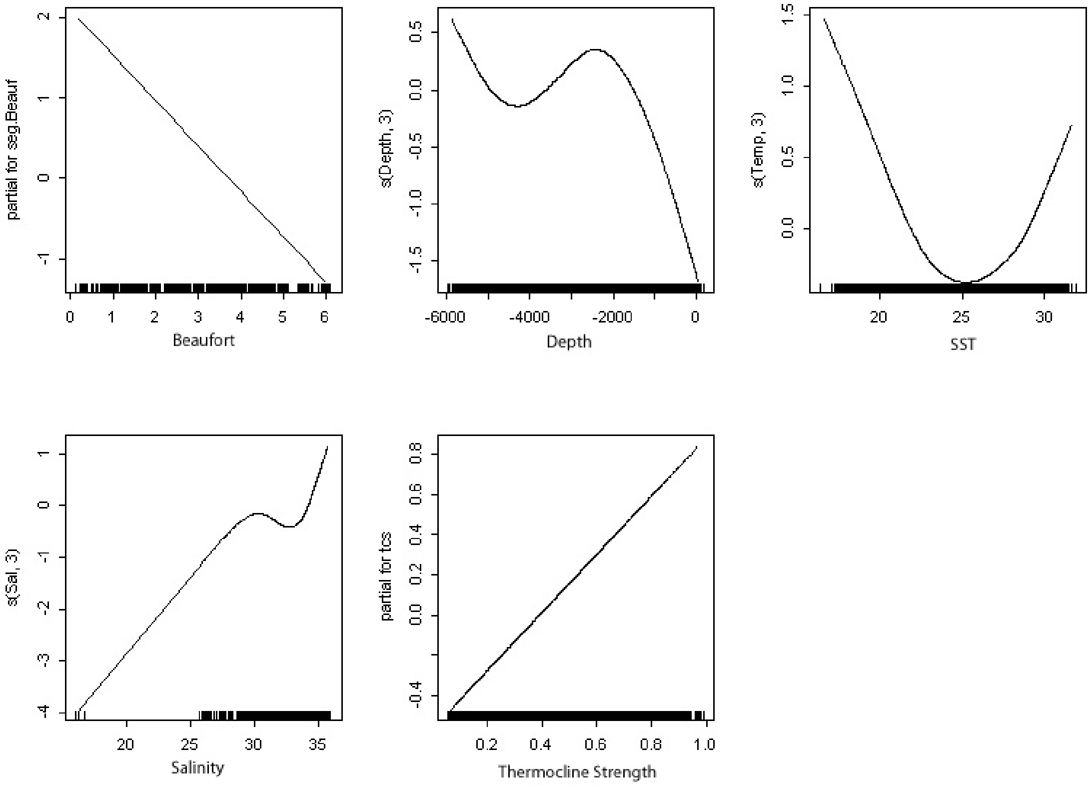

Figure 5.7. Smooth functions of the predictor variables incorporated into the final *Mesoplodon* beaked whale (*Mesoplodon* spp.) encounter rate GAM. Degrees of freedom for non-linear fits are in the parentheses on the y-axis. Tick marks above the x-axis indicate the distribution of observations in all segments (with and without *Mesoplodon* beaked whales).

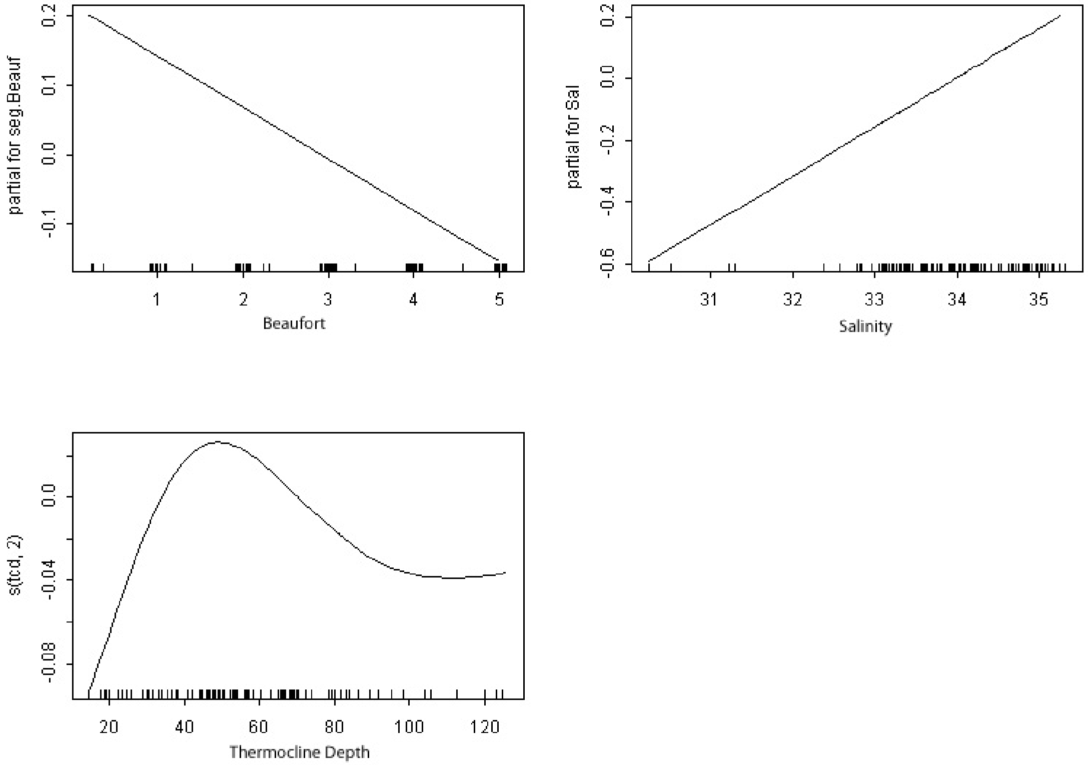

Figure 5.8. Smooth functions of the predictor variables incorporated into the final *Mesoplodon* beaked whale (*Mesoplodon* spp.) group size GAM. Degrees of freedom for non-linear fits are in the parentheses on the y-axis. Tick marks above the x-axis indicate the distribution of observations in all segments with *Mesoplodon* beaked whales.

