BEHAVIORAL ECOLOGY OF CETACEANS IN THE SOUTHERN CALIFORNIA BIGHT

A Dissertation

by

MARI ANN SMULTEA

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Chair of Committee,	Bernd Würsig
Committee Members,	Jane Packard
	Doug Biggs
	Jay Rooker
Head of Department,	Anna Armitage

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ABSTRACT

A behavioral ecology perspective on cetaceans in the Southern California Bight (SCB) can contribute to science-based adaptive management in the context of expanding anthropogenic activities. Objectives were to (1) identify behaviors associated with habitat resource selection, (2) evaluate species differences related to body size, group size, and group cohesion, and (3) determine temporal behavioral patterns.

Cetacean aerial surveys (87,735 km) were conducted in 2008-2013 in all months except December. Locations and behavioral data were recorded for blue whales (*Balaenoptera musculus*), fin whales (*B. physalus*), gray whales (*Eschrichtius robustus*), Risso's dolphins (*Grampus griseus*), common bottlenose dolphins (bottlenose; *Tursiops truncatus*), and common dolphins (*Delphinus delphis* and *D. capensis*). Response variables (occurrence, behavioral state, group size, group cohesion) were analyzed relative to the explanatory variables calf presence, bottom depth, shore distance, slope, aspect, time of day, Julian day, season.

Resource Selection Function (RSF) modeling predicted probability of habitat use relative to resource availability and behavioral state by contrasting environmental characteristics at locations of cetaceans and randomly selected points (n=35,167). During medium/fast travel, relative probability of habitat use by fin whales was highest in deep and eastern waters ($p<0.05$) of the San Nicolas and San Diego basins. Risso's dolphins selectively ($p<0.05$) used nearshore waters more than expected relative to availability, especially San Clemente Island, and habitat use differed by behavioral state (rest/slow travel, medium/fast travel; $p<0.05$). Bottlenose dolphins selectively used ($p<0.05$) nearshore shallow waters more frequently than available, particularly near Santa Catalina Island.

Behaviors varied by species, not solely by body size. Larger whales (blue, fin) and dolphins (Risso's, bottlenose) occurred in smaller, less cohesive groups and were more likely to occur alone. Species-specific group size was larger with calf presence; cohesion was higher during peak reproductive seasons (calving/mating). Time of day influenced behavioral state in nocturnal-feeding Risso's and common dolphins, which were less cohesive and more inactive (mill/rest/slow travel) near midday.

Spatiotemporal variation in cetacean distribution may reflect short-term changes in reproductive condition, resource availability, and anti-predator behavior. Applications of this behavioral ecology perspective are discussed relative to management opportunities within the framework of protecting areas, endangered species, and species-specific sensitive time periods.

DEDICATION

My dissertation is dedicated to my parents Ilie J. Smultea and Judith C. Smultea. They inspired in me the love of learning, pursuit of education, passion for culture, traveling, ethics of hard work, compassion for those in need, appreciation of nature, and nurturing of wayward animals. I am also grateful that they encouraged me to follow my own dreams and paths as far as they will take me. They also helped me to recognize reality and limitations and to appreciate the small things in life like butterflies and caterpillars. My work is dedicated to my two wonderful daughters Olivia and Iliana, to encourage them to follow their own dreams. A special dedication to my partner Dave, my kids, and all who supported me through this mid-life endeavor. This support endured my bouts of grumpiness with minimal sleep while juggling a business, full time work, a farm, a family, and my passion to pursue more knowledge through a PhD. All this in the hopes that this accomplishment will assist in further endeavors to promote and share scientific knowledge for practical management applications, among others.

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I was the principal scientist in all aspects of the research included herein. Statistical analyses in Chapters II and IV were selected and designed in consultation with West Inc. (Trent McDonald), with actual analyses in R conducted by West Inc. (S. Howlin, C. Nations, and S. Norman) and biological interpretation and direction conducted by me.

A team of field and office personnel assisted with data collection and management as well as compilation of data tables and summaries, figures, maps, and literature searching and citations. I was ultimately responsible for all aspects of the studies herein. Specifically, Chapter II was analyzed with assistance from T. McDonald, S. Howlin and T. Jefferson. Chapter IV was analyzed with assistance from T. McDonald and C. Nations. I thank all those who participated in

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NOMENCLATURE

AIC	Akaike’s Information Criterion
BIA	Biologically Important Area
BL	Body Length(s)
CCE	California Current Ecosystem
CI	Confidence Interval
CITES	Convention on International Trade in Endangered Species of Wild Fauna and Flora
DEM	Digital Elevation Models
DoN	Department of the Navy
DSL	Deep Scattering Layer
ESA	Endangered Species Act
ESE	East South-East
GPS	Global Positioning System
h	Hour(s)
HD	High Definition
ICMP	Integrated Comprehensive Monitoring Plan
IQR	Interquartile Range
km	Kilometer(s)
kt	Knot(s)
m	Meter(s)
MFA	Mid-Frequency Active
min	Minute(s)
MMPA	Marine Mammal Protection Act
MP	Megapixel
MPA	Marine Protected Area

MSMP	Marine Species Monitoring Plan
N	North
NAVFAC	Naval Facilities Engineering Command
Navy	U.S. Navy
NMFS	National Marine Fisheries Service
NMS	U.S. National Marine Sanctuaries
NOAA	National Oceanic and Atmospheric Administration
NW	Northwest
RSF	Resource Selection Function
SCB	Southern California Bight
SCI	San Clemente Island
SD	Standard Deviation
SE	Southeast
SNB	San Nicolas Basin
SOCAL	Southern California
SST	Sea Surface Temperature
SW	Southwest
SWFSC	Southwest Fisheries Science Center
U.S.	United States
WAAS	Wide-Area Augmentation System
WNW	West-Northwest

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CHAPTER I

INTRODUCTION

Principles of science-based adaptive management have been applied in both terrestrial and marine contexts (Katsanevakis et al. 2011; Geldmann et al. 2013). The adaptive management approach aids decision makers in setting short-term objectives for reaching explicit long-term goals and to utilize scientific information in evaluating success at achieving those narrowly-defined objectives. Typically, decision makers consider regulatory options related to protection of areas, species and times of high-risk anthropogenic activities. Behavioral ecology perspectives can provide a sound scientific basis for integrating species-specific spatio-temporal data into models (Blumstein and Fernández -Juricic 2010; Berger-Tal et al. 2011). To the extent that species-specific behavior varies in space and time, it should be considered in design of monitoring efforts yielding data useful in adaptive management.

Static spatial protection in the marine environment has been driven by policy such as Marine Protected Areas (MPA), U.S. National Marine Sanctuaries (NMS), and Designated Critical Habitat for U.S.-endangered species. Such protected areas can entail various levels of year-round protection of a geographic area characterized by sensitive marine habitats and associated species (Willis et al. 2004; Hooker et al. 2011). No-take protected areas, (i.e., reserves) prohibit all extractive uses (e.g., fishing, resource use) and exclude human activities that may directly or indirectly harm or disturb species or their habitats (Sissenwine and Murawski 2004; Sciberras et al 2015). Protected areas may exclude some activities but allow others. Many focus on protection of coral, fish, seabirds, sea turtles, or marine mammals. For example, the Gully MPA is designed to protect an important ecosystem that includes feeding habitat used by bottlenose whales in North Atlantic Canadian waters. The Gully MPA has three different levels of protective zones from full protection prohibiting disturbance, damage, and resource extraction to the lowest level where commercial activities are considered on a case by case basis (DFO 2008). NMS also prohibit similar activities and are designed to protect multiple invertebrate and vertebrate species (e.g., Channel Islands Marine Sanctuary off southern California) while typically allowing recreational fishing and tourism but excluding commercial fishing or other resource extractions (Botsford et al. 2014). Functions of NMS include enhancing production of young invertebrate and fish larvae and protecting seabird nesting populations and feeding and migration areas critical to larger taxa (e.g., sea turtles, marine mammals; NMS 2016; NOAA 2016).

Time is an important factor to be considered in MPA management, a concept identified as “Dynamic Ocean Management” (Maxwell et al. 2015). Spatial distribution of marine resources and anthropogenic activities are likely to change with short-term oscillations as well as long-term trends such as global climate change. Resources needed by a species may move outside a static protected area. Alternatively, anthropogenic activities may be restricted only during certain periods considered biologically important to one or more species (Mangel 2000; NRC 2001; Apostolaki et al. 2002). Examples for cetaceans include Designated Critical Habitat for the endangered Cook Inlet beluga whale (*Delphinapterus leucas*) in Cook Inlet, Alaska (NMFS 2008). During the ice-free season, seismic and other activities exceeding noise criteria regulated by National Marine Fisheries Service (NMFS) are prohibited within 18 km of the Susitna River mouth near Anchorage, coinciding with the peak migration of important beluga fish prey (NMFS 2008, 2015). Off Kaikoura, New Zealand, legislative mandates exclude tourism involving humans swimming with dusky dolphins during specific daily dolphin rest periods to avoid disturbing dolphins during this energetically important period (Lundquist et al. 2012, 2013). In the North Atlantic, Seasonal Management Areas (SMAs) for endangered North Atlantic right whales are designated at this species' southern calving grounds during winter, along the migration route during spring and fall migration, and on northern feeding grounds during summer (FR 2016). SMAs include restricting vessel speed to reduce the risk of vessels striking and injuring or killing right whales.

For species protected under the U.S. Endangered Species Act (ESA) or the Convention on International Trade in Endangered Species of Wild Fauna and Flora (CITES), management typically focuses on one species of conservation concern. For example, an MPA has been proposed based on critical habitat for the Chinese white dolphin (*Sousa chinensis*) in coastal waters of western Taiwan (Liu et al. 2015). This single-species approach contrasts with the multi-species approach recommended for MPA management (Schmiing et al 2015). However, a multiple-species approach may overlook critical needs of a single species. This paradox can be resolved if management for a single species also benefits multiple species in a MPA. When ecological communities derive benefits from single-species protection efforts, the focal species is termed an “umbrella species” (Wilcox 1984). Umbrella species are often wide-ranging with relatively large space requirements that maximize benefits to other species (Groom et al. 2006). For example, the northern spotted owl (*Strix occidentalis caurina*) is an umbrella species whose protection benefits smaller species (e.g., invertebrates, amphibians) in the old-growth forest that is the owl's habitat (Dunk et al. 2006). Similarly, a “flagship species” is a single-species conservation option based on the charismatic appeal to gain public support, thereby protecting other less-charismatic species inhabiting the same area (Ducarme et al. 2013). Examples of flagship species include the polar bear (*Ursus maritimus*) as well as whales and dolphins in the suborder *Mysticeti* (Leader-Williams and Dublin 2000; Barney et al. 2005).

Spatio-temporal habitat management for multiple species is a relatively new overarching concept for marine mammals in the face of growing anthropogenic pressures in the marine environment (Weilgart 2006; Dolman and Jasny 2015). Integrated spatial and temporal data analysis of marine environments is essential for effective adaptive management, particularly in cases where anthropogenic activity is outside a regulatory framework, such as shipping or military training activities (Fox et al. 2013). For example, buffer zones can be applied for voluntary compliance with best management practices reducing exposure to specific underwater noise levels (Weilgart 2006). The recent designation by NMFS of Biologically Important Areas (BIA) for multiple cetacean species is an example of a voluntary best management practices approach that focuses on areas encompassing critical seasonal feeding, calving and/or migratory habitat for cetaceans of concern (Calambokidis et al. 2015; Ferguson et al. 2015). Species-specific spatio-temporal data were useful in the development of an MPA, seasonal restrictions and closures for reducing ship collisions risks with the North Atlantic right whale (Garrison 2007; Conn and Silber 2013; Petruny et al. 2014).

Effective marine spatial planning and adaptive management require species-specific spatio-temporal data that identify when, how often, and why certain habitats are used by each species relative to critical biological functions (e.g., nursing, feeding), as animals may be more sensitive to disturbance during certain periods or behaviors (Dolman 2007; Brilot et al. 2012; Basille et al. 2013). There is increasing evidence across vertebrate taxonomic groups that species, location, animal activity (i.e., behavioral) state (e.g., feeding, migrating), and reproductive status (e.g., presence of young) affect individual response levels to anthropogenic activities (e.g., Brilot et al. 2012; Basille et al. 2013; Robertson et al. 2013). However, behavioral patterns (e.g., foraging, group size, social structure, habitat selection) vary spatiotemporally within and across populations and geographical regions in response to resource availability and predation risk (e.g., Gittleman 1989; Sterelny 2007; Kappeler et al. 2013).

Closely related species inhabiting the same environment are predicted to adapt distribution, group size, and social structure to dynamically changing time (diel, seasonal) and space gradients (e.g., ephemeral patchiness, habitat distribution) that affect resource availability (e.g., food, cover, mates), while still minimizing predation risk (e.g., Parrish and Edelstein-Keshet 1999; Beauchamp 2014). Predation pressure in particular is considered one of the strongest factors shaping the behavioral ecology of prey species (Norris and Schilt 1988; Kie 1999; Beauchamp 2014). Thus, identification of species-specific differences in behavioral ecology and factors influencing these differences are needed for effective conservation and adaptive management. Species-specific spatio-temporal data should be collected at a scale appropriate in the specific area of concern to appropriately interpret impacts and identify management measures (Meentemeyer and Box 1987; Wiens 1989).

1.1 Cetacean Behavioral Ecology Models

Several behavioral ecology models have been proposed to explain differences in the socioecology of cetacean species in different habitats as shaped by environmental variables. Gowans et al. (2008) proposed a conceptual framework predicting that delphinid social structure is influenced by spatial and temporal distribution of resources (e.g., food, habitat complexity providing cover from predators) that in turn affects home range patterns and social strategies (e.g., group size and stability).

The resulting social structure represents tradeoffs between group size, intra-group competition, and predation risk. For example, in structurally complex coastal and inland waters where predation risk is usually low and where food resources are predictable but limited, Gowans et al. (2008) predict that delphinid species should be resident and form small, relatively stable social groups (<10 dolphins), facilitating male sequestering of females for breeding. Example species include island-associated spinner dolphins (*Stenella longirostris*) and inshore bottlenose dolphins (*Tursiops* sp.). Gowans et al. (2008) compared the latter social grouping to African antelopes inhabiting structurally complex forests that provide reduced risk of predation. In contrast, Gowans et al. (2008) equated delphinids inhabiting deep oceanic waters (including the continental shelf and slope), such as short-beaked common dolphins, with large-bodied ungulate antelopes of the open African savannah. For both taxa, they suggested that living in large groups of ~100-1,000+ individuals may be the only anti-predator strategy possible in open habitat, where food patches are generally unpredictable and widely spaced, requiring individuals to travel long distances to forage.

Formation of large delphinid groups in open waters is hypothesized to (1) improve detection of fish and cephalopod prey (Norris and Schilt 1988; Gowans et al. 2008), (2) improve efficiency of cooperative herding and foraging of small fishes (Würsig and Würsig 1980), and (3) typically be associated with fission-fusion societies, where membership and group size often change spatiotemporally with resource availability (e.g., Norris and Dohl 1980; Connor et al. 2000;

Gowans et al. 2008). Gowans et al. (2008) further suggested a continuum related to variability in food availability across habitats in open water. Delphinids required to range medium distances to locate food are predicted to form medium-sized groups (10-100 dolphins), trading off reduced predation risk within a group with increased intra-specific competition, such as humpback dolphins (*Sousa* sp.). Gowans et al. (2008) concluded that their conceptual predictive framework remained to be tested empirically, but may provide a basis upon which to test further hypotheses related to the evolution of delphinid social strategies.

A number of delphinid studies have since shown patterns consistent with the Gowans et al. (2008) predictive framework. In shallow coastal waters characterized by relatively high structural complexity (e.g., vegetation, embayments), small delphinid groups form some stable associations and exhibit residency, presumably reflecting more predictable and localized prey availability. These include the Guiana dolphin (*Sotalia guianensis*), Commerson’s dolphin (*Cephalorhynchus commersoni*), and Australian snubfin dolphin (*Orcaella heinsohni*) (Santos et al. 2010; Coscarella et al. 2011; Parra et al. 2011).

While Gowans et al. (2008) considered the influences of habitat complexity, resource availability, home range, and predation pressure on delphinid social strategies, relatively few studies have considered the roles of body size and group cohesion (i.e., individual spacing) in cetacean social strategies. Gygax (2002a,b) compared intra- and inter-specific group sizes of mostly coastal delphinids and phocoenids (the family of porpoises) with body size, categorically rating variables for habitat complexity, predation pressure relative to habitat openness, diet, residency and other factors. Intra-specific comparisons revealed no consistent or general predictor of group size, with all eight investigated species exhibiting a unique set of correlative variables (Gygax 2002a). Inter-specific comparisons showed that designation of a species was the most important factor affecting group size, although Gygax (2002b) indicated that patterns may differ with more data. Group size also increased among some species as habitat openness increased (Gygax 2002b).

Among mysticete (baleen) whales, Ford and Reeves (2008) suggested that as body size and swim speed ability increase, predation risk decreases. They proposed that mysticetes have evolved divergent anti-predator strategies reflected by differences in body size, morphology and habitat selection: Balaenoptera (e.g., blue and fin whales) inhabiting primarily open pelagic waters have large streamlined bodies, and minimize predation by individually out fleeing killer whale (*Orcinus orca*) predators. In contrast, other mysticete genera (e.g., gray and bowhead whales, *Balaena mysticetus*) tend to have shorter, more robust bodies with slower swimming capability and are better suited for avoiding predators by seeking refuge in more structurally complex coastal waters (e.g., shallow depth, ice, kelp beds) or fighting off predators individually or in groups (Ford and Reeves 2008). In both strategies, Ford and Reeves (2008) concluded that one reason large mysticetes may have evolved large body size and/or fast swimming ability is to minimize predation risk by killer whales. Ford and Reeves (2008) suggested that fast-swimming balaenopterids require fast long chases by and risk of injury to predatory killer whales, traits that have evolved as a predator deterrent compared to preying on smaller-bodied cetaceans.

Based on the predictive framework for delphinids and mysticetes inhabiting open waters as described above, similar patterns are predicted to occur among less-described odontocete and mysticete species inhabiting deep open waters. Open waters are characterized by variability in the extent of clumped and patchy prey resources (e.g., Denman 1994), and presumed high predation risk. Thus, cetacean species and populations inhabiting open waters are predicted to exhibit strategies to minimize predation and maximize consumption of prey. As body size increases, cetacean group size and cohesion are predicted to decrease in open waters. However, the same comparative scale may not apply to mysticetes and odontocetes based on their further evolutionary separation and resulting ecological diversion (McGowen et al. 2009). For example, most mysticetes undertake long-distance seasonal migrations during summer to biologically rich, higher-latitude feeding grounds to consume invertebrates and small schooling fish; during winter, they migrate to lower-latitude breeding/calving areas where they generally fast (Ford and Reeves 2008; Jefferson et al. 2015). In contrast, most odontocete species do not make such long migrations, do not seasonally fast, and do not consume large quantities of small invertebrates (e.g., Jefferson et al. 2015). Some cetacean populations also exhibit behavioral plasticity in group size and cohesion in response to temporal and spatial changes in resource distribution (e.g., food, estrus females) (e.g., Würsig and Würsig 1980; Norris and Dohl 1980), similar to other mammal species including primates (Cowlishaw 1999) and ungulates (Kie 1999).

1.2 Statement of the Problem

The Southern California Bight (SCB) in the North Pacific Ocean off San Diego and Los Angeles, California, is characterized by relatively high levels of anthropogenic activities, including commercial shipping, military exercises, whalewatching, commercial and recreational fishing, and chemical runoff (DoN 2008a,b; Redfern et al. 2013; Calambokidis et al. 2015). These activities overlap with some of the highest densities and diversity of marine mammals attracted to the SCB by high biological productivity that peaks during spring and fall (Carretta et al. 2000;

Forney et al. 2012; Jefferson et al. 2014a). The Navy conducts military training exercises involving large ships, submarines, sonar, and underwater detonations within the Southern California Range Complex (SOCAL Range Complex; DoN 2008a,b, 2010, 2012) bounded by the SCB (Fig. 1-1). To address growing concerns over potential impacts of these activities on marine mammals, there is a need to describe and monitor the density, habitat use, and behavior of marine mammal species on the scale of the SCB (DoN 2010, 2012). Data are needed in sufficient sample sizes to be statistically valid and of appropriate duration to address naturally occurring environmental variability. Successful species management requires identification of biologically important habitat and temporal periods associated with behavior essential to species survival (e.g., birthing, breeding and feeding areas, migration). Knowing such information allows managers to develop spatio-temporal measures to effectively manage and enumerate impacts of anthropogenic activities on species of concern, and to monitor and evaluate effectiveness of protective measures.

Although an MPA network has been developed for other regions of California (Airamé et al. 2003; Botsford et al. 2014, Saarman et al. 2013), the viability of a spatiotemporal management approach has not yet been applied for cetaceans in the SCB (Fox et al. 2013). Efforts to systematically identify important species-specific habitat and sensitive biological periods on the scale of the SCB are generally lacking or problematic (Mills et al. 2015). Although BIAs have been identified for fin whales off southern California (Calambokidis et al. 2015), BIAs have no accompanying regulatory implications. There is a need to identify important habitats and sensitive biological periods for SCB cetacean species, given increasing anthropogenic activities.

Relatively little is known about the site-specific behavioral ecology of the approximately 19 cetacean species regularly inhabiting deep waters of the SCB, with the exception of blue whales (Calambokidis et al. 2007; Goldbogen et al. 2011; Lomac-MacNair and Smultea 2016). At the time of this study, data on the density and behavior of marine mammals were outdated, lacked systematic rigor, and/or were collected at much coarser or more localized scales than the SCB (Smultea and Jefferson 2014). Over the last 30+ years, previous studies in the region have focused primarily on population counts and predicting distribution and density of marine mammals relative to biotic and abiotic habitat factors on a much larger geographical scale. For example, multi-year vessel surveys involving widely spaced (>100 km) transect lines were conducted in the U.S. Exclusive Economic Zone extending 370 km (200 nm) offshore of the U.S. west coast, and within the California Current Ecosystem (CCE) extending along the length of California (e.g., Carretta et al. 2000; Becker et al. 2010; Campbell et al. 2015). More recently, SCB studies have focused on diving, movement or feeding behavior of beaked whales, and fin and blue whales based largely on tagging data (Falcone and Schorr 2014; Goldbogen et al. 2015; Mate et al. 2015). The latter studies have included behavioral responses of blue whales to military mid-frequency active (MFA) sonar noise (Melcon et al. 2012; Goldbogen et al. 2013). Henderson (2010, 2012) conducted focal group behavioral studies of cetaceans from a stationary platform north of San Clemente Island during fall of 2006-2008 using both visual and passive acoustic monitoring. Few other studies have considered the social context of cetacean behaviors (e.g., group size, composition, cohesion) that are known to affect cetacean behavioral ecology (e.g., common bottlenose dolphin, Shane et al. 1986; gray whale, Poole 1984; Risso’s dolphin, Hartman et al. 2008). Furthermore, past studies were conducted primarily during summer and fall, resulting in a data gap during winter and spring.

1.2.1 Background

In 2009, the Navy developed a Marine Species Monitoring Plan (MSMP) for the SOCAL Range Complex to monitor potential effects of military training activities on SCB marine mammals as required under the U.S. Marine Mammal Protection Act and ESA (DoN 2009). In 2010 (DoN 2010), an associated Integrated Comprehensive Monitoring Plan (ICMP) was developed to implement adaptive management and monitoring measures as new data become available. As part of the MSMP in the SOCAL Range Complex, I designed an aerial survey study to identify inter-specific relationships between cetacean habitat use, behavioral state, and group and environmental characteristics. The goal was to quantitatively identify important habitat and sensitive biological periods to provide a baseline against which to compare potential baselines shifts. Fig. 1-2 shows the systematic transect lines and the locations and names of bathymetric and topographic geographical locations in the study area mentioned in this dissertation. The study was planned to span a five-year period to address natural environmental variability. All survey effort conducted in the study area during the 2008-2013 survey period is shown in Fig. 1-3.

It is expensive to repeatedly access deep waters, and therefore group behavioral data on cetacean species in deep (>200 m) waters in the SCB and elsewhere are relatively sparse. Available information has primarily been collected from vessels (e.g., Shane 1995; Falcone et al. 2009), individually tagged animals (Baird et al. 2006; Falcone and Schorr 2014; Mate et al. 2015), a limited number of aircraft-based studies (Richardson et al. 1985; Würsig et al. 1985; Smultea and Würsig 1995), an offshore stationary platform (Henderson 2010, Henderson et al. 2014a,b), and more recently video recordings and photos from unmanned autonomous aircraft (currently limited by short observation durations, expense, and/or special permitting; Durban et al. 2015; Koski et al. 2015). Each of these approaches presents different perspectives, advantages and disadvantages (Dawson et al. 2008).

There are problems with the ability to discount potential effects of vessel- and tag-based studies on behavior, i.e., it cannot be known whether the mechanism or platform bias the observed or collected behavioral data. Vessel observation platforms produce underwater noise that can affect cetacean behavior (e.g., Constantine 2001; Henderson et al. 2014b). The tag and tagging procedures have short-term behavioral effects, generally involving fast approach by a vessel and launching or deploying a device to place the tag on the animal's body, or in some cases capture and release of the animal (Read 2009); potential longer-term confounding effects on behavior are problematic to assess. Cetaceans, especially delphinids, are social animals that often travel in cohesive synchronized groups, and their behavior is influenced by social and environmental context (Norris and Dohl 1980; Norris et al. 1994; Trillmich 2009). Remote processing of a single individual's tag lacks ground truthing of behavioral activity, including the ability to assess effects of group dynamics on the individual's behavior.

Observing cetacean behavior from aircraft, especially when documented with video or photography, offers the advantage of a bird's eye view of animals at and below the water surface (to an estimated 30-40 m depth when water clarity is good in the SCB). A distinct advantage of the aerial platform is the ability to avoid potential acoustic disturbance of observed cetaceans. This can be accomplished from a flying plane whose sound transmission through the water is theoretically limited to a relatively small 26-degree cone directly below the plane on a flat sea (Urick 1972), or by circling at lateral distances and altitudes beyond this cone during higher Beaufort sea states (e.g., Richardson et al. 1985, 1995; Smultea and Würsig 1995). Use of a small aircraft in this manner provides an unobtrusive and unique three-dimensional perspective for studying cetacean behavioral ecology.

1.2.2 Study Species: Ecology and Life History

Life history traits and related ecological gradients for each of the six cetacean species addressed herein are summarized below (Tables 1-1, 1-2) and in detail in Appendix A to position results in a meaningful biological context, using data from the SCB as available. Table 1-1 focuses on documented and predicted ecological and social parameters for the cetacean study species relative to the Gowans et al. (2008) model for delphinids and the Ford and Reeves (2008) model for mysticetes discussed above. The blue whale, fin whale, Risso's dolphin, and common dolphins inhabit primarily semi-pelagic and deep open waters, foraging along slopes on spatially clumped food resources. The gray whale migrates through the SCB primarily close to the mainland coast and to a lesser extent offshore migratory corridors through the Channel Islands. The remaining apparent island-associated ecotype of bottlenose dolphin appears to closely associate with coastal and adjacent slope waters near San Clemente and Santa Catalina islands.

1.3 Chapter Organization, Study Questions and Goals

This dissertation is organized into five chapters as summarized below. Chapters II-IV have their own introduction, methods, results and discussion following the TAMU OGAPS Journal Thesis Template and the journal Behavioral Ecology and Sociobiology. My three overarching study questions and goals are listed below by chapter. More detailed specific study objectives are identified in each of Chapters II, III and IV. To address my study goals, cetacean response (i.e., dependent) variables were selected that (1) have been demonstrated to change when exposed to a potential threat, (2) may be quantitatively collected during aerial surveys, and (3) provide baseline data useful to identify potential future changes in behavior-location and behavioral indicators.

1.3.1 Chapter I

Chapter I introduces theoretical concepts in conservation biology and cetacean socioecology, linking relevance of the topics discussed in the three following main chapters. It also includes a short summary of the Problem Statement and Background information focusing on data available from the SCB study area as possible. A summary of how the six cetacean species examined during my study would be expected to fit into various conceptual models for predicting delphinid and mysticete social structure and strategies within an ecological framework is also presented. This combined information is meant to provide a context within which to understand the relevance of the study results.

1.3.2 Chapter II

Chapter II entitled *Modeling Cetacean Habitat Selection* applies Resource Selection Function (RSF) analysis (Manly et al. 1993, 2010) to identify high-probability selection of environmental parameters for four cetacean species as a function of behavioral state relative to eight static habitat parameters. Static habitat parameters were chosen to facilitate geo-referencing and prioritization of habitat relative to decisions on the relatively fine management scale of the SCB. RSF is unique from other habitat-use analyses as it compares the ratio of environmental variables selected by a species to the availability of those variables in a given area. For example, in my study, habitat parameters associated with sighting locations were compared with habitat variables associated with >35,000 randomly selected points in the study area. Thus, an RSF estimates "selection" (i.e., "preference") rather than "use" by quantifying the ratio between which habitat variables are used versus available to animals. Separate RSF models were run for different behavioral states to determine the role of behavioral state in habitat selection and to evaluate the relative functional importance of habitat to cetacean species. The overarching question and goal of this chapter are identified below.

Question: How do cetacean species in the SCB select habitat relative to availability and behavioral state?

Goal: Determine if behavioral state and abiotic environmental factors can be used to predict relative habitat selection among cetacean species in the SCB.

Target Journal: Marine Ecology Progress Series

1.3.3 Chapter III

Chapter III entitled *Cetacean Body Size, Group Size and Group Cohesion* examines relationships between cetacean body size (using species as a proxy), group size, and group cohesion in deep (>200 m) open waters. Predictive frameworks proposed for ungulates (closely related ancestors of cetaceans) in open savannah and delphinids in the open ocean per the Gowans et al. (2008) model lead to development of the following study prediction for the SCB study area: as cetacean body size increases, group size and group cohesion decrease. Results are discussed relative to phylogenetic and ecological constraints associated with living in a semi-pelagic and open ocean environment. Observed relationships are expected to represent trade-offs between reducing predation risk and adapting to patchily distributed food resources characteristic of slope and open-ocean waters. The overarching question and goal of this chapter are identified below.

Question: Does social behavior, as indicated by group size and group cohesion, differ among cetacean species in the SCB?

Goal: Determine whether cetacean species body size is inversely related to group size and group cohesion in the SCB, and compare the possible reasons for these differences across species.

Target Journal: Behavioral Ecology and Sociobiology

1.3.4 Chapter IV

Chapter IV entitled *Spatiotemporal Behavioral Patterns of Cetaceans in the Southern California Bight* uses first-observed sighting data of cetaceans to examine how the response variables behavioral state, group size, and group cohesion are affected by social, temporal, and environmental factors. The eight explanatory variables examined include calf presence, time of day, day of the year (i.e., Julian day), season, water depth, distance from shore, slope, and slope-face aspect. Resulting patterns across species may reflect varying reproductive phase, resource availability and adaptations to predation risk. This information is important in identifying species-specific and biologically sensitive temporal periods. Observed natural variations in group size, group cohesion and behavioral state should be considered when differentiating potential effects of increasing anthropogenic activities of concern in the SCB. Three related overarching study questions are addressed in this chapter:

Question 1: Does calf presence influence group size and cohesion of cetacean species in the SCB?