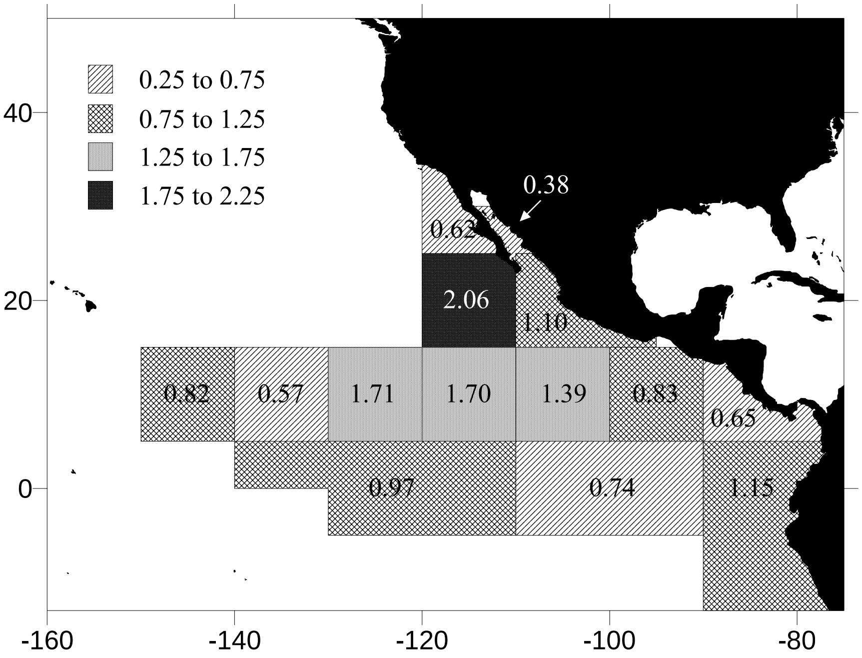

Figure 5.9. Geographic distribution of residuals for Cuvier's beaked whale (*Ziphius cavirostris*) encounter rates measured as the ratio: $R_{ER}$=[sum(predicted)/sum(observed)] $R_{ER}$ values are shown in each stratum. Predictions were based on observed oceanography data from SWFSC survey cruises in 1986-1990 and 1993.

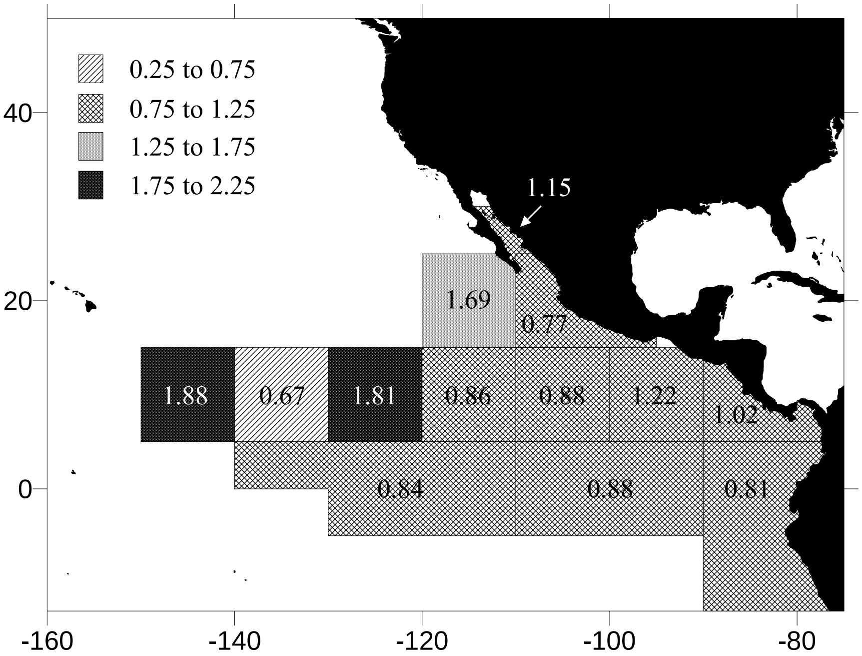

Figure 5.10. Geographic distribution of residuals for *Mesoplodon* beaked whale encounter rates measured as the ratio: $R_{ER}$=[sum(predicted)/sum(observed)] $R_{ER}$ values are shown in each stratum. Predictions were based on observed oceanography data from SWFSC survey cruises in 1986-1990 and 1993.

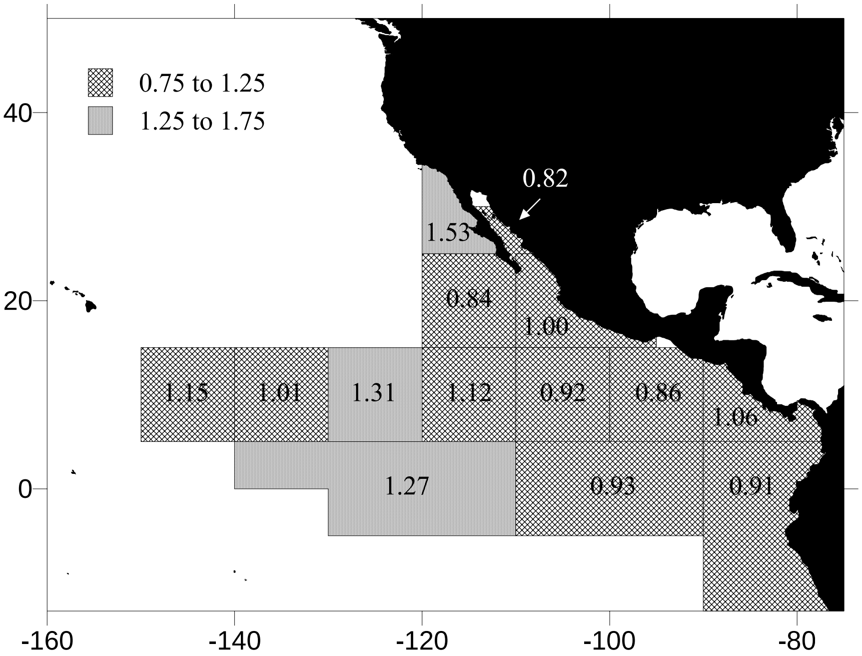

Figure 5.11. Geographic distribution of residuals for Cuvier's beaked whale (*Ziphius cavirostris*) group sizes measured as the ratio: $R_{SS}$=[sum(predicted)/sum(observed)] $R_{SS}$ values are shown in each stratum. Predictions were based on observed oceanography data from SWFSC survey cruises in 1986-1990 and 1993.

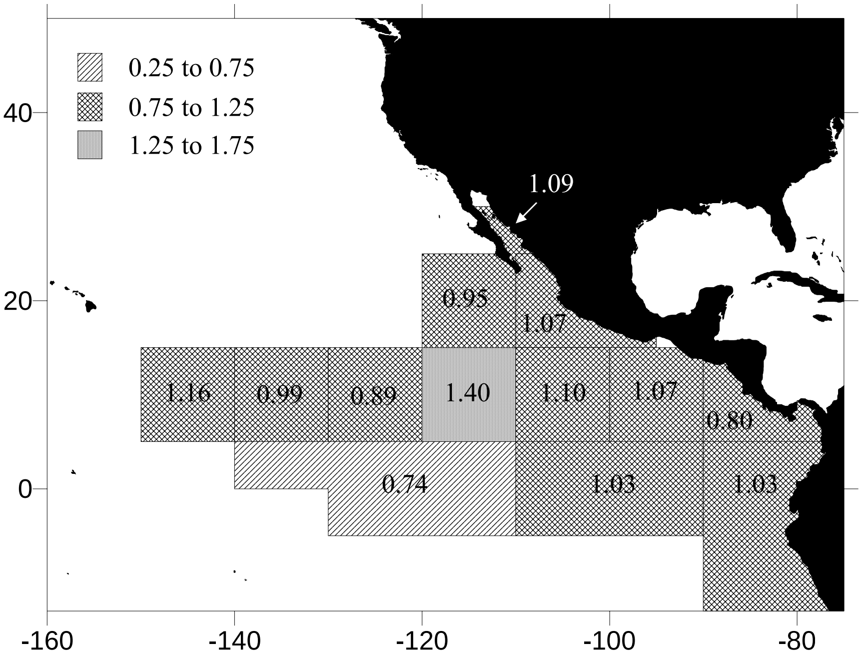

Figure 5.12. Geographic distribution of residuals for *Mesoplodon* beaked whale group sizes measured as the ratio: $R_{SS}$=[sum(predicted)/sum(observed)] $R_{SS}$ values are shown in each stratum. Predictions were based on observed oceanography data from SWFSC survey cruises in 1986-90 and 1993.

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# CHAPTER SIX

# VARIANCE ESTIMATION FOR A SPATIAL MODEL OF CUVIER'S BEAKED WHALE DENSITY

BY

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## Abstract

A parametric bootstrap method is used to estimate variance for Cuvier's beaked whale (*Ziphius cavirostris*) density (number of individuals per unit area) predictions derived from generalized additive models (GAMs) relating encounter rate (number of groups per unit transect length) and group size to environmental variables. The variance estimate includes estimates of uncertainty due to model selection, stochasticity in the encounter rates and group sizes, and line-transect parameter estimation. Estimated CV's ranged from 0.462 to 3.01 and were highest where survey effort was low. The predictor variables included in the original models of encounter rate and group size were consistently included in the bootstrap models, and those variables were selected more often than the remaining variables. The degrees of freedom associated with the selected variables in the bootstrap models were not consistently the same as those selected for the original models. Several sources of uncertainty were left out of the variance estimates presented herein. Future efforts to model cetacean density should investigate the magnitude of the remaining components of uncertainty to the total variance estimate for the density predictions.

## Introduction

An ecological model is designed to identify meaningful relationships while cutting through the multitude of less important relationships. That is, every ecological system has thousands of interactions but only a few strong interactions that define the patterns of interest. A model of beaked whale "habitat" may be a map of the Pacific Ocean overlaid with beaked whale sightings, or it may be a mathematical equation relating the number of beaked whale sightings in a given area to functions of the animals' environment. In other instances, ecologists build models to describe the dominant sources of variation inherent in a system. Regardless of model type, the ultimate goal is to weed through the noise (unexplainable variation) in order to better understand nature or to predict a future state of nature.

The output from an ecological model is an approximation to truth (Burnham and Anderson, 1998); as such, it has two components: a point estimate (such as the observed sighting locations in a distribution map or the predicted number of whales resulting from a mathematical equation) and an estimate of the uncertainty associated with the point estimate. In many instances, uncertainty estimates are either not computed or not presented with the model output. Ellison (2004) states that "Recognizing uncertainty in parameter estimates and predictions of ecological models and communicating the uncertainty in the range of ecological models considered can lead to better understanding by ecologists of the power and limitations of statistical inference and prediction." Estimates of uncertainty help keep ecologists honest, and good models help them understand the processes controlling ecosystems.

The goal of this analysis is to provide estimates of uncertainty associated with Cuvier's beaked whale (*Ziphius cavirostris*) density (number of individuals per unit area) estimates derived from generalized additive models (GAMs) fit to cetacean sightings from shipboard line-transect surveys and oceanographic data from the eastern tropical Pacific (ETP) (Ferguson *et al.*, 2005, Chapter Five). Ferguson *et al.* (2005, Chapter Five) used GAMs to model Cuvier's beaked whale encounter rate (number of sightings per unit transect length) and group size. The encounter rate and group size predictions, in addition to estimates of the line-transect sighting parameters from Ferguson *et al.* (2005, Chapter Two), were then incorporated into the standard line-transect equation for estimating density (Buckland *et al.*, 2001). Ferguson *et al.*'s (2005, Chapter Five) method for estimating cetacean density contains multiple steps, each with an unknown but estimable amount of uncertainty.

The numerous sources of uncertainty in Ferguson *et al.*'s (2005, Chapter Five) spatial model of Cuvier's beaked whale density are as follows. The survey design is a source of uncertainty because altering the spatial or temporal specifications of the shipboard survey tracklines would have produced a different set of cetacean and oceanographic observations. The process of sighting the animals is stochastic, with some unknown probability that animals within sighting distance will be detected. The environmental data used as predictor variables in the GAM have measurement error. Sampling error arises from the stochasticity inherent in the sampling process generating the encounter rates and group sizes. Error is introduced when parameters are estimated in fitting the sighting and spatial models. Model selection errors are associated with choosing the appropriate variables and their corresponding degrees of freedom. Finally, there is a component of uncertainty due to a disassociation between the animals' distribution and the predictor variables used to try to understand the ecology of the system. The sources of error outlined above are not necessarily independent, making analytical methods for estimating variance largely intractable. In addition, the Cuvier's beaked whale density model described above, like many predictive models in ecology (Hamazaki, 2004), are affected by inflated sample size due to non-independence among samples, which is another situation in which analytical variance estimation methods fail. Where analytical methods fail, computer-intensive methods often succeed (Efron and Tibshirani, 1991); therefore, we pursue computer-intensive strategies to estimate variance in the density predictions.

Hedley *et al.* (1999) developed spatial models within a GAM framework to estimate the density and abundance of cetacean groups based upon line-transect survey data. They used a parametric bootstrap to estimate the components of variance due to spatial modeling (the stochasticity in encounter rates). Hedley *et al.*'s (1999) parametric bootstrap method involves the following steps. First, a spatial model is fit to the observed cetacean sighting data, then the spatial model is used to estimate group density at closely-spaced points along the survey trackline. A probability density function (pdf) for detections along the trackline is computed by dividing the estimated densities at each point by the total density along the line (computed by numerical integration). For each bootstrap pseudosample, the number of values generated from the detection pdf is distributed as a Poisson random variable with expectation equal to the total number of detections in the original data. Random variates are drawn from two uniform distributions, one ranging from zero to the total transect length and the second ranging from zero to the maximum value of the detection pdf; these random variates represent a point in two dimensions which, if located below the curve in the detection pdf, is accepted in the bootstrap pseudosample; otherwise it is rejected. The accepted points are projected onto the transect line, their positions are calculated, and they serve as the sightings for the bootstrap pseudosample. Given the collection of sightings in each bootstrap pseudosample, the model selected from the original data is refitted to obtain density and abundance estimates, and the sample variances of the pseudosample density and abundance estimates reflect the variance attributed to the spatial modeling process. Hedley *et al* (1999) incorporate uncertainty due to the estimation of the line-transect sighting parameters via the delta method.

The parametric bootstrap method that Hedley *et al.* (1999) implemented addresses the stochasticity in encounter rates, and their overall variance estimate incorporates uncertainty due to estimating the sighting parameters, but a number of components contributing to the overall variance in the predicted values were not accounted for. We build on Hedley *et al.*'s (1999) work, estimating the variance in Cuvier's beaked whale density estimates using a parametric bootstrap to quantify the uncertainty due to model selection and stochasticity in encounter rates and group sizes, and the delta method to add uncertainty due to the line-transect parameter estimation process. Furthermore, we use the bootstrap results to examine the relative importance of the environmental predictor variables, providing insight into how consistent the GAM machinery is in building models and suggesting which of the environmental factors we observed are good indicators of Cuvier's beaked whale habitat. We acknowledge that our method does not incorporate all sources of uncertainty in the density estimation process, but we believe that we have captured components that contribute to a large proportion of the true variance.