Question 2: Are group size and group cohesion influenced by species and Julian day as related to the calving and mating seasons?

Question 3: Are group size, group cohesion and behavioral state among presumed nocturnal feeding delphinid species influenced by time of day as related to nocturnal prey behavior?

Goal: Determine if behavioral state, group size, and group cohesion of cetaceans inhabiting the SCB are influenced by calf presence, temporal and environmental factors.

Target Journal: Behavioral Ecology and Sociobiology

1.3.5 Chapter V

Chapter V entitled *Summary* summarizes and integrates results of the three primary chapters, tying them back to concepts and goals presented in the Chapter I *Introduction*. It discusses how study results contribute to applied science by providing information needed to monitor potential impacts on cetaceans relative to growing anthropogenic activities of concern in the SCB, including the Navy’s Strategic Planning Process for Marine Species Monitoring through adaptive management in the SCB. The chapter ends with recommendations for future research useful for applied science and adaptive management process applications relative to cetaceans.

1.4 Ecological Gradients of Cetaceans Relative to Existing Models

Life history traits and related ecological gradients for each of the six cetacean species addressed herein are summarized below and in detail in Appendix A to position results in a meaningful biological context, using data from the SCB as available. Table 1-1 focuses on documented and predicted ecological and social parameters for the cetacean study species relative to the Gowans et al. (2008) model for delphinids and the Ford and Reeves (2008) model for mysticetes, as discussed above. The blue whale, fin whale, Risso’s dolphin and common dolphin spp. inhabit primarily semi-pelagic and deep open waters, foraging along slopes on spatially clumped food resources. The gray whale migrates through the SCB primarily close to the mainland coast and to a lesser extent offshore migratory corridors through the Channel Islands. The remaining apparent island-associated ecotype of bottlenose dolphin appears to closely associate with coastal and adjacent slope waters near San Clemente and Santa Catalina islands.

CHAPTER II

MODELING CETACEAN HABITAT USING BEHAVIOR

2.1 Synopsis

The role of behavioral state in cetacean habitat selection was examined relative to eight environmental variables in deep (>200 m) waters of the Southern California Bight (SCB) from 2008-2012. Fifteen aerial transect surveys totaling 18,831 km of systematic and connecting line effort were conducted. Resource selection function (RSF) models predicted relative probability of occurrence by contrasting environmental characteristics at cetacean locations with random point locations. Analyses involved 59 endangered fin whale, 40 gray whale, 134 Risso's dolphin, and 31 bottlenose dolphin groups. Each species model was fit for up to three behavioral states (mill, rest/slow travel, medium/fast travel) and all behaviors pooled. Behavioral state influenced habitat use, and some regions and features were selected for important biological functions (foraging, resting) at higher rates than expected based on availability of those features. Fin whales were most likely to display rapid travel over deep flat basins, while rest/slow travel was associated more frequently than expected with nearshore waters including islands. Migrating gray whale habitat use probability decreased east to west from the mainland coast, with rapid travel predicted to occur along the San Clemente Island shoreline. Risso's dolphins were most likely to display rapid travel near San Clemente Island and the mainland coast. Bottlenose dolphins were closely affiliated with shallow nearshore waters particularly of Santa Catalina Island for all behaviors (including foraging, feeding, and calf nurturing). Results improve understanding of how behavioral state influences habitat selection of little-studied offshore cetaceans. Such knowledge is useful to identify potential opportunities for spatiotemporal management relative to sensitive areas and periods for cetaceans. Data provide an important 5-year baseline for little-known species to compare potential future changes in habitat selection patterns, assisting in conservation and management decisions in a relatively high-anthropogenic use area.

Key words: cetacean, blue whale, fin whale, Risso's dolphin, bottlenose dolphin, resource selection function, habitat

2.2 Introduction

Numerous studies have successfully used habitat modeling to quantitatively link habitat use to ecological attributes based on the underlying premise that an animal's distribution reflects its response to the environment (Barry and Elith 2006; Elith and Leathwick 2009; Becker et al. 2014). However, data on the underlying biological function of habitat use is often lacking, especially in offshore marine environments (Hastie et al. 2004; Becker et al. 2014). Information on spatial use of habitat resources is needed for applied species management, as it indicates how individuals are distributed in space relative to those resources. With such knowledge, effective management and monitoring can be developed to minimize impacts to species of concern (Hooker et al. 1999; Cañadas et al. 2002; Redfern et al. 2013), including modification of human activities in time or space relative to sensitive biological periods and locations (Lusseau and Bejder 2007; Halpern et al. 2013; Dolman and Jasny 2015).

Resource selection function (RSF) analyses have been applied to identify terrestrial animal habitat use, including anthropogenic effects from oil and gas exploration, construction, tourism, and climate change (e.g., Manly et al. 1993, 2010; McDonald and McDonald 2002; Sawyer et al. 2006). The RSF method assumes that resources (e.g., food items, cover types, or any quantifiable habitat characteristic) important to individuals are used disproportionately to availability, and numerically compares the availability of attributes throughout a study area to those associated with animal locations (Johnson 1980; Manly et al. 2010). In marine ecosystems, RSFs have been used to identify preferred habitat attributes of marine mammals and subsequent changes induced by anthropogenic disturbance among endangered polar bears (*Ursus maritimus*; Amstrup et al. 2001; Durner et al. 2009), Pacific walrus (*Rosmarus divergens*; Jay et al. 2014), endangered Cook Inlet beluga whales (*Delphinapterus leucas*; Goetz et al. 2007), Hector's dolphins (*Cephalorhynchus hectori*; Bräger et al. 2003), bottlenose dolphins (Fortuna 2006), and dugongs (*Dugong dugon*; Sheppard et al. 2010). The tools afforded by the RSF method have enabled managers to successfully identify preferred habitat, adverse effects, and viable mitigation and management opportunities, by correlating changes in habitat use with changes in anthropogenic activity. However, behavioral states that can represent how preferred habitats function biologically, have rarely been incorporated into habitat-modeling studies.

The SCB is encompassed by the California Current Ecosystem, one of the richest areas of year-round biological productivity and diversity in the world (Dailey et al. 1993; Hayward and Venrick 1998). A distinct feature of the SCB is deep water close to shore characterized by alternating deep (~500-2,500 m) underwater basins, 9 islands, 12 large canyons, and 18 marine basins (Emery 1960; Fig. 1-2). The SCB is used by over 30 marine mammal species (Forney and Barlow 1998; Campbell et al. 2015; Smultea and Jefferson 2014) as well as growing anthropogenic activities of concern to these species (McDonald et al. 2006; DoN 2008b; Falcone et al. 2009). Peak seasonal spring and fall plankton blooms in the SCB are linked with dynamic oceanographic processes. These processes include upwelling, fronts, eddies, gyres, and mixing of four different water masses along the mainland and Channel Islands coasts, seamounts, and underwater canyon slopes that serve to aggregate prey consumed by many cetaceans (Hayward and Venrick 1998; Mann and Lazier 2013; Munger et al. 2009). Ongoing human activities include fishing, commercial shipping, recreational boating, marine tourism, oil and gas development, and military operations involving mid-frequency active sonar (McDonald et al. 2006; DoN 2008b, 2010).

Despite over two decades of directed studies of cetacean density and distribution off California (e.g., Forney and Barlow 1998; Carretta et al. 2000; Campbell et al. 2015), habitat-use patterns and social and behavioral characteristics of most species are not well understood. Most such information comes from limited numbers of tagged individuals (Falcone et al. 2009; Goldbogen et al. 2011; Mate et al. 2015) that may represent behavior biased by the effects of tagging (Watkins and Tyack 1991; Schneider et al. 1998) and observations from noise-creating vessels. Passive acoustic monitoring has linked calling behavior with spatiotemporal characteristics including presumed foraging sounds for some SCB cetacean species (Soldevilla et al. 2011), though accompanying social and behavioral influences are mostly lacking and non-calling animals are not represented.

Spatially explicit habitat-based modeling, including predictive modeling, has linked occurrence/density of some cetacean species with broad environmental parameters in the expansive California Current Ecosystem (e.g., sea surface temperature and water depth ranges; Forney 2000; Becker 2007; Becker et al. 2010, 2014; Campbell et al. 2015) and the eastern tropical Pacific Ocean (e.g., Ferguson 2005; Ferguson et al. 2006; Barlow et al. 2009). A goal of these predictive models is to identify locations, features and/or periods most important to species survival, to assist in developing and implementing management and conservation strategies (Becker 2007; Becker et al. 2014). However, the latter approach can give an incorrect picture of habitat needs, especially if a critical habitat is rare and unlikely to be observed on the transect line (Manly et al. 2010). Unlike habitat-based density models (e.g., kernel density models), RSF is considered a better representation of actual habitat needs because it estimates use in the context of the distribution of environmental characteristics from thousands of randomly selected point locations, not just habitat attributes at animal locations (Manly et al. 2010; Fig. 2-1). Such modeling has also not considered how behavioral state or function may affect habitat use, and Becker et al. (2010) indicated that the ability to predict cetacean abundance is problematic if an animal's behavioral state (e.g., foraging, migrating, breeding) varies, including across seasons. Furthermore, due to the large spatial scale of past surveys (transect lines spaced >100 km apart; Forney et al. 2012; Becker et al. 2014; Campbell et al. 2015), the ability of habitat models to assist with management decisions on smaller scales such as the SCB is limited. Moreover, existing data are limited to summer-fall periods.

In summary, there is a clear need to identify characteristics of high-use habitat relative to behavioral function on the scale of the SCB to provide information relevant to managers concerned with potential impacts of ongoing localized anthropogenic activities. Integration of such information for multiple species is also needed to address potential cumulative effects of anthropogenic activities (Ruckelhaus et al. 2008; Halpern et al. 2013; Redfern et al. 2013). The primary objective of this study was to develop RSFs to identify specific environmental characteristics and areas commonly used by four SCB cetacean species (the gray whale, fin whale, Risso's dolphin, and bottlenose dolphin), and to relate habitat choices to functional behavioral states important for survival and reproduction. In doing so, we provide localized information useful for further refinement of marine resource management plans via the adaptive management approach (DoN 2010, 2015).

2.3 Materials and Methods

2.3.1 Study Area and Aircraft

Aerial surveys were conducted in two sub-areas: the Santa Catalina Basin (8,473 km^2) and the San Nicolas Basin (4,180 km^2) including the South of San Clemente Island area (4,903 km^2) (Fig. 1-1). Parallel transect lines were flown primarily along a WNW to ESE orientation generally perpendicular to bathymetric contours to obtain a random sample of individuals and thereby avoid biasing results if selection was associated with depth contours (Buckland et al. 2015). The prescribed area was intensively surveyed by following transect lines spaced approximately 14 km apart between the coast and San Clemente Island in the Santa Catalina Basin, and spaced 7 km apart to the west in the San Nicolas Basin and South San Clemente Island (Fig. 1-2). Surveys were flown at speeds of approximately 185 km hr^{-1} and altitudes of approximately 227-

357 m from a small high-wing, twin-engine airplane equipped with bubble observer windows on the left and ride sides of the middle seats.

2.3.2 Data Collection

Two trained biologists observed cetaceans from the middle seats of the aircraft while a dedicated recorder/photographer sat in the front and/or rear seats. Basic sighting and environmental data (e.g., observation effort, Beaufort sea state, visibility, glare, etc.; see Jefferson et al. 2014a) were recorded using the following hardware and software. In 2008 and 2009 BioSpectator was used on a Palm Pilot TX or an Apple iPhone or iTouch. In 2010 and part of 2011 a customized Excel spreadsheet on a Windows-based notebook computer was used. During part of 2011 and all of 2012 customized observation software (Mysticetus Observation Platform, Mysticetus™) was used on a notebook computer. During all surveys, a wide-area augmented system-enabled Global Positioning System (GPS) was used to automatically assign a time stamp, a sequential sighting number, and a GPS position. A Suunto handheld clinometer was used to measure horizontal angles to sightings that were converted to a GPS position by Mysticetus™.

Following the protocol of Smultea (1994), we recorded the initial sighting location and first-observed group behavioral state relative to movement type/speed of travel for each sighting (mill, rest/slow travel, medium/fast travel; Table 2-1). A “group” was defined as >50% of individuals engaged in the same polarized behavioral state up to 100 Body Lengths (BL) apart within visual range of observers (after Norris and Schilt 1988; Baird and Dill 1996; Lusseau et al. 2004; Table 2-1). Within observed groups, individuals were typically within 10-20 BL of each other but occasionally up to 50-100 adult BL apart. For common dolphins that formed much larger groups than other cetaceans (on the order of hundreds to thousands), cohesion was based on distinct subgroups that met the above group definition. Species, sighting time, group size, and number of calves were also recorded. Sightings were circled at radial distances of approximately 500-1000 m to confirm sighting information as needed. The latter included using Steiner 7 X 25 or Swarovski 10 X 32 binoculars o photo-documentation with a Canon EOS 40D or 60D or Nikon D300 or D7000 DSLR camera with a 100-400 mm f/4.5-5.6 IS USM lens). High Definition (HD) video was also recorded when conducting focal behavioral follows as part of a separate study using a Sony Handycam HDR-XR550 or HDR-XR520 video camera.

2.3.3 Data Analysis

RSFs were developed for cetacean sighting (i.e., group) locations obtained along systematic transect lines and shorter connecting lines during conditions suitable for sighting cetaceans (Beaufort sea state ≤ 4; Jefferson et al. 2014a). For the RSF analysis, site characteristics at marine mammal locations were contrasted to site characteristics at 35,167 randomly selected "available" points obtained at a randomly placed systematic grid of locations within the study area. However, the bottlenose dolphin was modeled only for the Santa Catalina Basin region with a set of 23,455 available site points, as none were seen in the region west of this island.

The RSFs we estimated related the relative probability of the species selecting a location, Π, as a function of p explanatory variables x_1, x_2, ..., x_p that characterized the habitat at the location. The form of the RSF model was

$$\Pi(x_1,x_2,...,x_p) = \exp(\beta_0 + \beta_1 x_1 + \beta_2 x_2 + \ldots + \beta_p x_p)$$

where β values were parameters (Manly et al. 2010; McDonald 2013). Thus, the response variable was location of sighting. Eight habitat variables were considered for inclusion in each model: latitude, longitude, water depth (meters [m]), northness calculated as the cosine of aspect, eastness calculated as the sine of aspect, closest distance to shore (km), slope (degrees of an underwater slope calculated as the maximum, three-dimensional rise over the run) and aspect (the compass direction of the slope of the seafloor face) (Table 2-2). Similar to other ocean studies (e.g., Becker et al. 2010), slope was used as a proxy for upwelling and geographically referenced biological productivity, consistent with SCB oceanographic and biological conditions (Hayward and Venrick 1998; Mann and Lazier 2013). Mysticetus™ Geographic Information Systems (GIS) used the following National Oceanic and Atmospheric Administration (NOAA) National Geophysical Data Center - Digital Elevation Models (DEM) databases to determine the values of depth, slope, distance from shore, slope and aspect: (1) Locations near San Diego, CA: Tsunami Inundation project, 1/3 arc-second DEM http://www.ngdc.noaa.gov/dem/squareCellGrid/download/3543; (2) Locations outside the 1/3 arc-second DEM: U.S. Coastal Relief Model, Southern California (region 6), 3 arc-second DEM http://www.ngdc.noaa.gov/mgg/coastal/grddas06/grddas06.htm.