### Methods

## Data Collection and Model Building

The entire ecological model building process can be broken down into 5 steps: 1.) data collection; 2.) model specification, including identifying the range of models to consider and selecting the best model framework; 3.) parameter estimation; 4.) variance estimation; and 5.) model evaluation (Redfern *et al.*, in prep.). Thus, we report on the fourth step, but we will briefly summarize the methods that preceded our analysis.

The Cuvier's beaked whale sighting data and *in situ* oceanographic data were collected on Southwest Fisheries Science Center (SWFSC) research cruises conducted during the summer and fall of each year from 1986 to 1990, and in 1993 (Figure 6.1). Two National Oceanic and Atmospheric Administration (NOAA) research vessels, the *David Starr Jordan* and the *McArthur*, followed standard line-transect protocols (Buckland *et al.* 2001) to survey cetaceans in the eastern tropical Pacific Ocean, while concurrently collecting a suite of oceanographic data over the length of the trackline. Kinzey *et al.* (2000) provide a complete description of the SWFSC cetacean data collection procedures followed during the ship-based line-transect surveys. The *in situ* oceanographic data collected during the line-transect surveys, and considered as potential predictor variables in the encounter rate and group size models, were: sea surface temperature (SST), sea surface salinity, thermocline depth, thermocline strength, and surface chlorophyll concentration. Details of the oceanographic data collection methods for each ship and each year between 1986 and 1990 are available in Thayer *et al.* (1988a, 1988b, 1988c, 1988d), Lierheimer *et al.* (1989a, 1989b, 1990a, 1990b), and Philbrick *et al.* (1991a, 1991b). Oceanographic methods and results from the 1993 cruise have not yet been published. The fixed geographic variables depth, slope, distance from shore, latitude, and longitude were also considered as predictor variables. In addition, Beaufort sea state was recorded while the marine mammal observers were on-effort and was updated whenever conditions changed. Beaufort sea state is a dominant factor affecting the visibility of cetaceans; therefore, Beaufort was included in all models to account for potential biases due to visibility. For the GAM analysis, the sighting and environmental data were summarized as 9km segments of on-effort trackline (Ferguson *et al.*, 2005, Chapter Five). Detailed methods of the GAM model-building process can be found in Ferguson *et al.* (2005, Chapter Five), but we highlight pertinent features of that process below.

A GAM may be represented as

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

where each of the $X_j$ is a predictor variable and the $f_j$ are nonparametric functions of the predictors that are estimated from the data using smoothing operations (Hastie and Tibshirani, 1990; Chambers and Hastie, 1991; Insightful Corporation, 2001). There are three pieces to a generalized additive model: a random component, a systematic component, and a link function, which links the two components together (Hastie and Tibshirani, 1990). The random component specifies the sampling distribution of the response variable, $Y$. The link function, $g(\mu)$, relates the expectation of the response variable given the predictor variables, $\mu = E(Y|X_1,\ldots,X_p)$, to the additive predictor $\eta$ (the systematic component) as $g(\mu) = \eta = \alpha + \Sigma f(X)$.

The encounter rate and group size GAMs were built using S-PLUS 6 for Windows. The encounter rate data were essentially clustered counts; therefore, the number of sightings in each segment was modeled using a quasi-likelihood error distribution with variance proportional to the mean and a logarithmic link function (approximating an over-dispersed Poisson distribution). The proportionality constant relating the mean to the variance is referred to as the dispersion parameter, $\phi$, with $\mathrm{var}(Y) = \phi \cdot \mathrm{var}(\mu)$. Encounter rate models were built using all 9km segments, regardless of whether they contained sightings. Observed distributions of cetacean group sizes in the ETP region typically have long tails and are restricted to the positive real values. Therefore, GAMs were built using the natural logarithm of group size as the response variable and a Gaussian error distribution with the identity link function. The dispersion parameter for Gaussian GAMs is equal to var($Y$). Group size models were built on only the 9km segments that contained Cuvier's beaked whale sightings with valid group size estimates. The model selection process involved forward-backward stepwise selection of variables, testing up to three degrees of freedom (df) for each predictor variable, using Akaike's Information Criterion (AIC) to select the best model at each step. The stepwise selection process was conducted in five parallel runs, each time one of the years between 1986-1990 was excluded from the fitting procedure (1993 contained relatively little data), resulting in five candidates for the overall best model. During the cross-validation step, each candidate model was tested on the excluded year of data, and average squared prediction error (ASPE) was used to determine the overall best model. The final encounter rate model consisted of a linear fit for Beaufort sea state and smoothing splines for offshore distance (with two df) and depth (with three df). The final group size model included latitude, Beaufort sea state, and thermocline strength as linear terms and thermocline depth as a smoothing spline with two degrees of freedom. To fine-tune the GAM smoothing parameters, the overall best encounter rate and group size models were re-fit to all years' data using the predictor variables and degrees of freedom listed above for each model.

Density estimates were computed using the standard line-transect equation (Buckland *et al.*, 2001)

$$D = \left(\frac{n}{L}\right) \cdot S \cdot \frac{1}{2 \cdot ESW \cdot g(0)} \qquad (2)$$

where, *n/L* = encounter rate,

*S* = expected (or mean) group size,

*ESW* = effective strip half-width, or 1/*f(0)*, where *f(0)* is the sighting probability density at zero perpendicular distance

*g(0)* = probability of detecting an animal on the trackline.

Output from the encounter rate and group size GAMs provide the values for *n/L* and *S* in equation (2). If group size predictions are needed in arithmetic space, it is necessary to apply a bias-correction factor to the GAM output because the models were built in log space and transforming the results to arithmetic space also transforms the group size point estimate to a geometric mean (Finney, 1941; Smith, 1993). The ratio estimator was used to correct for this back-transformation bias (Smith, 1993). The values of *f(0)* and *g(0)* were those for Cuvier's beaked whales in the ETP and Gulf of California in Ferguson and Barlow's (2001) analysis. Cuvier's beaked whale densities resulting from applying the encounter rate and group size GAMs to the environmental data used to build the models are shown in Figure 6.2.

## Variance Estimation

A parametric bootstrap was used to quantify the contribution of model selection uncertainty and stochasticity in encounter rates and group sizes to the variance in predicted Cuvier's beaked whale densities (Figure 6.3). The bootstrap algorithm began by predicting encounter rates and group sizes from the oceanographic and geographic data collected during all survey years (1986-1990 and 1993). Consequently, point estimates were computed for every 9km segment used to build the original GAMs. In each bootstrap iteration (*B*=500 total iterations), these point estimates were perturbed to generate bootstrap pseudosamples using the estimates of variance for encounter rate and group size from the final GAMs. The dispersion factor for the encounter rate was estimated to be 0.981, which is close to the value of 1.0 expected under a simple Poisson model. Therefore, bootstrap encounter rate pseudosamples were generated from Poisson distributions (one for each 9km segment) with the mean for each distribution set equal to the corresponding point estimate. Similarly, bootstrap group size pseudosamples were generated from Gaussian distributions (one for each 9km segment) with the mean for each distribution equal to the corresponding point estimate (the natural logarithm of group size) and the variance equal to the estimated value of the dispersion parameter for the group size model. The encounter rate and group size pseudosamples were then run through the model selection procedures and density estimation methods summarized above and described in Ferguson *et al.* (2005, Chapter Five). The original environmental data were used to build the bootstrap models and to compute the bootstrap density estimates. Upon completion of each bootstrap iteration, the point estimates of density for each 9km segment (derived from the bootstrap encounter rate and group size models) and the predictor variables (and their associated degrees of freedom) found in the best bootstrap group size and encounter rate models were saved.