To select a final RSF model, all 127 models were fitted representing all possible combinations of the eight explanatory variables. Models were run separately for all sightings and for each behavioral state. Pearson correlations between all pairs of continuous variables were calculated and correlations >0.6 in absolute value were not permitted to enter regression models together.

Each pair of categorical variables was cross-tabulated and results were examined for evidence of association. If Fisher's two-sided exact test was significant ($p<0.05$), the two variables were not permitted to enter any model together. All models were ranked with Akaike's Information Criterion (AIC) (Burnham and Anderson 2002) to evaluate model fit based on the log likelihood and a penalty for parameter inclusion. Observations with missing values for any variables were excluded from analyses.

The models associated with the minimum AIC value for each species and behavior were selected as the final models. Direction (positive or negative value) of the parameter estimate indicated whether the relationship between the variable and use was positively or negatively correlated. Significance of the parameter estimate (i.e., testing that the parameter was significantly different from zero) was computed from the corresponding *t*-ratio (parameters estimate divided by standard error). P values<0.05 were considered statistically significant. Final RSF models were used to predict the relatively probability of selection for sub-areas within the study area. The resulting predicted RSF values were illustrated on maps color-coded based on five predicted classes rated from low to high relative probability of use.

2.4 Results

In 2008-2012, 15 aerial surveys of systematic line transects totaling 127 flights were conducted over 86 days. At least one survey occurred during all months except December. We limited RSF estimation to 264 cetacean sightings made during 18,831 km of systematic line-transect and connector effort (Fig. 2-2). Overall, 99 percent of the total flight time was associated with a Beaufort sea state less than 4. There were sufficient sightings ($n \geq 30$ groups each) to develop an RSF for the gray whale ($n=40$ groups), fin whale ($n=59$), Risso's dolphin ($n=134$), and bottlenose dolphin ($n=31$) (Table 2-3). Due to the low number of mill behavioral states, mill and rest/slow travel sightings were pooled into the same rest/slow travel model for all species except the Risso's dolphin. Statistical results for the RSF modeling are summarized below by species in phylogenetic order and in Tables 2-3 and 2-4. Referenced underwater feature locations are identified in Fig. 1-2. Specific patterns of habitat selection are also discussed, based on predicted RSF values illustrated on maps in Figs. 2-3 through 2–6.

2.4.1 Fin Whale

Most of the 59 fin whale groups used in RSF modeling displayed medium/fast travel ($n=36$), followed by rest/slow travel ($n=20$), and mill ($n=2$), with one group whose behavior was unknown

(Table 2-3). Due to small sample size, the two mill groups were pooled with rest/slow travel for analysis. This resulted in fitting of three RSF models for fin whales: all sightings, rest/slow travel, and medium/fast travel. The final RSF model for rest/slow travel contained only distance to shore, but did not account for a significant amount of variation in the data (p=0.3970; Table 2-3). For medium/fast travel, the final RSF model contained longitude (p=0.0276) and depth (p=0.0017) (Table 2-3). Both variables were positively correlated with relative probability of use, meaning that during medium-fast travel, fin whales used deeper eastern waters more than expected relative to availability. Pooling all behaviors, fin whale habitat selection was associated with four variables: latitude, longitude, depth and distance to shore (Tables 2-3 and 2-4). Latitude and distance from shore were negatively correlated with relative probability of use, while longitude and depth were positively correlated. Thus, assuming equal access to all parts of the study area, fin whales used deeper waters as close to shore as possible in the eastern and southern parts of the study area (Table 2-3).

Maps of predicted relative probability of habitat selection indicated that overall and for medium/fast travel, fin whales selectively used the center of the San Nicolas Basin and the San Diego Trough characterized by low bathymetric relief (Figs.1-2 and 2-3). In contrast, rest/slow travel among fin whales was not significantly related to any variable, although distance from shore produced the best-fitting model according to AIC (Table 2-4; Fig. 2-3).

2.4.2 Gray Whale

Most of the 40 gray whale groups used in RSF modeling displayed rest/slow travel (*n*=18) or medium/fast travel (*n*=21), with only one group observed to mill (Table 2-3). Mill was therefore pooled with rest/slow travel. This resulted in fitting of three RSF models for gray whales: all sightings, rest/slow travel, and medium/fast travel. The final RSF model for rest/slow travel contained the variables longitude and northness aspect. Longitude (i.e., eastness) was positively associated with rest/slow travel, but did not account for a significant amount of variation in the data (p=0.0639; Tables 2-3 and 2-4, Fig. 2-4). The gray whale was the only species for which seafloor aspect (i.e., the compass direction of the slope of the seafloor face) occurred in the top model, with rest/slow travel less likely to occur over north-facing aspects, but aspect did not account for a significant amount of variation in the data (p=0.0958) (Table 2-3). For medium/fast travel, although the final RSF model contained the variables longitude and distance from shore, they did not explain a significant portion of variation in the data (p=0.1480; Tables 2-3 and 2-4). Pooling all behaviors, the final RSF model for gray whales contained only longitude (p=0.0074), which was positively correlated with relative probability of use. Thus, assuming equal access to all parts of the study area, gray whales selected eastern parts of the study area (Fig. 2-4).

Maps of predicted relative probability of habitat use indicated that overall, gray whales selectively used waters closest to the mainland coast, with probability of use decreasing with increasing distance from the mainland coast (Table 2-3, Fig. 2-4). Although behavioral state was not significantly related to any variable, longitude produced the best-fitting model for rest/slow travel, suggesting that this behavior was relatively higher to the east along the mainland coast (Table 2-3, Fig. 2-4).

2.4.3 Risso's Dolphin

Most of the 134 Risso's dolphin groups used in RSF modeling displayed rest/slow travel (*n*=63), followed by medium/fast travel (*n*=56), or mill (*n*=11) (Table 2-3). This resulted in fitting of more (*n*=4) RSF models than any other species: all sightings, rest/slow travel, medium/fast travel, and mill. The final RSF model for rest/slow travel contained longitude, distance from shore, and depth, although only longitude (p=0.0149) and distance from shore (p=0.0084) addressed a significant amount of variation in the data (Tables 2-3 and 2-4). Longitude was positively correlated with use, meaning that for rest/slow travel, Risso's dolphins used eastern areas more than expected relative to availability. Distance from shore was negatively correlated with use, thus for rest/slow travel, dolphins selectively used areas closer to shore (including islands) more often than expected relative to availability. A positive but insignificant (p=0.0803) correlation was also found between depth and rest/slow travel, with deeper waters associated with higher use.

The final RSF model for medium/fast travel among Risso's dolphins contained latitude, distance from shore, longitude, and depth, all which accounted for a significant amount of variation in the data (p≤0378) except depth (p=0.1298) (Tables 2-3 and 2-4). Latitude and shore distance were negatively correlated while longitude was positively correlated with relative probability of use. Thus, assuming equal access to all parts of the study area, Risso's dolphins used nearshore southern and eastern waters of the study area for medium/fast travel more than expected relative to availability (Fig. 2-5). Depth was negatively correlated with use (i.e., increasing relative use with decreasing depth), but did not account for a significant amount of variation in the data (Tables 2-3 and 2-4).

For mill behavior, the final RSF model contained only longitude, but did not represent a significant amount of data variation (p=0.2370). Pooling all behaviors, the final RSF model for Risso’s dolphins included three variables, all of which contributed significantly to data variation: latitude, longitude, and distance to shore (p≤0.0190; Tables 2-3 and 2-4). Correlations for pooled behaviors were the same as those for medium-fast travel except that depth was not in the final RSF model: latitude and distance from shore were negatively correlated with use, while longitude was positively correlated (Tables 2-3 and 2-4).

Maps of predicted relative probability of habitat selection indicated that overall, Risso’s dolphins selectively used waters close to San Clemente and Santa Catalina islands and the mainland coast, with relatively lower than expected use in the western half of San Nicolas Basin and the southcentral part of the study area (Fig. 2-5). In addition, relative probability of habitat use also differed by behavior in some areas as follows. Along the northeast and east side of San Clemente Island and south of Santa Catalina Island, relative probability of use was higher for rest/slow travel and lower for medium/fast travel than expected, coinciding with the deep Catalina Basin (~1000-1300 m) and around Emery Knoll (Figs.1-2 and 2-5). In contrast, southeast of San Clemente Island, relative probability of use for medium/fast travel was higher but rest/slow travel was lower than expected (Figs.1-2 and 2-5). The latter subarea is associated with the western edge of Fortymile Bank, a moderately deep (~500-800 m) flat area that drops off steeply into San Clemente Canyon to the west and Coronado Canyon to the east (Figs. 1-2 and 2-5). Along the mainland coast relative probability of use was similarly higher than expected for mill, rest/slow travel, and medium/fast travel in the subarea approximately 10 to 40 km offshore, where bottom depth ranges from about 200-800 m (Fig. 2-5).

2.4.4 Bottlenose Dolphin

Most of the 31 bottlenose dolphin groups used in RSF modeling displayed medium/fast travel (*n*=19) or rest/slow travel (*n*=11), with one remaining group exhibiting mill (Table 2-3). Due to small sample size, the one mill group was combined with rest/slow travel for analysis. An RSF model was not fitted for the San Nicolas Basin west of San Clemente Island because no bottlenose dolphins were sighted there during systematic effort. This resulted in fitting of three RSF models for bottlenose dolphins: all sightings, rest/slow travel, and medium/fast travel. The two final RSF models for pooled behaviors and medium/fast travel contained longitude, depth, and distance to shore, all of which accounted for a significant amount of variation in the data (p≤0.0419) except for medium/fast travel and longitude (p=0.0579) (Tables 2-3 and 2-4). All three variables were negatively correlated with relative probability of use. Thus, assuming equal access to all parts of the study area, for all sightings and during medium/fast travel, bottlenose dolphins used shallower nearshore western waters more than expected relative to availability (Fig. 2-6). For rest/slow travel, the final RSF model contained only latitude, but did not account for a significant amount of variation in the data (p=0.1328; Tables 2-3 and 2-4).

Maps of predicted relative probability of habitat selection indicated that overall and for medium-fast travel, bottlenose dolphins primarily selected nearshore waters of San Clemente Island and the mainland, and few subareas near San Clemente Island associated with Emory Knoll and bank edges (Figs. 1-2 and 2-6). In contrast, rest/slow travel was not significantly related to any variable, although latitude produced the best-fitting model according to AIC; the resulting map of predicated relative probability of habitat use suggested that bottlenose dolphins selected northern waters more often than expected relative to availability (Fig. 2-6).

2.5 Discussion

In offshore SCB waters (>10 km from the mainland), RSF modeling indicated that the four cetacean species I examined differentially utilized habitat features and subareas based on behavior. Implications of results within the behavioral ecology and regional context for each species are discussed below.

Relative probability of habitat use by gray whales was positively correlated with eastern waters closer to the mainland coast. Overall, Risso’s dolphins selected nearshore southern and eastern waters close to islands and the mainland, with differential probability of use during medium/fast travel correlated with latitude relative to Santa Catalina and San Clemente islands. During medium/fast travel and all behaviors pooled, bottlenose dolphins selected nearshore shallow waters more often than available in the study area, with a preference for western waters near Santa Catalina Island during medium/fast travel. Migrating gray whale habitat use decreased east to west, with medium/fast travel in offshore areas linked closely with coastal San Clemente Island waters. Risso’s dolphins primarily medium/fast traveled in the western study area over steep bathymetry close to San Clemente Island, with a trend for rest/slow travel in deep eastern nearshore waters. Bottlenose dolphins (including calves) were closely affiliated with shallow nearshore waters of Santa Catalina Island for foraging, feeding, and calf nurturing.

2.5.1 Fin Whale

During medium/fast travel, fin whales selected deep (1000-2000 m), southern, and eastern parts of the study area with higher relative probability than other areas. Rest/slow travel and faster travel are believed to serve different biological functions. Rest/slow travel is associated with resting, feeding, and socializing while medium/fast travel is typically associated with directed point-to-point movement. Mate et al. (2015) reported that four blue whales tagged in the SCB for a median of 19.4 days exhibited primarily slow and fast behavioral states based on analysis of dive and GPS data. Slow behavior presumably involved feeding based on deeper dives occurring within a small (median 1.5 km^2) area for <1 – 13.3 h, with most foraging dives during daytime (Mate et al. 2015). Similarly, fin whales spent most of their time in relatively small areas engaged in rest/slow travel presumed to involve feeding and foraging based on data from 53 fin whales satellite-tagged for a median duration of 20 days in the SCB in 2008-2014 (Falcone and Schorr 2014). During my study, rest/slow travel also included open-mouthed lunge feeding, logging at the surface, and apparent courting similar to humpback whales *Megaptera novaeangliae* based on video recordings. In contrast, Mate et al. (2015) reported that fast behavior involved point-to-point movement with few turns and was consequently associated with traveling and migrating rather than feeding. Likewise, medium/fast travel was associated with directed point-to-point movement, with minimal changes in heading based on fin whales video recorded for 10-60+ minutes (min) (Smultea unpublished data).

Higher relative probability of use of deep waters by fin whales during medium/fast travel (when feeding is unlikely) is consistent with expected low densities of prey in deep areas with low bathymetric relief. The deepest parts of our study area were predominately flat basins west of San Clemente Island and southeast relatively near shore. Fin whale prey (small invertebrates and schooling fish) are less likely to concentrate in such areas given the lack of bathymetric features associated with high upwelling and biological productivity that aggregate them (Hayward and Vernick 1998; Schoenherr 1991; Fiedler et al. 1998). Thus, faster travel over deep waters instead likely represents transit between locally productive areas associated with feeding and socializing or farther migratory destinations. In contrast, data from 56 tagged SCB fin whales indicated that travel speed between estimated satellite GPS positions was faster over shallow vs. deep water (Falcone and Schorr 2014). Ground-truthing of fin whale speed and headings relative to behavioral states such as feeding/ foraging and point-to-point traveling are needed to further clarify differences across studies in the SCB.

Overall, during 2008–2012, RSF modeling indicated highest relative probability of fin whale use in deep waters of the San Nicolas Basin and the San Diego Trough in the southeastern SCB. The fin whale was the only cetacean species with relative high probability of use of the San Nicolas Basin west of San Clemente Island, consistent with previous studies off southern California (e.g., Falcone and Schorr 2014; Jefferson et al. 2014a; Calambokidis et al. 2015). The Cuvier's beaked whale is the only other cetacean species within the SCB exhibiting high affinity to the San Nicolas Basin (Falcone et al. 2009). Relatively high use of the San Nicolas Basin by fin whales is consistent with estimated fin whale densities being over three times higher there than the Santa Catalina Basin during both the cold- and warm-water periods in 2008–2013 (Jefferson et al. 2014a). Similarly, Falcone and Schorr's (2014) tagging results showed extensive fin whale use of the northern San Nicolas Basin in 2008–2014. However, they also reported high use of the northern Santa Catalina Basin in contrast to my results indicating relatively highest use of the southeastern Santa Catalina Basin. Differences may be due to spatiotemporal disparities in effort and/or seasonal differences in fin whale habitat use. For example, in 2008–2014, Falcone and Schorr (2014) also reported an apparent seasonal distributional shift by fin whales differing from historical data. During fall and winter, fin whales apparently concentrated along the mainland coast and northern Santa Catalina Basin, while during spring and summer they tended to be more dispersed throughout the SCB; the northern San Nicolas Basin was used year-round (Falcone and Schorr 2014; Calambokidis et al. 2015). Other cetacean surveys in the California Current Ecosystem indicated that fin whale abundance and density were higher during the warm-water (summer-fall) vs. the cold-water period (winter-spring) (Forney and Barlow 1998; Douglas et al. 2014; Calambokidis et al. 2015). However, 2008–2012 data reported herein showed that fin whale density and abundance was nearly identical during these two periods, and in fact higher than historically reported SCB densities (Smultea and Jefferson 2014; Jefferson et al. 2014a). The latter is consistent with the documented increase in fin whale abundance along the U.S. west coast, presumably due largely to protection from whaling by the International Whaling Commission since 1976 (Moore and Barlow 2011; Calambokidis et al. 2015; Jefferson et al. 2015).

2.5.2 Gray Whale

As expected, migrating gray whales selectively used eastern waters of the study area closer to the mainland coast, despite the availability of other areas and environmental attributes and regardless of behavioral state. Nearly all directed research on migrating gray whales from the SCB to the Pacific Northwest has focused on coastal (<10 km) mainland waters within the main migration corridor (e.g., Reilly et al. 1983; Poole 1984; Sumich and Show 2011). While these waters provide an important migratory path, gray whales use the entire SCB study area during winter and spring migration. Gray whales were regularly observed offshore at these times, although the lowest relative probability of use was at the westernmost edge of the study area (Fig. 2-4).

Maps of predicted relative probability of habitat use suggested that gray whales were more likely to select nearshore waters close to San Clemente and Santa Catalina islands in the offshore migration corridor, though this prediction was not supported by a significant correlation. Sumich and Show (2011) reported during winter 1988-1990 that more southbound gray whales used this offshore migratory corridor and another corridor 80-90 km farther west, than the coastal mainland corridor. Based on photogrammetry data, Sumich and Show (2011) suggested that smaller (<11.5 m), presumably younger gray whales preferentially use the coastal migratory corridor in the SCB, along with most mothers with young calves, presumably to avoid documented killer whale *Orcinus orca* predation by hugging shallow waters and kelp forests (Weller 2009). However, we observed four separate gray whale mother-calf pairs approximately 10 to 50 km from the nearest coastline, including two pairs 10 and 25 km west of San Clemente Island.

There was some indication that north aspects may have been negatively correlated with relative probability of use by migrating gray whales during rest/slow travel, though aspect did not account for a significant amount of variation in the data ($p=0.0958$). This potential correlation may be related to localized currents or other oceanographic features (e.g., upwelling, water temperature changes) that influence gray whale behavior and migration movement patterns. It is possible that whales use these contours for migration cues during generally east-west movements between the mainland coast and outer islands in the SCB. Avoidance of predators may also influence observed migratory travel-speed differences related to habitat features. The possible role of aspect in relative probability of habitat use by gray whales may warrant further study.

2.5.3 Risso's Dolphin

Overall and during medium-fast travel, Risso's dolphins showed a clear relative preference for southern and eastern nearshore waters of the study area, particularly near San Clemente island and the mainland coast, where . This is consistent with other studies indicating that this species inhabits deep waters over steep slopes, at least during daytime (Kruse 1989; Shane 1994; Kruse et al. 1999; Carretta et al. 2000; Baird 2009; Carretta et al. 2015; Jefferson et al. 2014b, 2015).

However, differences emerged among habitat use when behavioral state was considered in the RSF model, suggesting that different habitat features and subareas serve different biological functions. Contrasting differences in behavior and habitat use were most evident along eastern San Clemente Island, where the probability of rest/slow travel was highest in nearshore water along steep underwater slopes. Based on daytime video recordings and field observations during extended focal behavior sessions in the SCB, rest/slow travel frequently involved rest and socializing characterized by tight group cohesion (≤ 2 - 3 adult body lengths apart), sometimes in tight layers of animals, with individuals occasionally touching and crisscrossing through the group (Smultea unpublished data). On one occasion, apparent mating or other socio-sexual behavior was photographed close to southeastern San Clemente Island during spring (Smultea unpublished data). Similarly, Shane (1995) reported that Risso's dolphins most frequently rested and slow traveled up and down the coastline over a steep underwater drop off within several kilometers of Santa Catalina Island. Slow daytime behavior is characteristic of night-time foraging cetaceans such as spinner dolphins *Stenella longirostris* (e.g., Norris and Dohl 1980; Norris et al. 1994; Benoit-Bird and Au 2003; Thorne et al. 2012), sperm whales *Physeter macrocephalus* (Davis et al. 2007), and some regional dusky dolphin *Lagenorhynchus obscurus* populations whose nighttime foraging correlates with darkness when prey associated with the Deep Scattering Layer (DSL) move closer to the water surface (Benoit-Bird et al. 2004; Vaughn et al. 2007; Würsig et al. 2007; Würsig and Würsig 2010). Similarly, Risso's dolphins presumably feed at night on squid associated with the DSL (Leatherwood and Reeves 1983; Baird 2009; Jefferson et al. 2014b, 2015).

In contrast to rest/slow travel over deep nearshore water, medium/fast travel among Risso's dolphins was strongly associated with shallower nearshore water. This medium/fast travel may represent directed point-to-point movement foraging and searching for prey as exhibited by Southern Resident killer whales (Heimlich-Boran 1988). Alternatively, Risso's dolphins fast traveling over shallower water may be the most efficient way to cross less-productive habitat to reach deeper steep drop-offs in coastal areas used for daytime resting/socializing. Similarly, near dusk, Hawaiian spinner dolphins (Norris and Dohl 1980; Norris et al. 1994) and dusky dolphins off Kaikoura, New Zealand (Benoit-Bird et al. 2004; Vaughn et al. 2007; Würsig et al. 2007; Würsig and Würsig 2010), muster and then travel fast directly to offshore nighttime feeding areas to prey on DSL fishes and squid; near dawn, dolphins return at fast travel to coastal waters to rest and socialize much of the day. However, unlike spinner dolphins and dusky dolphins, Risso's dolphins may forage at night over habitat similar to that used for daytime resting and socializing. In the SCB, tagged Risso's dolphins made deep foraging dives primarily at night over steep coastal drop offs, with deepest dives occurring near dusk and dawn (Schorr, unpubl. data). Apparent foraging was observed and video recorded just three times, always over a steep underwater drop off, during over 18 daytime hours (h) of conducting focal observations of 51 Risso's dolphin groups (mean duration of 22 min; Smultea unpublished data). Individuals or pairs of foraging Risso's dolphins sprinted a short (~25 - 50 m) distance then dove steeply and rapidly, surfacing 1-2 min later, with several northern right whale dolphins *Lissodelphis borealis* following behind in some instances. Risso's dolphins may also employ an alternative foraging strategy of kleptoparasitism. SCB Risso's dolphins were video recorded harassing and charging sperm whales, with northern right whale dolphins following closely, and hypothesized this was to induce sperm whales to regurgitate squid parts (Smultea et al. 2014). In summary, during daytime, Risso's dolphins in the SCB preferred nearshore waters near San Clemente and Santa Catalina islands and the mainland over steep underwater drop offs for essential resting, socializing, and young-rearing, with a trend for rest/slow travel to occur over deeper water than medium/fast travel.

2.5.4 Bottlenose Dolphin

I found a clear preference by bottlenose dolphins for waters east vs. west of San Clemente Island during the study period, with no systematic sightings made west of the island; furthermore, all 96 bottlenose dolphin groups seen during our aerial surveys in 2008-2013 were east of San Clemente Island (Smultea unpublished data). Survey lines began >8 km from the island coast (Fig. 1-2), though three aerial surveys circumnavigated the island <0.2 km from shore (Smultea and Bacon 2012). Small-boat based studies have reported relatively few bottlenose dolphins off the western San Clemente Island, with most sightings near the eastern shoreline (Campbell et al. 2010, 2011; Falcone and Schorr 2011, 2013).

Regardless of behavior, all three RSF models indicated that bottlenose dolphins selectively used nearshore shallower waters more than expected based on availability, assuming equal access to all parts of the study area. These preferences corresponded with coastal waters of Santa Catalina Island, the mainland, and subareas off eastern San Clemente Island (Fig. 2-6). This pattern is generally consistent with the coastal common bottlenose dolphin worldwide (Jefferson et al. 2015). Small, vessel-based photo-identification studies suggest that some individual bottlenose dolphins demonstrate long-term site fidelity to both San Clemente and Santa Catalina islands (Campbell, unpubl. data). However, sightings are generally more common near Santa Catalina Island (Shane 1995; Campbell et al. 2010, 2011).

For medium-fast travel, western nearshore shallow waters of Santa Catalina Basin were positively correlated with high relative probability of use by bottlenose dolphins. Rest/slow travel and faster travel likely are associated with different biological functions. Shane (1994) indicated that fast traveling individuals near Santa Catalina Island were likely foraging. Similarly, Heimlich-Boran (1998) reported that killer whales in the San Juan Islands travel rapidly while foraging. Faster travel in deeper waters could also be related to fast transit between feeding or other areas. In contrast, winter behavioral studies of bottlenose dolphins near Santa Catalina Island in 1983-1991 reported that rest/slow travel was typically associated with socializing (i.e., touching, orienting towards one another) and active feeding (diving repeatedly in one area, facing in varying directions when surfacing; Shane 1994). Similarly, mill and rest/slow travel during our 2008-2013 aerial surveys often included socializing and probable feeding (individuals criss-crossing while performing short dives) based on extended focal follows recorded on video (Smultea unpublished data).

Data and studies indicate that nearshore shallow waters of Santa Catalina and eastern San Clemente islands, and the coastal mainland provide important year-round habitat for bottlenose dolphins, including for calf rearing, resting, socializing, foraging, and feeding (Shane 1994, 1995; Smultea and Bacon 2012; also see Chapter IV). Ten percent of 96 bottlenose groups in the SCB during 2008-2013 contained at least one calf (Smultea and Bacon 2012; Smultea unpublished data). Bottlenose dolphins, particularly young, are vulnerable to shark and killer whale predation (Jefferson et al. 1991; Weller 2009). Selecting nearshore shallow waters presumably reduces predation risk for bottlenose dolphins.

2.6 Conclusion

Behavioral state was related to habitat use of fin whales, gray whales, Risso's dolphins, and bottlenose dolphins in deep waters of the SCB. RSF modeling showed that some subareas and environmental features were selected proportionally more frequently than available in the study area, assuming equal access to all parts of the study area. However, the fundamental behavioral functions of these preferences remain poorly understood. Point-sampling protocol used to gather behavioral state data was commonly limited to relatively short (~10-30 sec) periods with animals observable at or near the water surface from the aircraft (to an estimated depth of 20-30 m). However, the plane circled back to confirm species, group size for ≥5-60+ min during ~19% of all sightings, and 52% of large whale sightings. Another caveat is that it was unknown what animals were doing while diving beyond view. However, SCB satellite tagging results (Falcone and

Schorr 2014; Mate et al. 2015) are consistent with the premise that rest/slow travel (including mill) is more likely to include feeding than fast travel. Detailed analysis of the over 50 h of behavioral data collected from our circling aircraft with HD video may further elucidate the functional importance of behavioral states relative to differential habitat use.

Additional environmental variables not addressed here may also influence habitat use and RSF values. For example, chlorophyll a and Sea Surface Temperature (SST) have been used to predict some cetacean densities on the larger regional scale of the California Current Ecosystem (Becker et al. 2010, 2012, 2014). Collaborations are planned with other researchers to develop and refine density prediction models by integrating and comparing our relatively small-scale data with other data collected on a larger scale relative to SST, chlorophyll a, etc. (E. Becker, SWFSC/ManTech, unpublished data). Incorporating measures of general prey distribution and abundance would also improve the accuracy of predicting habitat-use preferences. Unfortunately, these data are generally lacking on the scale of the SCB with a few exceptions (e.g., Munger et al. 2009; NOAA 2016).

In summary, results provide a better understanding of how behavioral state influences habitat selection of little-studied offshore cetaceans, illustrating the complexity of differentiating naturally occurring behavioral variability from potential anthropogenic disturbance of cetaceans in the SCB. Findings are useful for adaptive management relative to concerns regarding increasing anthropogenic activities. For example, some areas of relative high probability of use for important cetacean behaviors (e.g., resting, feeding, foraging) overlap with areas used regularly for military training activities involving Mid-frequency Active (MFA) sonar (DoN 2008b, 2011, 2014). While this study provides an important five-year baseline, further research is needed to refine cetacean habitat use relative to critical behaviors and periods, and to monitor potential changes in habitat usage and species viability in the face of climate change and growing anthropogenic activities.

CHAPTER III

CETACEAN BODY SIZE, GROUP SIZE AND GROUP COHESION

3.1 Synopsis

In open environments, prey are hypothesized to reduce predation risk through increased body size, group size, or tighter group cohesion. Cetacean group size and spacing change in response to natural and human-related factors (e.g., predators, behavior, noise exposure, close vessel approaches). A comparative approach was used to test the prediction that as cetacean species body size increases, group size decreases, cohesion decreases, and individuals are more likely to occur alone. Sighting data were collected in the Southern California Bight (SCB) from 2008-2013 during 18 one-week-long aerial surveys totaling 87,735 km along systematic transect and other effort. Point-sampling protocol was used to document the first-observed group cohesion (i.e., maximum nearest-neighbor distance estimated in adult Body Lengths [BL]) of cetacean sightings. Non-parametric statistical analyses were used to examine relationships between group size, cohesion and body length (using as a proxy). A total of 66 blue whale, 130 fin whale, 68 gray whale groups, 320 Risso's dolphin, 107 bottlenose dolphin, and 362 common dolphin spp. groups were observed. Among each taxonomic group, as body size increased, group size decreased, group cohesion decreased (i.e., individuals were spaced farther apart), and individuals were more likely to be alone. Differences in the same habitat may reflect evolutionary adaptations to predation risk and food resource availability, as predicted by terrestrial mammal group-living patterns. Larger group size benefits may include reduced predation pressure and improved prey detection/mate access, at the risk of increased resource competition.

Key words: cetacean, blue whale, fin whale, Risso's dolphin, predation, cohesion

3.2 Introduction

In open environments where predation risk is high, prey are hypothesized to reduce such risk through increased body size, group size, and/or tighter group cohesion (e.g., Krebs and Davies 1997, Ch 2; Ramakrishnan and Coss 2001; Davies et al. 2012). Species body size, group size and group cohesion are thought to represent adaptive trade-offs between the costs and benefits of group living. Large body size requires increased energy costs while large group size increases intra-specific competition for resources. Each strategy is commonly considered an adaptive response to predation pressure in open habitats lacking cover from predators, due to the dilution effect and other anti-predator benefits attributed to group formation (e.g., Jarman 1974; Norris and Dohl 1980; Gowans et al. 2008). Sociality and huddling are thought to reduce predation risk through predator confusion and improved sensory integration that enhances information transfer regarding predator detection (Norris and Dohl 1980; Kie 1999; Hebblewhite and Pletscher 2002).

Given the costs and benefits to forming groups, behavioral ecology theory predicts that group size should reflect surrounding environmental pressures, resulting in an optimal group size relative to body size (Jarman 1974; Wittenberger 1980; Owen-Smith 1988). A classic example of evolutionary tradeoffs between larger body size or larger group size is illustrated by comparative studies of African ungulates in open savannah habitat characterized by high predation risk. Jarman (1974) reported that in the open African savannah, as ungulate body size increases, group size decreases. This inverse relationship is believed to be a functional tradeoff between increased energy needs of larger body size leading to increased home ranges or seasonal migrations with decreased risk of predation. At the extreme, the energy required for carnivore predators to kill and consume an Eland buffalo (*Taurotragus oryx*) or giraffe (*Giraffa camelopardalis*) is presumably higher (due to the potential of predator injury relative to strength of the prey) than to kill an antelope such as an impala (*Aepyceros melampus*) that is over one-third smaller (Davies et al. 2012, Ch 2). The anti-predator behavior of the impala relies more on larger group sizes and the dilution and predator confusion effects. In open habitats, trade-offs between increasing group size and decreasing body size are predicted to follow a continuum.