The delta method (Seber, 1982) was used to incorporate uncertainty due to estimation of *f(0)* and *g(0)* into the overall variance estimate.

## Results

Results from the bootstrap simulation will be discussed as coefficients of variation instead of variances to present the variability on the same scale as the density estimates. Estimates of the coefficients of variation for the Cuvier's beaked whale density predictions range from 0.462 to 3.01 (Figure 6.4). The region with lowest CV's (Figure 6.4) correspond to the region with the greatest survey effort (Figure 6.1). Summary statistics for the results of the bootstrap simulations on a sample of nine out of the 13,872 total segments located throughout the study area (Figure 6.4) are presented in Table 6.1. In addition, histograms of the bootstrap density estimates for the sample of nine segments are shown in Figure 6.5. The distributions for these bootstrapped density estimates have long right tails, suggesting that the bootstrap samples generated very high densities on occasion.

Overall, only two out of 500 bootstrap simulations selected exactly the same encounter rate model as the original, and none of the simulations selected the same group size model. Of all the predictor variables included in the scope of the encounter rate GAMs, Beaufort, offshore distance, and depth (the three variables found in the original model) had the highest frequencies of inclusion in the bootstrap models (Table 6.2). All of the bootstrap encounter rate models selected Beaufort, and approximately 68.6% of the models incorporated it as a linear term, as in the original model. Offshore distance and depth were not as consistent in the bootstrap encounter rate models, being included in 43.2% and 70.2% of the simulations, respectively, with under 15% of the simulations including offshore distance with the same number of degrees of freedom as in the original model. In the bootstrap group size models, the variables with the highest frequencies of inclusion were latitude, Beaufort, thermocline depth, and thermocline strength, which were the only four variables in the original group size model (Table 6.3). Latitude, Beaufort, and thermocline strength were selected for the bootstrap models with the same number of degrees of freedom as the original model in 87%, 71%, and 61.2% of the iterations, respectively. Thermocline depth was unusual in that none of the bootstrap group size models accepted it with the same number of degrees of freedom as the original model.

## Discussion

We have presented the first variance estimates for cetacean density predictions derived from spatial models. Our methods quantify the contribution of model selection uncertainty, sampling errors in encounter rates and group sizes, and line-transect parameter estimation uncertainty to the overall variance estimate. In addition, we used bootstrap selection probabilities to provide a measure of relative importance for each of the predictor variables that were considered in building the GAMs. Quantifying the uncertainty in cetacean density predictions and in ecological model specifications is important because it informs ecologists and decision-makers of the limitations of our knowledge, and can provide guidance on where to concentrate future efforts to better understand cetacean ecology.

For example, there is a great amount of uncertainty in the Cuvier's beaked whale density predictions in the Gulf of California as measured by the coefficient of variation (Figure 6.4). Knowing that Cuvier's beaked whale density predictions for this area are relatively imprecise is particularly meaningful in light of the events in September of 2003, when a Cuvier's beaked whale mass stranding event closely corresponded to the timing of seismic research cruise during which intense acoustic pulses were transmitted into the water (Peterson, 2003). Efforts to avoid or mitigate potential harm to beaked whales caused by such human activities should incorporate the limitations of our knowledge of beaked whale habitat to properly weigh the risks of negatively affecting the animals against the costs of modifying, relocating, or discontinuing the human actions. It is noteworthy that the spatial coverage of the SWFSC line-transect survey in the Gulf of California was thorough (Figure 6.1), yet it is a region where the density models were the least precise. This apparent irony may be explained by the fact that the Gulf of California was surveyed extensively during only one year. It is also possible that factors other than the measured environmental variables that were considered in building the models are influential in characterizing Cuvier's beaked whale habitat in the Gulf of California.

Examination of the bootstrap variable selection frequencies produced three valuable results. First, the variables that were included in the original Cuvier's beaked whale encounter rate and group size GAMs were *consistently* included in the bootstrap models. Second, the three variables in the original encounter rate model and the four in the original group size model had much higher bootstrap selection frequencies than any of the other variables when summed over all functional forms (*i.e.*, linear or smoothing splines with 2, 3, or 4 df). Finally, although the GAMs consistently selected certain variables, the functional forms appearing in the final bootstrap models were highly variable; this is particularly evident for offshore distance in the encounter rate model and thermocline depth in the group size model, both of which had bootstrap selection probabilities less than 0.15 (Tables 6.2 and 6.3). This inconsistency may be a weakness of the GAM methodology, or it may be a consequence of using proxy predictor variables to characterize encounter rate and group size.

Future efforts to model cetacean density should investigate the magnitude of the remaining components of uncertainty to the total variance estimate for the predictions. In addition, more resources should be applied to understanding cetaceans as predators and the ecology of their prey because a better understanding of these relationships could provide more insight into the mechanisms that structure cetacean distributions, which may result in ecological models with greater precision.

## Acknowledgements

We would like to thank Karin Forney, Dan Goodman, and Jessica Redfern for providing ideas on how to proceed with this analysis. Paul Dayton, Teresa Chereskin, and Jim Leichter provided thoughtful comments on earlier drafts of this manuscript.

Funding for this research came from the National Science Foundation Graduate Research Fellowship, the Department of Navy through the Office of Naval Research, and the Strategic Environmental Research and Development Program.

The dissertation author was the primary researcher and author of Chapter Six, and the co-author listed directed and supervised the research which forms the basis for this chapter.

Table 6.1. Summary statistics for the results of the bootstrap simulations on nine segments, randomly located throughout the study region. Each segment is labeled and shown as a black cross on Figure 6.4.

| Segment Label | Bootstrap | | | | | | Original Model Estimated Density |
|---|---|---|---|---|---|---|---|
| | Minimum | 5th percentile | Mean | 95th percentile | Maximum | CV | |
| A | 0.701 | 1.556 | 4.687 | 8.732 | 17.247 | 0.629 | 4.474 |
| B | 0.933 | 1.816 | 3.873 | 6.275 | 8.926 | 0.527 | 3.446 |
| C | 0.134 | 1.211 | 4.076 | 8.333 | 17.967 | 0.699 | 2.970 |
| D | 0.623 | 2.029 | 5.460 | 10.238 | 15.152 | 0.596 | 5.059 |
| E | 0.715 | 1.727 | 3.489 | 5.628 | 9.117 | 0.528 | 2.430 |
| F | 1.110 | 2.130 | 4.505 | 7.394 | 11.296 | 0.529 | 3.850 |
| G | 0.413 | 2.211 | 6.098 | 11.465 | 25.737 | 0.648 | 6.674 |
| H | 0.235 | 1.202 | 4.571 | 9.808 | 17.699 | 0.709 | 3.678 |
| I | 0.125 | 0.891 | 3.753 | 8.014 | 22.347 | 0.757 | 2.839 |