Group cohesion patterns may also follow a continuum as a function of tradeoffs between ecological pressures. Pitcher (1983) proposed the elective group size concept, assuming that distance between individuals within a group is a functional trade-off between the benefits and costs of living in a group. For example, animals tend to increase cohesion when frightened or after feeding, but disperse when hungry and foraging (Romey 1997; Krause and Ruxton 2002; Würsig and Pearson 2014). In the open ocean, small schooling fishes such as herring and anchovy occur in large, tightly spaced schools of highly synchronized individuals (e.g., Norris and Dohl 1980). Tighter spacing and density changes in motion between individuals induce the “dilution effect” and the “confusion effect”, decreasing predation risk (e.g., Scott-Samuel et al. 2015). Tight cohesion and coordinated movement are also beneficial by reducing energy expenditure due to “drafting” (Marras et al. 2015). In contrast, the much larger bluefin tuna occur in smaller, less-cohesive groups presumably related to increased body size resulting in reduced predation pressure (Newlands and Porcelli 2008). Group cohesion is further influenced by behavioral and physiological motivation and perceived threat. If threatened, many species increase group cohesion. In contrast, the same individuals may spread out to forage and feed in areas where predation risk is perceived to be lower or the benefits (e.g., high prey density, increased mating opportunities) appear to outweigh the risk of predation (Frid and Dill 2002).

Following the group formation theory of behavioral ecology, small-sized odontocetes inhabiting open-ocean habitat form relatively large, tightly spaced groups (in the hundreds to thousands) as perhaps the only way to minimize predation in a seascape void of hiding structures (Norris and Schilt 1988; Norris and Dohl 1980; Gowans et al. 2008). This behavior appears to be viable as long as sufficient resources can be found to support the group (Acevedo-Gutierrez 2009). Among such odontocetes, group size is also hypothesized to be positively correlated with relatively large home ranges and patchy yet dense food sources, such as small schooling fish (Gowans et al. 2008). Odontocete feeding efficiency on fish schools is increased through cooperation among group members to corral and take turns consuming the fish (Würsig and Würsig 1980; Benoit-Bird and Au 2009; Vaughn-Hirshorn et al. 2013). Success of cooperative feeding strategies is hypothesized to rely on intraspecific communications to orchestrate and finely tune spacing and coordination between individuals (Norris and Schilt 1988). For example, killer whales, spinner dolphins, common dolphins, dusky dolphins and pilot whales spread out laterally while foraging to maximize prey detection, and then decrease individual spacing while feeding and resting, the latter to minimize predation (Norris and Dohl 1980; Gowans et al. 2008; Henderson 2010; Würsig and Pearson 2014).

Based on behavioral ecology theory and terrestrial and marine studies, species adapt to the same environment in different ways, while adaptations may differ between populations of the same species in different environments across invertebrates, amphibians, fishes, birds, terrestrial carnivores, and cetaceans (e.g., Würsig and Würsig 1980; Basolo and Wagner 2004; Hoare et al. 2004). The optimal adaptive balance between body size, group size, and group cohesion relative to resource availability and predation pressure may vary across a continuum. Additional variation is predicted to occur relative to local, diurnal, seasonal, and geographical variations in resource availability and predation risk. Group size and morphology among the same species of odontocetes can vary regionally and temporally depending on site-specific ecological conditions including habitat complexity, distribution and abundance of preferred prey, predation pressure, and behavioral state (e.g., Perrin et al. 1999; Henderson 2010; Würsig and Pearson 2014). Studies of various fishes and terrestrial mammals suggest that in open habitats where predation risk is high, group size and body size are larger and group cohesion is tighter. Larger group size of dolphins in open waters has been hypothesized to be linked to increased predation pressure (Norris and Schilt 1988; Gygax 2002a; Gowans et al. 2008). Dusky dolphin populations inhabiting three distinct marine habitats exhibit different foraging and social strategies related to variations in availability of prey, habitat, and predation risk, with larger group sizes found in more open habitats, and small stable group formation where predation risk is low (Würsig and Pearson 2014). A review of limited empirical studies and general trends in the degree of habitat complexity (i.e., openness) and home range have led to a framework predicting that delphinid group size and home range increase with habitat openness; however, this framework remains to be empirically tested across more cetacean species (Gowans et al. 2008).

Group size and group cohesion often increase or sometimes decrease (i.e., disaffiliation, individuals fleeing) in response not only to predators but also apparent threatening anthropogenic stimuli such as vehicles, vessels, helicopters, human hunters and tourism (e.g., Frid and Dill 2002; elk *Cervus elaphus*, Hebblewhite and Pletscher 2002; bottlenose dolphins, Smultea and Würsig 1995; sperm whales, Smultea et al. 2004, 2014). Frid and Dill (2002) reviewed numerous animal taxa and situations and concluded that reactions to predators and non-lethal disturbance stimuli have similar negative costs: a reduction in time spent in critical behavioral functions (e.g., parental care, feeding, mating) that can lead to decreased fitness and reproductive success if chronic or repetitive. However, as group size varies inter- and intra-specifically as a function of a number of interacting ecological pressures (e.g., resource distribution, predation risk, behavioral activity; Jarman 1974; Connor et al. 2000; Gowans et al. 2008), baseline data on naturally occurring group size and cohesion and the influence of site-specific ecological factors (e.g., species body size, food distribution) need to be established for a particular region, set of species and seasonal distribution of resources before using these parameters as behavioral indicators. For example, Henderson (2010) found that behavioral state of common dolphins in the SCB was correlated with group cohesion: dolphin were less cohesive while traveling rapidly than while resting or milling; vocalizations were also higher while spread-out during fast travel.

The objective of this study was to determine whether there is a predictable relationship between cetacean body length (using species as a proxy), group size, and group cohesion. Frameworks proposed for terrestrial and marine species lead to development of the study prediction that as cetacean body size increases, group size and group cohesion should decrease as trade-offs to reduce predation risk and adapt to patchily distributed food resources characteristic of open-ocean environments. Group size and cohesion data contribute to further understanding what constitutes a socially synchronized group and the variations thereof (Krause and Ruxton 2002). Both group size and cohesion are known to change in response to natural and human-related factors (e.g., predation risk, behavioral state such as resting or foraging, noise exposure, close vessel approaches; Richardson et al. 1995; Smultea and Würsig 1995; Visser et al. 2011). Data on group size and cohesion of poorly known offshore cetacean species may also provide a reference scale for potential behavioral indicators of anthropogenic disturbance. The proposed predictive framework builds on the predictive framework of Gowans et al. (2008) for delphinids by considering group cohesion, incorporating an additional dimension to understanding the evolution of cetacean social strategies.

3.3 Methods

3.3.1 Study Area and Species

The study area in the SCB encompassed waters extending from approximately 10 km off the mainland coast up to approximately 200 km offshore, and from San Diego to approximately 100 km north near Los Angeles (approximately 17,555 km^2; Fig. 3-1). The study area includes San Clemente and Santa Catalina islands, the southernmost California Channel Islands. Water depth in the study area ranged from 0 to approximately 2000 m. Bathymetric topography is highly variable, characterized by underwater canyons, seamounts, a relatively narrow continental shelf, deep flat basins, and steep slopes (Fig. 3-1). Aerial surveys were flown out of Montgomery Airport, San Diego using primarily (79 of 90 flight days) a small high-wing, twin-engine Partenavia P68-C or P68-OBS (glass-nosed) airplane equipped with bubble observer windows on the left and ride sides of the middle seats. A high-winged twin-engine Aero Commander airplane was used on nine days and a Bell 206 helicopter on two days. Aerial survey periods were typically one-week long and occurred at least once during every month of the year except December from 2008 - 2013. Observations usually occurred between 9:00-15:00 Pacific Standard Time (depending on survey conditions) to maximize overhead light and sighting conditions.

Analyses were limited to the six most commonly sighted cetacean species with sample sizes considered adequate to conduct meaningful statistical analyses (n>20). In descending order of body length these six species included the blue whale, fin whale, gray whale, Risso's dolphin, bottlenose dolphin, and unidentified common dolphin spp. From the aircraft, short- and long-beaked common dolphins were difficult to differentiate given the subtle physical differences between the two species (Heyning and Perrin 1994; Perrin 2009; Smultea and Jefferson 2014) from the high survey altitude (213-305 m), and the image quality and resolution (10.1-18 megapixels) limitations of cameras at the time. Only 23% of the 564 common dolphin sightings photographed and examined by a species expert (T.A. Jefferson, Clymene Enterprises, Inc.) were confirmed to species: 17% as short-beaked common dolphin and 6% as long-beaked common dolphins. Species confirmation was typically only based on one or at most a few individuals in large groups of hundreds of individuals. Thus, for the purposes of this study all three species were pooled to increase sample size.

3.3.2 Data Collection and Equipment

The survey team consisted of one (2008-2010) or two pilots (2011-2013), two trained marine mammal biologists and a data recorder. Two biologists observed from center seats; the data recorder operated from the front right co-pilot seat (2008-2010) or rear left bench seat (2011-2013). Survey design followed line-transect protocol (Buckland et al. 2015) to obtain sighting data for estimating density and abundance (Jefferson et al. 2014a). Systematic survey lines were oriented generally southeast-northwest perpendicular to bathymetric contours (Fig. 1-2). Surveys were flown at speeds of approximately 100 knots ground speed and altitudes of 227-357 meters (m).

Sightings used for analysis were collected during observation effort along systematic line transect and connector survey legs (shorter lines connecting and perpendicular to systematic lines) to ensure systematic data collection. Data collected included date, time, species, Global Positioning System (GPS) location, best estimated group size including estimated number of calves, group cohesion (maximum distance between nearest neighbors within a group, estimated in adult BL), observation effort on or off, survey leg type, and environmental data (Beaufort sea state, visibility, glare, cloud cover). Typical photos for each of the study species from the aerial perspective of the aircraft showing examples of group cohesion are provided in Fig. 3.1 and 3-2. For the purposes of this study, a “group” was defined as >50% of polarized individuals engaged in the same behavioral state (e.g., travel, mill, rest) within visual range of the observers to a maximum of 100 BL apart (after Norris and Schilt 1988; Baird and Dill 1996; Lusseau et al. 2005; Table 1). Within observed groups, individuals were typically within 10-20 BL of each other but occasionally up to 50-100 adult BL apart. For common dolphins that formed much larger groups than other cetaceans (on the order of hundreds to thousands), cohesion was based on distinct subgroups that met the above group definition. A “calf” was defined as an animal less than or equal to one-half the body length of the adult individual with which it was closely associated (within 0.5 adult BL). Point-sampling (Mann 2000; Martin and Bateson 2011) was used to record the first-observed group size and cohesion. Sightings were circled as needed to confirm these parameters including with photographs or High Definition (HD) video. This sometimes included conducting a focal behavioral group session for up to 60 min as part of a separate study (Smultea et al. 2014; Lomac MacNair and Smultea 2016).

Data were collected using a variety of software and hardware that changed with technological advances. In 2008-2009, BioSpectator software was used on a Palm Pilot TX or an Apple iPhone or iTouch. In 2010-2011, a customized Excel spreadsheet was used on a Windows-based laptop. In 2011-2013, customized Mysticetus™ System (Mysticetus™) software was used on a laptop. GPS data were recorded using a Wide-Area Augmentation System (WAAS) handheld and aircraft Garmin, and a Bluetooth or USB GPS. Each new entry was automatically assigned a time stamp, a sequential sighting number, and a GPS position. Photographs and video recordings were made through a small opening porthole through either the co-pilot seat window (2008-2010) or the rear left bench-seat window (2011-2013). Species and group size were documented as needed with a DSLR camera (Canon EOS 40D or D60 or Nikon D300 or D7000 with 100-400 mm Image Stabilized zoom lenses), a Sony Handycam HDR-XR550 or HDR-XR520 video camera, and Steiner 7 X 25 or Swarovski 10 X 32 binoculars.

3.3.3 Data Analysis

The three variables of interest consisted of one response variable (group size) and two explanatory variables; (group cohesion and species [as a proxy for species body length]). Table 3-2 identifies the mean reported body lengths of the six study species, prioritizing data collected nearest to the SCB. Statistical analyses were conducted using R software. Due to the non-parametric nature of the data, Mann-Whitney U tests and Kruskal-Wallis tests were applied to determine if group size and group cohesion varied significantly between suborder (Mysticete relative to Odontocete) and also between species or pooled species within each suborder. For investigations into group cohesion only those groups with two or more animals were included, while all investigations into group size included single animals. Where there were significant differences within the suborder, post-hoc tests were applied to determine which species differed significantly from another. These non-parametric post-hoc tests were achieved using functions available in the R-package ‘PMCMR’ (The Pairwise Multiple Comparison of Mean Ranks Package, Pohlert 2016).

3.4 Results

During 18 aerial surveys conducted in 2008–2013, there were a total of 670 sightings of an estimated 88,487 individuals of the six study species during approximately 82,502 km of observation effort (Fig. 3-3). Overall, 97 percent of the total flight time was associated with a Beaufort sea state less than 4. Numbers of groups seen for each species in descending order of frequency were 362 common dolphin spp., 320 Risso's dolphin, 130 fin whale, 107 bottlenose dolphin, 68 gray whale, and 66 blue whale. Associated summary statistics, total number of individuals by species, and total number of sightings by species are shown in Table 3-1 and 3-2 and Fig. 3-3 through 3-6 and include frequency plots and box plots.

Frequency distributions of group size and group cohesion by species are shown in Fig. 3-3 and 3-4. Blue whale group size ranged from 1-6 and fin whales occurred in groups of 1-4 animals (Table 3-1). Gray whale group size ranged from 1 to 9 animals, however the most common group size for these baleen species was 1. In contrast, the three dolphin species were rarely seen as a single individual (Fig. 3-4). Common dolphins (pooled) occurred in the largest group sizes (estimated maximum 2,500 individuals) while bottlenose and Risso's dolphins occurred in groups of no more than 150 animals (estimated maximum 120 Risso's dolphins and 150 bottlenose dolphins, respectively) (Table 3-2 and Fig. 3-4).

The non-parametric analysis found significant differences in both group size (Mann-Whitney U test, W=198359.5, $p<0.001$) and group cohesion (Mann-Whitney U test, W=63433.5, $p<0.001$) between mysticete and odontocete suborders. Group size and group cohesion also differed significantly for both the odontocete species (Kruskal Wallis, group size chi-squared=356.84, df=2, $p<0.001$, Kruskal Wallis, group cohesion chi-squared=10.54, df=2, $p=0.005$) and the mysticete species (Kruskal Wallis, group size chi-squared=8.65, df=2, $p=0.013$, Kruskal Wallis, group cohesion chi-squared=27.97, df=2, $p<0.001$). For the odontocete species, common dolphin species were found to occur in significantly larger groups than both Risso's ($p<0.001$) and bottlenose dolphins ($p<0.001$), but there was no significant difference in the group sizes of Risso's and bottlenose dolphins. There was also no significant difference in the group cohesion of Risso's and bottlenose dolphins; however, bottlenose dolphin group cohesion was found to differ significantly to that of common dolphin species ($p=0.008$). There was no significant difference between the group cohesions of Risso's dolphins and common dolphin species. Of the mysticete species gray whales had a significantly tighter group cohesion than both blue whales ($p<0.001$) and fin whales ($p<0.001$), though there was no significant difference in the group cohesion of blue and fin whales. In terms of group size only blue whale group size differed significantly to gray whales (p=0.015) but not to fin whales, and gray whale group size also did not vary significantly to fin whale group size.