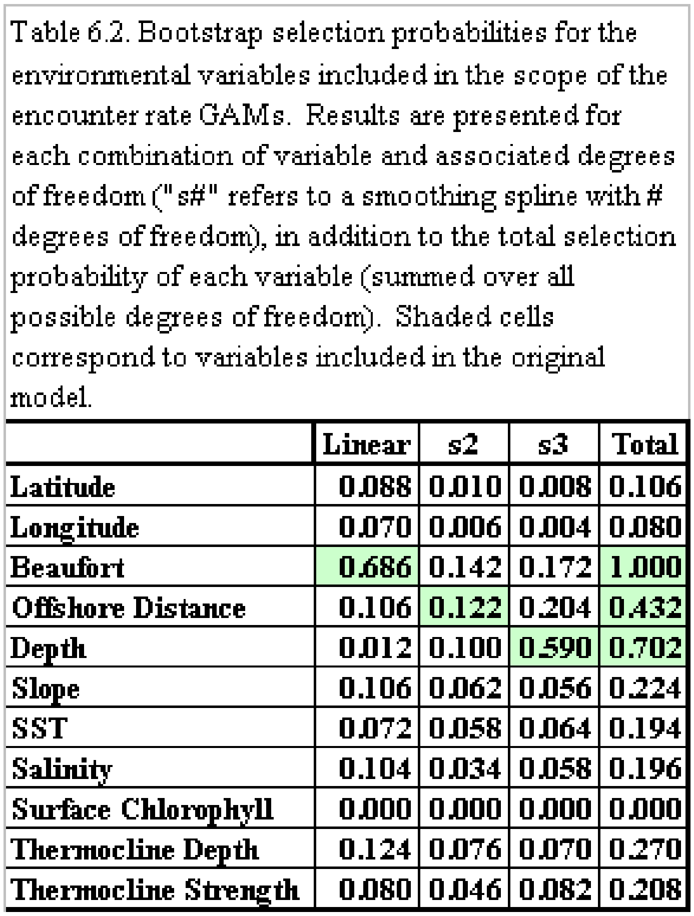


Table 6.2. Bootstrap selection probabilities for the environmental variables included in the scope of the encounter rate GAMs. Results are presented for each combination of variable and associated degrees of freedom ("s#" refers to a smoothing spline with # degrees of freedom), in addition to the total selection probability of each variable (summed over all possible degrees of freedom). Shaded cells correspond to variables included in the original model.

| | **Linear** | **s2** | **s3** | **Total** |
|---|---|---|---|---|
| **Latitude** | **0.088** | **0.010** | **0.008** | **0.106** |
| **Longitude** | **0.070** | **0.006** | **0.004** | **0.080** |
| **Beaufort** | **0.686** | **0.142** | **0.172** | **1.000** |
| **Offshore Distance** | **0.106** | **0.122** | **0.204** | **0.432** |
| **Depth** | **0.012** | **0.100** | **0.590** | **0.702** |
| **Slope** | **0.106** | **0.062** | **0.056** | **0.224** |
| **SST** | **0.072** | **0.058** | **0.064** | **0.194** |
| **Salinity** | **0.104** | **0.034** | **0.058** | **0.196** |
| **Surface Chlorophyll** | **0.000** | **0.000** | **0.000** | **0.000** |
| **Thermocline Depth** | **0.124** | **0.076** | **0.070** | **0.270** |
| **Thermocline Strength** | **0.080** | **0.046** | **0.082** | **0.208** |

Table 6.3. Bootstrap selection probabilities for the environmental variables included in the scope of the group size GAMs. Results are presented for each combination of variable and associated degrees of freedom ("s#" refers to a smoothing spline with # degrees of freedom), in addition to the total selection probability of each variable (summed over all possible degrees of freedom). Shaded cells correspond to variables included in the original model.

| | **Linear** | **s2** | **s3** | **Total** |
|---|---|---|---|---|
| **Latitude** | 0.870 | 0.038 | 0.088 | 0.996 |
| **Longitude** | 0.150 | 0.008 | 0.010 | 0.168 |
| **Beaufort** | 0.710 | 0.174 | 0.116 | 1.000 |
| **Offshore Distance** | 0.222 | 0.122 | 0.112 | 0.456 |
| **Depth** | 0.154 | 0.082 | 0.140 | 0.376 |
| **Slope** | 0.112 | 0.046 | 0.076 | 0.234 |
| **SST** | 0.096 | 0.168 | 0.304 | 0.568 |
| **Salinity** | 0.126 | 0.134 | 0.154 | 0.414 |
| **Surface Chlorophyll** | 0.000 | 0.000 | 0.000 | 0.000 |
| **Thermocline Depth** | 0.000 | 0.000 | 1.000 | 1.000 |
| **Thermocline Strength** | 0.612 | 0.154 | 0.234 | 1.000 |

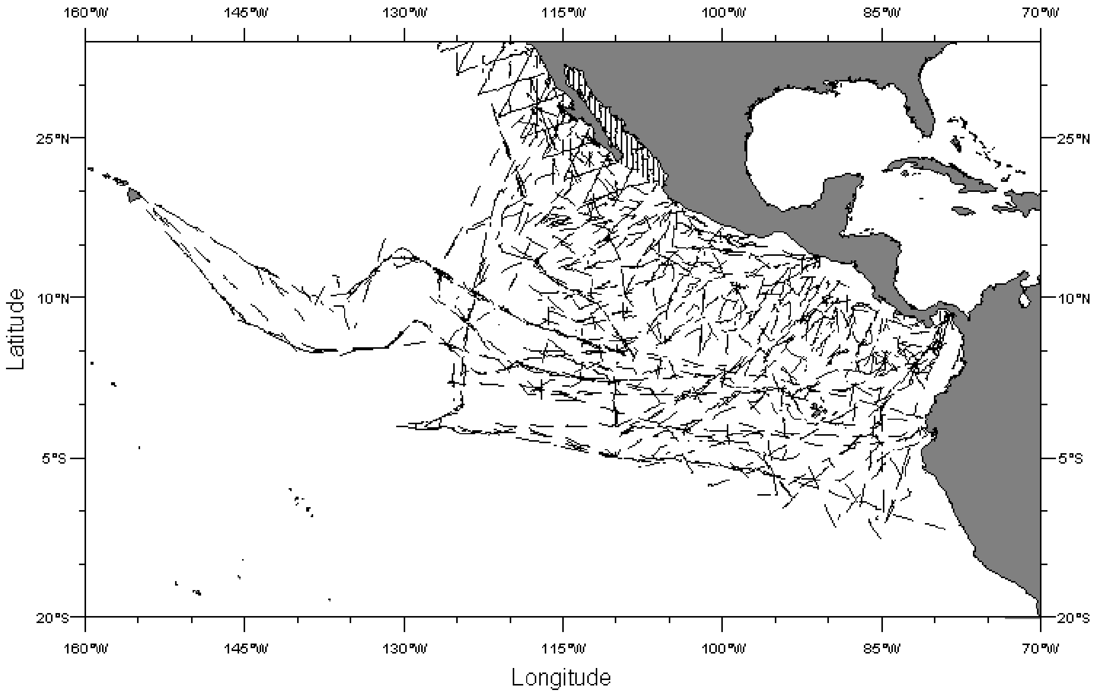


Figure 6.1. Transect lines covered during the 1986-1990 and 1993 line-transect surveys conducted by the Southwest Fisheries Science Center.

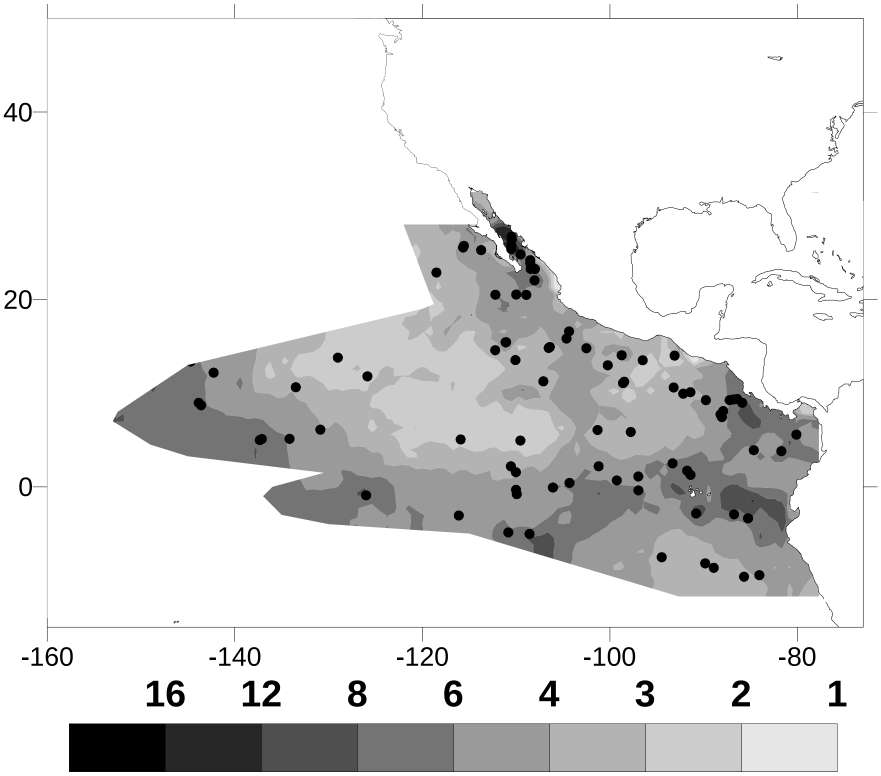
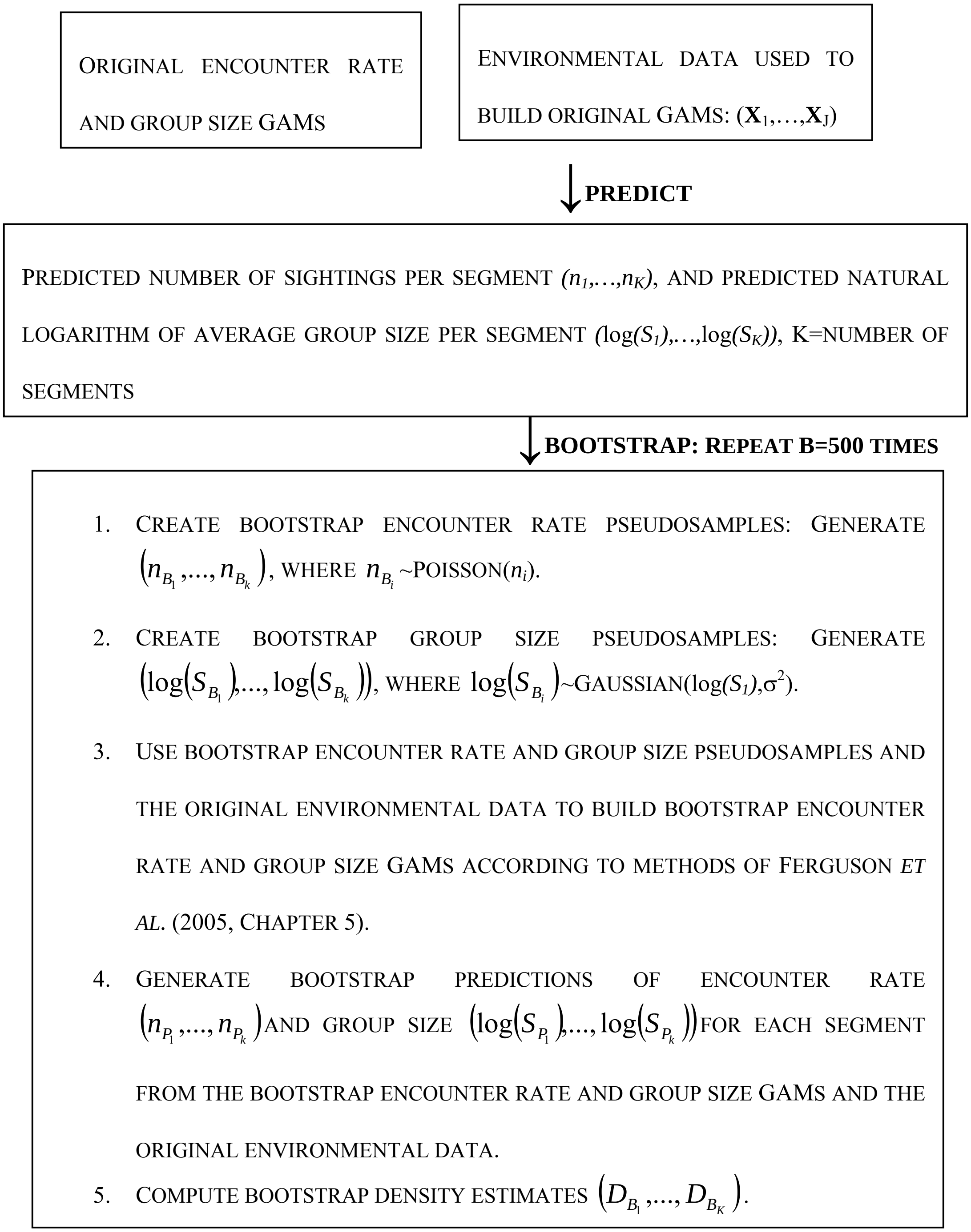


Figure 6.2. Predicted Cuvier's beaked whale (*Ziphius cavirostris*) density (# individuals/1000 km$^2$) in the eastern tropical Pacific Ocean. Predictions are for Beaufort sea state of 1. Black circles mark locations of all transect segments with on-effort Cuvier's sightings and oceanography data from Southwest Fisheries Science Center surveys in 1986 to 1990 and 1993.