Mean group sizes for the three mysticetes (gray whale 2.1, Standard Deviation [SD] 1.40; fin whale 1.7, SD 0.90; and blue whale 1.6, SD 1.10) were much smaller than for the three odontocetes (Tables 3-1 and 3-2). Mean group size was largest for the pooled common dolphins (254.9, SD 408.50), followed by the bottlenose dolphin (18.3, SD 21.70) and Risso's dolphin (16.6, SD 16.30). Group cohesion among baleen whales was closest for gray whales (1.7 BL, SD 3.30), followed by blue and fin whales (12.0 BL, SD 2.62 and 4.9 BL, SD 6.40, respectively). Group cohesion for the three odontocetes were similar: Risso's dolphin (7.7 BL, SD 12.80), bottlenose dolphin (5.2 BL, SD 9.90), and common dolphin spp. (5.3 BL, SD 5.30).

The blue whale sample size for at least two individuals in a group was too small to be tested, as most blue whales were single individuals. However, when proportional comparisons were made assessing the probability of each species occurring in group size of 1, the results supported the overall gist of the hypothesis: blue whales were the most likely to occur in a group size of one, which is actually the "largest" group spacing among all the species examined. Furthermore, the probability of a species occurring in group size of 1 generally decreased with increasing group size.

3.5 Discussion

Examination of species-specific relationships for body size, group size and group cohesion suggested predictable patterns as a function of presumed semi-pelagic and pelagic predation pressure and clumped, unpredictable prey patches. Group-size patterns of odontocetes in deep waters of the SCB match predictions for social structure (in terms of group size and cohesion) in open terrestrial habitat reported for distant-related open-savannah ungulates (e.g., Jarman 1974; Davies et al. 2012, Ch 2), and semi-pelagic and pelagic deep delphinids (Gygax 2002a,b; Gowans et al. 2008).

Separate correlative but parallel relationships were found within odontocetes and mysticetes, respectively. Species body size was inversely related to group size and group cohesion within each of these taxonomic groups on a different scale. The separate scaling patterns found between mysticetes and odontocetes may be related to phylogenetic differences that led to different foraging strategies, body size, energy requirements, and anti-predator responses (Ford and Reeves 2008). Shared ancestry between closely related species may result in similar behaviors (Beauchamp 2014, Ch 9).

Among mysticetes, blue whales were most likely to be observed alone, in the smallest groups, and with the largest separation distance between individuals within groups. This pattern changed on a continuum for the smaller-sized fin whale and the even smaller-sized gray whale. Gray whales had the largest mean group size and the tightest group cohesion among the three mysticete species. Killer whale predation on whales is common in California waters, while shark predation is likely most common on small dolphins and pinnipeds (Weller 2009). Smaller-body-sized species are presumably more vulnerable to predatory attacks. Forming larger group sizes is predicted to reduce predation pressure on individuals by diluting the odds of being preyed upon, among other benefits (Gowans et al. 2008; Acevedo-Gutierrez 2009; Würsig and Pearson 2014). In contrast, the largest body-sized cetaceans in the SCB, the blue and fin whales, are presumably less likely to be attacked than smaller-sized species. Though both species and in fact all cetacean species are known to be consumed at least occasionally by killer whales (Jefferson et al. 1991), large baleen whales and sperm whales are presumably a higher risk prey target than smaller more defenseless delphinids, and have been documented to inflict serious injuries to attacking killer whales (Ford and Reeves 2008). Larger, tighter common dolphin and gray whale groups match presumed higher predation pressure associated with smaller relative body size among odontocetes and mysticetes, respectively. Similarly, common dolphins had much larger group sizes and tighter group cohesion than the larger-bodied Risso’s and bottlenose dolphins. The lack of significant difference between Risso’s and bottlenose dolphins may be related to similar body sizes.

While results suggested general trends, cetacean group size and group cohesion are known to vary spatiotemporally and by behavioral state, particularly among delphinids (e.g., Henderson 2010), and presumably also influence general group size and cohesion patterns. These influences are examined in Chapter IV, as this chapter focused on examining a simple potential predictive framework within which to compare inter-specific differences and relationships between body size, group size and cohesion. Based on a literature review, this correlation does not appear to have been previously examined among cetaceans and merits further investigation and testing.

3.6 Conclusion

In conclusion, the initially proposed hypothesis was supported when mysticetes were considered separately from odontocetes. Within each of these two groupings, as species body length decreased, group size increased and group cohesion decreased with decreasing likelihood of occurring alone. Different cetacean species have exhibited ecological diversion in the same habitat in response to differing predation pressure and food resource availability as predicted by terrestrial mammal group-living patterns. As hypothesized, blue whales as the largest cetacean, occurred in small, dispersed groups and were most likely to occur alone compared to all other smaller cetaceans. The latter pattern progressively continues with other species as body size decreases. While these correlative patterns were apparent in the SCB, further research is needed to corroborate or reject this trend in other open marine habitats. Group cohesion data are difficult to collect from the low vantage point of vessels, but the “bird’s eye” perspective of an overflying aircraft operating outside the zone of sound disturbance to cetaceans offers a unique 3-dimensional and wide-angle view of group structure and spacing.

In summary, similar to their terrestrial counterparts, cetacean group size and social complexity appear to vary with body size and environmental conditions related primarily to resource distribution and availability, balanced with presumed predation risk. As summarized by others (e.g., Gowans et al. 2008; Acevedo-Gutierrez 2009; Würsig and Pearson 2014), open-ocean habitats presumably represent the most formidable ecological pressures to form large groups to minimize predation pressures as well as challenges to finding dispersed patches of food sufficient to sustain large group of cetaceans.

Data lend insight into baseline behavior and ecological triggers influencing behavior, and provide site-specific life history information on group size and group cohesion patterns of cetaceans inhabiting offshore SCB waters. These parameters define species-specific behavioral indicators. Such information is needed to differentiate naturally occurring behavior relative to potential impacts of anthropogenic sources. Correlative patterns reported here between species body size, group size and group cohesion present a preliminary predictive framework for semi-pelagic and pelagic-dwelling small odonotocete and mysticete species that remains to be examined in other environments and among other populations and species.

CHAPTER IV

INFLUENCES ON CETACEAN BEHAVIOR, GROUP SIZE AND COHESION, SOUTHERN CALIFORNIA

4.1 Synopsis

Factors influencing variation in intra- and interspecific group size, cohesion (inter-individual spacing), and behavioral state of cetaceans inhabiting semi-pelagic and pelagic waters are poorly known. Such information is needed to differentiate potential effects of increasing anthropogenic activities in the Southern California Bight (SCB) from natural stressors. Anthropogenic activities of concern in the SCB include shipping, fisheries, recreational boating, tourism, offshore resource extraction, and military exercises. From 2008-2012, 15 week-long aerial surveys were conducted in the SCB to examine the influence of diurnal, seasonal, environmental, and calf presence factors on cetacean behavior, group size, and group cohesion (maximum nearest neighbor distance in adult body lengths). Sighting data (species, location, group size, calf presence) were collected during all observation effort based on line transect design. Point sampling was used to record initially observed group cohesion and behavioral state. Environmental data at cetacean locations were determined using GIS: water depth, closest distance to shore, slope, and aspect. A total of 62 blue whale, 115 fin whale, 78 gray whale, 293 Risso's dolphin, 96 bottlenose dolphin, and 566 common dolphin spp. groups were observed. Regression modeling indicated that (1) groups with calf presence were larger, (2) groups were more cohesive (less space between individuals) during expected calving and mating seasons, and (3) nocturnal foraging Risso's and common dolphins displayed rest/slow travel relatively more during midday, and traveled faster during early morning and late afternoon. Temporal differences in group size, cohesion, and behavior may reflect varying reproductive phase, resource availability, and adaptations to predation, as reported among related ungulates and other cetaceans inhabiting open environments. Results indicate that spatio-temporal and group composition influences on group size, cohesion, and behavioral state must be included when evaluating potential influences of anthropogenic activities.

Key Words: cetacean, group cohesion, calf, behavioral indicator, Southern California Bight

4.2 Introduction

Phylogeny and the environment are predicted to shape behavioral ecology through adaptation relative to the distribution of resources (e.g., food, mates) balanced with predation risk (Jarman 1974; Sumpter 2010). Animal behavior, group size, and group cohesion may thus vary intra- and interspecifically in response to local variability in ecological factors. It is important to identify environmental and social factors that influence animal behavior and habitat use to assess the opportunity for potential spatiotemporal management and conservation measures, and to understand and differentiate how these patterns may change in response to anthropogenic activities (Blumstein and Fernández -Juricic 2010; Berger-Tal et al. 2011). Conservation behavior focuses on linking ecological principles with practical applied conservation and management (Blumstein and Fernández -Juricic 2010). The practical conceptual framework suggested for effective implementation of conservation behavior by Berger-Tal et al. (2011) is to develop standardized approaches for quantifying behavior and habitat use, subsequently measure potential changes related to anthropogenic effects, and then evaluate effectiveness of management and conservation strategies. Two recommended primary behavioral ecology domains (i.e. pathways) to accomplish this step-wise approach are studies of: (1) social and reproductive behavior patterns, and (2) foraging and predator-prey related behaviors and patterns (Berger-Tal et al. 2011)

Among terrestrial and aquatic animals, spatiotemporal distribution and availability of needed resources influence behavior and habitat use (e.g., Gittleman 1989; Kappeler et al. 2013; Rooker et al. 2013). Different species in the same region may adjust group size, spacing between individuals, distribution and behavioral tactics (e.g., foraging patterns) in response to changes in resource availability and related tradeoffs between group size and predation risk (Burkepile et al. 2013; Hopcraft et al. 2014). Spatiotemporal variations and patterns in cetacean behavior, group dynamics, and habitat use are better described for easily accessible coastal cetaceans than for more offshore open and semi-pelagic ocean environments (Gowans et al. 2008; Würsig 2009; Würsig and Pearson 2014). These studies show that behaviors are strongly influenced by calving and mating seasons, distribution and behavior of prey, and presumed predation pressure that vary accordingly across regions and populations.

Most inter- and intra-specific comparisons showing variable behavioral patterns across cetaceans have involved coastal gray whales, humpback whales, and coastal bottlenose dolphin and dusky dolphin populations (Darling et al. 1998; Defran et al. 1999; Würsig and Würsig 2010).

Some pelagic sperm whale populations have also been well-studied from relatively large, live-aboard vessels that follow behind the whales for extended weeks and months (Biggs et al. 2000; Whitehead 2003; Jochens et al. 2008). Coastal feeding bowhead and gray whales display different feeding strategies depending on regional and seasonal prey availability (Würsig et al. 1985; Dunham and Duffus 2002). Dusky dolphin populations off Argentina feed during daylight, cooperatively herding bait fish (Würsig and Würsig 1980; Vaughn et al. 2007, 2010). In contrast, dusky dolphin populations off Kaikoura, New Zealand rest nearshore during the day and forage in offshore deep waters at night when vertically migrating fish are closer to the surface (Benoit-Bird et al. 2004; Würsig and Würsig 2010). In comparison, relatively little has been described for social or group characteristics or foraging patterns of less accessible, oceanic species including blue and fin whales, and Risso’s, offshore bottlenose and common dolphins, as well as offshore migrating gray whales (Jefferson et al. 2014b, 2015; Perrin 2009; Henderson 2010; Visser 2014). However, similar to more well-described coastal cetacean species, semi-pelagic and pelagic cetacean species are expected to display behavioral tactics adapted to diurnal and seasonal changes in food resources as well as availability of mates and presence of calves.

Because it is expensive and difficult to track offshore cetaceans, and they are at the surface for only brief periods, data on group behavior are limited or lacking. Most such studies have been based from vessels, though these platforms are challenged by relatively low vantage points, and the vessel itself can be a potential source of disturbance (Constantine 2001; Dawson et al. 2008; Henderson et al. 2014b). An aerial platform (e.g., fixed wing aircraft, helicopter, dirigible, blimp, unmanned aerial system), as used in this study, provides the advantage of an overhead three-dimensional view of animals at and somewhat below the water, such that near-surface numbers, behaviors, and intraspecific orientations and spacing can be seen and video recorded (Würsig et al. 1985; Smultea and Würsig 1995; Durban et al. 2015). This latter technique has the further advantage of not disturbing the animals when proper protocols are followed, including sufficient altitude, flying outside the air-to-water cone of sound, and other precautions such as not letting the airplane’s shadow fall on members of a group (Richardson et al. 1995; Patenaude et al. 2002; Lomac-MacNair and Smultea 2016).

4.3 Objectives and Hypotheses

The purpose of this study was to look beyond simplified inter-specific correlations and predictive framework between cetacean species with respect to body size, group size and group cohesion explored in Chapter III by adding in temporal, spatial environmental, and calf presence explanatory factors to examine their influence on behavioral state, group size and group cohesion. To maximize sample size, analyses focused on the same six most commonly observed cetacean species as used in Chapter III. Hypotheses focused on whether (1) calf presence relative to reported peak calving and mating seasons influenced group characteristics, and (2) diurnal and seasonal behavioral state patterns followed presumed prey distribution based on reported predominant nocturnal foraging tactics of Risso's and common dolphins.

Response variables were selected based on results of other studies identifying quantifiable parameters shown to be responsive to natural threats (e.g., predators) and human-related disturbance: group size and group cohesion (i.e., inter-individual distance). Similar to Chapter III, the study goal included gathering species- and SCB-specific baseline data on group size and cohesion to provide a source of comparison at the scale of the SCB to evaluate whether these parameters change as a result of anthropogenic disturbance. Baseline data were further meant to provide potential behavioral indicators of future anthropogenic disturbance.

The general null hypothesis inversely matching the study objectives above was as follows:

- **Null Hypothesis:** Behavioral state, group size, and group cohesion of cetaceans in the SCB are not influenced by calf presence and environmental factors.

The three specific alternative hypotheses were as follows.

1. **Alternative Hypothesis 1**: Groups with calf presence are larger with tighter group cohesion than groups without a calf across cetacean species.
2. **Alternative Hypothesis 2:** For nighttime foraging Risso's and common dolphins, rest/slow travel peak during midday while faster travel peaks in the early morning and late afternoon.
3. **Alternative Hypothesis 3**: Individual spacing within groups is closer during the calving and mating seasons across cetacean species.

4.4 Methods

4.4.1 Study Area and Survey Design

The study area consisted of the SCB extending from offshore the mainland coast to ~70 km west of San Clemente Island, and from the Mexican border north to near Los Angeles (Fig. 1-1). Surveys were flown out of San Diego using three types of aircraft: (1) most (88%; *n*=79) of the 90 survey days were conducted from a small high-wing, twin-engine Partenavia P68-C or P68-

OBS (glass-nosed) airplane equipped with bubble observer windows on the left and ride sides of the middle seats; (2) the remaining 11 survey days (12%) occurred from an Aero Commander airplane (9 days) or a helicopter (2 days). The 15 surveys occurred at least once during 11 of the 12 calendar months: October and November 2008; June, July and November 2009; May, July/August and September 2010; February, March, April, and May 2011; and January, February, and March/April 2012. Daily field observations typically occurred between 9:00-15:00 Pacific Time to maximize overhead light and sighting conditions. The survey team consisted of one (2008-2010) or two pilots (2011-2012), three professionally trained marine mammal biologists (two with over 10 years of related experience) or two such biologists and a computer scientist. Two biologists observed from center seats; the third biologist (or computer scientist) recorded data from the front right co-pilot seat (2008-2010) or rear left bench seat (2011-2012). Surveys were flown at speeds of approximately 100 kt and altitudes of approximately 227-357 m (averaging 261 ± 49 m per the Wide-Area Augmentation System-enabled GPS).