ORIGINAL ENCOUNTER RATE AND GROUP SIZE GAMS

ENVIRONMENTAL DATA USED TO BUILD ORIGINAL GAMS: ($\mathbf{X}_1,\ldots,\mathbf{X}_J$)

↓ **PREDICT**

PREDICTED NUMBER OF SIGHTINGS PER SEGMENT $(n_1,\ldots,n_K)$, AND PREDICTED NATURAL LOGARITHM OF AVERAGE GROUP SIZE PER SEGMENT $(\log(S_1),\ldots,\log(S_K))$, K=NUMBER OF SEGMENTS

↓ **BOOTSTRAP: REPEAT B=500 TIMES**

1. CREATE BOOTSTRAP ENCOUNTER RATE PSEUDOSAMPLES: GENERATE $\left(n_{B_1},\ldots,n_{B_k}\right)$, WHERE $n_{B_i}$ ~POISSON($n_i$).
2. CREATE BOOTSTRAP GROUP SIZE PSEUDOSAMPLES: GENERATE $\left(\log\left(S_{B_1}\right),\ldots,\log\left(S_{B_k}\right)\right)$, WHERE $\log\left(S_{B_i}\right)$~GAUSSIAN($\log(S_1),\sigma^2$).
3. USE BOOTSTRAP ENCOUNTER RATE AND GROUP SIZE PSEUDOSAMPLES AND THE ORIGINAL ENVIRONMENTAL DATA TO BUILD BOOTSTRAP ENCOUNTER RATE AND GROUP SIZE GAMS ACCORDING TO METHODS OF FERGUSON *ET AL*. (2005, CHAPTER 5).
4. GENERATE BOOTSTRAP PREDICTIONS OF ENCOUNTER RATE $\left(n_{P_1},\ldots,n_{P_k}\right)$ AND GROUP SIZE $\left(\log\left(S_{P_1}\right),\ldots,\log\left(S_{P_k}\right)\right)$ FOR EACH SEGMENT FROM THE BOOTSTRAP ENCOUNTER RATE AND GROUP SIZE GAMS AND THE ORIGINAL ENVIRONMENTAL DATA.
5. COMPUTE BOOTSTRAP DENSITY ESTIMATES $\left(D_{B_1},\ldots,D_{B_K}\right)$.

Figure 6.3. Parametric bootstrap algorithm used to estimate variance in Cuvier's beaked whale (*Ziphius cavirostris*) density predictions.

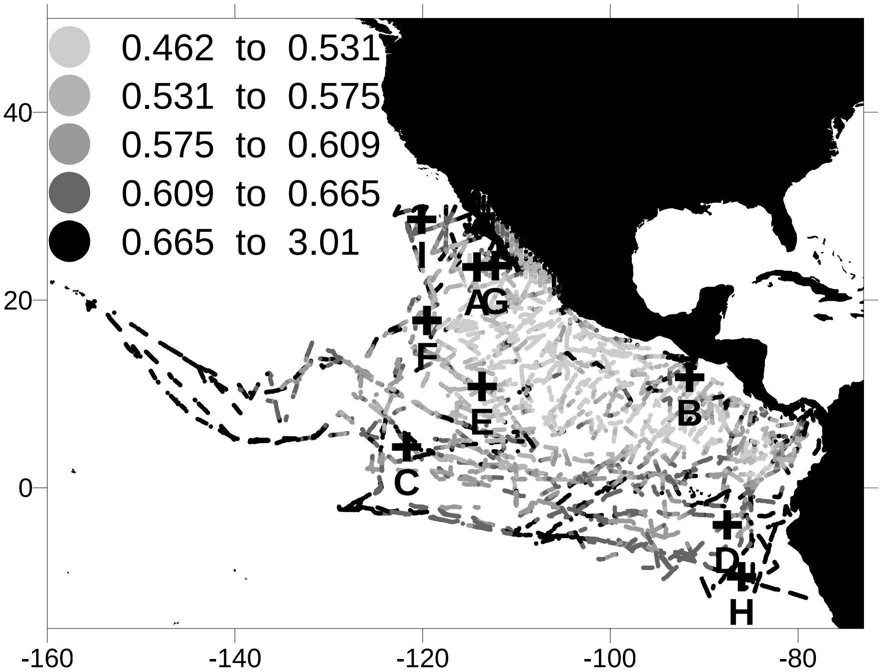


Figure 6.4. Estimated coefficients of variation for Cuvier's beaked whale (*Ziphius cavirostris*) density predictions. Summary statistics of bootstrap simulations for segments identified by black crosses are provided in Table 6.1.

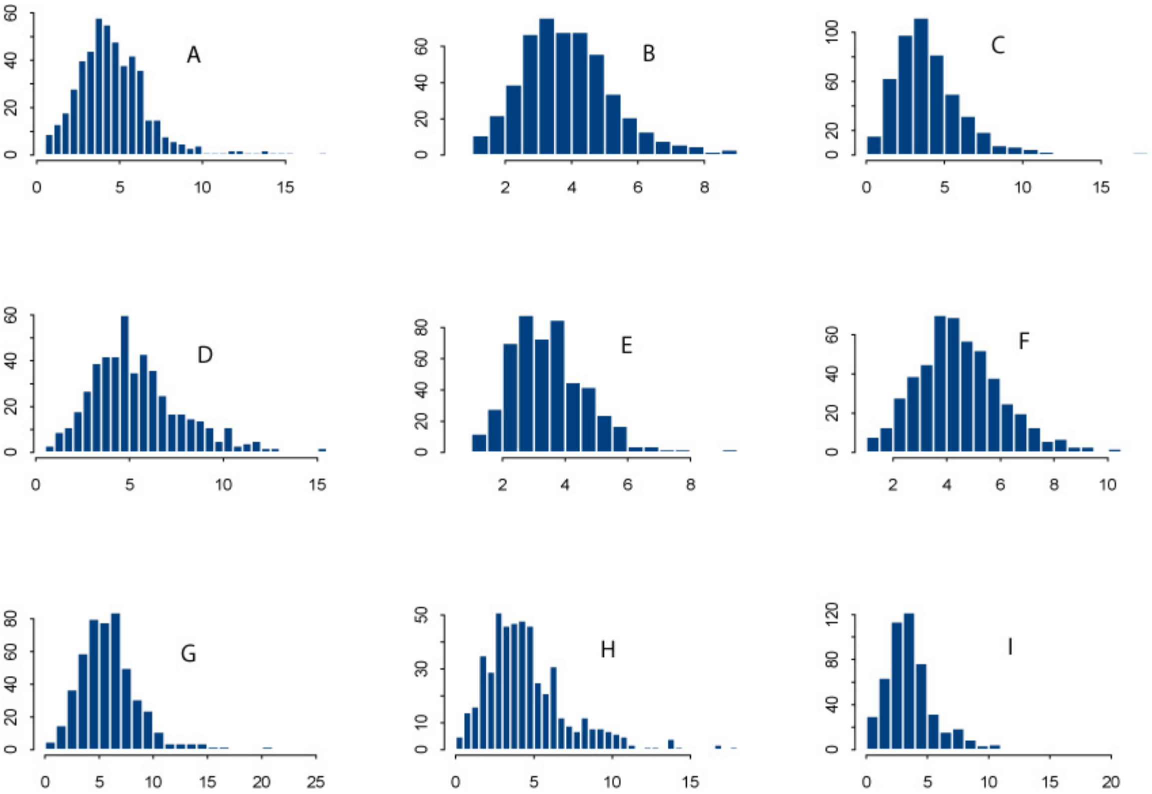


Figure 6.5. Histograms of bootstrap density estimates for nine segments randomly located throughout the ETP study area. Density estimates (# individuals/1000km$^2$) are given on the x-axis and number of bootstrap simulations are given on the y-axis. Summary statistics of the bootstrap simulations for the nine segments are provided in Table 6.1. Locations of the nine segments are shown as black crosses in Figure 6.4.

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