Surveys followed line-transect protocol (Buckland et al. 2015) along generally east-west-oriented lines perpendicular to bathymetric contours (Jefferson et al. 2014a). Observations included in this analysis occurred during both systematic and connector effort (i.e., shorter perpendicular lines connecting longer systematic survey lines). Point-sampling (Martin and Bateson 2011) was used to record the first-observed group behavioral state (mill, rest/slow travel, medium/fast travel; Table 2-1) (Shane 1990; Smultea 1994; Henderson 2010), and (2) group cohesion (maximum nearest neighbor distance within a group, estimated in adult species body lengths (BL) (Table 2-2 and Fig. 4-1). A group was defined as all individuals within 10-20 adult BL but occasionally as many as 50 BL apart, interacting or engaged in similar activities (after Shane 1990; Smultea 1994). For common dolphins that formed much larger groups (on the order of hundreds to thousands) than other cetaceans, cohesion was based on individual spacing within distinct subgroups that met the above stated definition of “group”. A calf was defined as a smaller individual ≤one-half the BL of the closely accompanying larger animal. For common dolphins, the minimum number of calves observed was estimated because it was not possible to count all calves in the characteristically larger groups; for other species, the estimated number of calves was indicated as a minimum or the actual observed number. From the aircraft, short - and long-beaked common dolphins were difficult to differentiate given the subtle physical differences between the species (Jefferson et al. 2015), and the lower resolution (12 megapixels (MP)) of camera lenses used during 2008-2011. However, starting in 2012, a higher-resolution (24 MP) camera lens allowed the identification of a higher subset of photos in situ and post-field by a species identification expert. Of the total 564 common dolphin sightings, 12% were identified to contain short-beaked common dolphin(s), and 6% to include long-beaked common dolphin(s).

Environmental data were collected at the beginning of each effort type and whenever conditions changed. Sightings were circled to photo-document and confirm species, group size, and calves. Blue, fin, and gray whales, bottlenose and Risso's dolphins, and occasionally other cetacean species were sometimes circled for longer (>5 min) periods to conduct a detailed focal group or individual behavioral session by increasing altitude to ~365 - 455 m and radial distance ~0.5-1.0 km and video recording animal behavior. Field data (sighting, effort, and environmental data including Beaufort sea state, visibility, glare, and cloud cover) were collected with various hardware and software that changed across the study period with development of new systems. In 2008-2009, BioSpectator software was used on a Palm Pilot TX or an Apple iPhone or iTouch in. In 2010-2011, a customized Excel spreadsheet on a Windows-based notebook computer was used. In 2011-12, customized Mysticetus Observation (Mysticetus™) Software was used on a notebook computer. Locations were determined using a WAAS handheld and aircraft Garmin, and a Bluetooth or USB Global Positioning System (GPS). Each new entry was automatically assigned a time stamp, a sequential sighting number, and a GPS position. A Suunto handheld clinometer was used to measure declination and horizontal angles to sightings. In 2008-2010, declinations were converted post-survey to perpendicular sighting distance; in 2011-2012, declinations were instantly converted to perpendicular and radial sighting distances by Mysticetus.

Photographs and video recordings were made through a small opening porthole on either the co-pilot seat window (2008-2010) or the rear left bench-seat window (2011-2012). Photographs were collected using a Canon EOS 40D or D60 or D300 or D7000 Nikon digital camera with 100 -400 mm Image Stabilized zoom lenses. A Sony Handycam HDR-XR550 or HDR-XR520 video camera was used to document behaviors while circling focal groups. Observers used Steiner 7 X 25 or Swarovski 10 X 32 binoculars as needed to identify species, group size, behaviors, etc.

4.4.2 Data Analysis

Analyses focused on three response variables and explored potential relationships with 11 explanatory variables (Table 2-2). For analyses, time of day was represented as the number of minutes from sunrise each day, calculated using sunrise tables for San Diego, California. Julian day was used to represent the integer day number beginning with 1 on January 1 of each year of the study (Table 2-2). Water depth, closest distance to shore (including islands), slope, and slope aspect were determined using geo-spatial analysis capabilities of Mysticetus (Table 2-2). Aspect was transformed into a variable pair via the cosine and sine transformations, and was subsequently treated as a single variable in the model selection process.

Statistical analyses were conducted using the software program R and included Pearson Correlation, Fisher’s two-sided exact test, t-test, and regression modeling. Pearson correlations between all pairs of continuous variables were calculated; correlations >0.6 in absolute value were not permitted to enter regression models together (described below). Each pair of categorical variables was cross-tabulated and results were examined for evidence of association. If Fisher’s two-sided exact test was significant (p<0.05), the two variables were not permitted to enter any model together. The association between each mixed pair of categorical and continuous variables was examined via an independent sample t-test; if the test was significant (p<0.05), the two variables were not permitted to enter any model together. The cosine and sine transformations of aspect were treated as a single variable: either both transformations entered a model together or both were excluded. If either member of the pair was associated with any other variable using the criteria above, neither member of the pair was permitted to enter a model with the associated variable.

Separate regression modeling was conducted for the three response variables. A different type of model was used based on the results of each type of response. Only models with five or fewer variables were examined. An automated routine was used to generate all main effects models with 1, 2, 3, 4, or 5 variables that met the criteria above for absence of strong pairwise associations. Because observations with missing values do not contribute to regression models, observations with missing values were excluded from further analyses. Each resulting reduced dataset was then re-examined for associations among variables. As dictated by the criteria for associations among variables, different candidate sets of models were constructed as necessary.

Akaike’s Information Criterion (AIC) (Burnham and Anderson 2002) was calculated for each candidate model. The top 10 models with the lowest (best-fitting) AIC value were evaluated, and, the difference between this AIC value (AICi) and that of the top-ranked model (AIC1) was calculated as

∆_i= 〖AIC〗_i-〖AIC〗_1

Akaike weights were then calculated for all 10 models from these differences as

w_i=exp (-1/2 Δ_i)/(∑_(m=1)^10 exp (-1/2 Δ_m))

The importance value for each variable was then calculated based on the sum of the Akaike weights for each model within which that variable appeared. The importance value represented the number of times a variable appeared in the top 10 models. For example, if a variable appeared in all 10 models, its importance value equaled 1; otherwise, the importance value was bounded between 0 and 1.

Each of the three response variables (behavior, group size, and group cohesion) were evaluated with separate regression models based on variable characteristics. The response variable behavioral state (with three categories) (Table 2-2) was analyzed using multinomial logistic regression. This involved pooling medium/fast travel as the reference category, with the odds of being in either of the other two categories (rest/slow travel or mill) calculated relative to the reference. Log-linear models were used for the response variable group size, since it was an integer count variable. Poisson and negative binomial regression models were both examined for group size. Because variance was generally greater than expected under the Poisson distribution, Vuong's (1989) test was applied to compare the fit of Poisson and negative binomial regression models. The negative binomial model described variance better than the Poisson model. When negative binomial regression models exhibited convergence problems, a Poisson regression was used. The variable "group cohesion" was log transformed to approximate a normal distribution. Standard multiple linear regression was applied to model the relationship between individual spacing and the variables.

4.5 Results

A total of 588 sightings of an estimated 160,494 individuals were made during the approximately 82,502 km of observation effort conducted during the 15 aerial surveys in 2008–2012 (Fig. 4-1). Overall, 99 percent of the total flight time was associated with a Beaufort sea state less than 4. Numbers of groups seen by species in descending order of frequency were 564 common dolphin spp., 286 Risso's dolphin, 115 fin whale, 96 bottlenose dolphin, 78 gray whale, and 65 blue whale.

4.5.1 Blue Whale

For blue whale group size, Julian day was the only significant and most important response variable among the Poisson regression models (importance value 0.95) (Tables 4-1 and 4-2). Group size increased with increasing Julian day from 1.0 whale in spring to 3.5 whales in fall. Depth had a much lower importance value of 0.42 and was non-significant. For group cohesion, none of the candidate variables accounted for significant variation in cohesion, and the best model contained only slope with importance value of 0.62.

4.5.2 Fin Whale

The best predictors of fin whale behavioral state were (1) distance to shore and (2) Julian day (importance value 1.0 for Julian day and 0.96 for distance to shore) (Tables 4-1 and 4-3). All remaining explanatory variables were nonsignificant for behavioral state. Milling was most likely to occur close to shore: for each 10 km increase in distance, the odds of milling decreased by a factor of 0.2. Fin whales were also 0.8 times more likely to slow travel earlier relative to later in the year, with odds decreasing by a factor of 0.22 for each 100 days. The best model for fin whale group size included (1) calf presence and (2) time of day. Mean observed group size with a calf was 3.2 fin whales relative to 1.6 whales with no calf. Although insignificant, there was some indication ($p<0.10$) that group size decreased with increasing time since sunrise. All remaining variables were nonsignificant for group size. The best predictors of group cohesion were (1) calf presence followed by (2) subregion (importance values 0.93 and 0.41, respectively). The top model showed that cohesion was closer with calf presence (1.0 BL apart) than absence (2.5 BL). In contrast, cohesion tended to be farther apart (4.7 BL apart) when compared to the subregion East of San Clemente Island (2.5 BL) (Tables 4-1 and 4-3).

4.5.3 Gray Whale

The best predictor of behavioral state for gray whales was aspect and was the only explanatory variable in the best model (importance value 0.72) (Table 4-1). Odds ratios showed that rest/slow travel was five times more likely than medium/fast travel to occur over south-facing vs. north-facing slope aspects. Inversely, medium/fast travel was primarily associated with north-facing slopes. All other variables were nonsignificant for behavioral state. The best predictors of gray whale group size were (1) subregion and (2) to a lesser extent aspect (importance values 0.92 and 0.72, respectively). Group size tended to be larger west vs. east of San Clemente Island (2.7 vs. 1.7 whales, respectively; $p<0.10$). Predicted group size as a function of aspect suggested a trend for highest group size over east-northeast-facing slope aspects. Correspondingly, lowest predicted group size was associated with west-southwest-facing slope aspects. Remaining variables in the top-ranked group size models were insignificant (p>0.10). For group cohesion, the best predictors were: (1) subregion, (2) aspect, and (3) Julian day (importance values >0.72). Gray whale groups tended to be less cohesive when west vs. east of San Clemente Island (1.4 BL vs. 0.7 BL, respectively; p<0.10). Group cohesion also tended to decrease across the winter-spring from 0.8 BL in February to 0.5 BL in April, though this trend was not significant (p<0.10).

4.5.4 Risso's Dolphin

The best predictors of behavioral state for Risso's dolphins were: (1) distance to shore, (2) Julian day, and (3) to a lesser extent time of day (Table 4-4 and 4-5). Distance to shore and Julian day appeared in all top models (importance value 1.0). Milling increased across the year but slow travel decreased (both relative to medium/fast travel). Odds ratios indicated that for each 100 days of the year, Risso's dolphins were 1.67 times more likely to mill than medium/fast travel. As time progressed within a day, dolphins were less likely to either mill or rest/slow travel than medium/fast travel. The time of day odds ratios showed that for each hour (60 min) after sunrise, dolphins were 0.93 times as likely to mill and 0.89 times as likely to rest/slow travel (both relative to medium/fast travel). Risso's dolphins milled more (by a factor of 1.39) and rest/slow traveled less (by a factor of 0.84) with each 10 km increase in distance from shore. The best group size predictors were: (1) calf presence, (2) other cetacean presence, and (3) Julian day, all appearing in all top models. Predicted group size was higher with calf presence vs. absence (25 vs 15 dolphins), and also when another cetacean species was present vs. absent (26 vs 15 dolphins). As Julian day increased from February to late-November, predicted group size increased linearly (on a log scale) from approximately 12 to 23 dolphins (including calves). The best predictors of group cohesion were: (1) time of day, (2) Julian day, and (3) to a lesser extent depth. All 10 models contained time of day and Julian day as important predictors of cohesion. A relatively high importance value for depth (0.88) explained variability in cohesion among models. Like common and bottlenose dolphins, Risso's dolphin group cohesion increased (dolphins were closer together) with time of day (6.5 BL in early morning to 2.1 BL in late afternoon) and decreased across the year (2.4 BL in February to 6.0 BL in November). Cohesion also decreased with deeper bottom depth: from 2.3 BL over 100-m bottom depth compared to 5.7 BL over 2000 m depth.

4.5.5 Bottlenose Dolphin

The best predictors for bottlenose behavioral state were (1) depth, (2) slope aspect, (3) Julian day, and (4) time of day (Table 4-4 and 4-6). All top 10 models had 3–5 explanatory variables; simpler models did not perform as well. Rest/slow travel increased with deeper water depths (by a factor of 1.3 for every 100 m increase in depth). Mill behavior increased across the year (by a factor of nearly 3 for every 100 Julian days). Mill progressively increased ($p<0.05$) as slope aspect changed from southeast to west-northwest. Dolphins were 100 times more likely to mill over west-northwest-facing vs. southeast-facing slope aspects. In addition, the odds of slow travel increased progressively as slope aspect changed from approximately south-southeast to northwest by a maximum factor of 12. Bottlenose dolphin group size was significantly ($p<0.05$) higher with calf presence vs. absence by a factor of 2.3 (mean=38.9 vs 17.1, respectively; importance value 1.0). No explanatory variables appeared in any of the 10 regression models for group cohesion. However, in the best model, the three most frequently occurring variables were distance to shore, time of day, and Julian day, and all three had relatively high importance values. Cohesion was closer in afternoon compared to morning (mean=2.9 vs. 4.9 BL, respectively). Dolphin groups were significantly ($p<0.05$) less cohesive as Julian day progressed, from a mean of 2.2 BL in February to 5.8 BL in October. Dolphins were also significantly ($p<0.05$) more likely to swim close together near shore vs. offshore, though this effect was small (3.3 BL within 300 m of shore vs 3.0 BL near 8 km from shore).

4.5.6 Common Dolphin spp.

The best predictors for common dolphin behavioral state were (1) subregion and (2) water season (importance values 0.91 and 1.0, respectively) (Table 4-4 and 4-7). Rest/slow travel was 4.1 times more likely to occur in waters west of San Clemente Island ($p<0.05$). The odds of milling was 1.9 times greater in the warm versus cold season ($p<0.05$). The best group size predictors were (1) calf presence, (2) slope aspect, and (3) to lesser extent Julian day (importance values 1.0, 1.0 and 0.92, respectively). Mean size of groups with calf presence had over twice as many individuals (n=485) as groups without a calf ($p<0.05$) (Table 4-4 and 4-7). Group size was also highest for north-facing slopes and lowest for south-facing slope aspects ($p<0.05$). Group size decreased significantly ($p<0.05$) across the calendar year from a mean of 245 to 170 individuals. The best group cohesion predictors were (1) calf presence and (2) time of day (importance values 1.0). Cohesion decreased significantly ($p<0.05$) with calf presence from a mean of 3.4 to 5.1 BL. Cohesion also significantly ($p<0.05$) increased across the day from a mean of 4.8 BL in early morning to 2.8 BL near dusk.

4.6 Discussion

The biological meaning of significant behavioral patterns may be linked to species-specific foraging strategies, and reproductive, calving and migratory periods. Some observed behavioral patterns were also hypothesized to be influenced by relative predation risk, though the latter factor cannot be easily ascertained and lacks consistent enumeration in available literature (e.g., Weller 2009).

4.6.1 Group Size: Calf Presence and Reproductive Timing

Mean group size of fin whales, Risso's dolphins, bottlenose dolphins, and common dolphins was larger with calf presence, consistent with the hypothesis that groups with a calf are larger than groups without a calf. Samples sizes of groups with a calf were too small ($n<5$) to conduct meaningful analyses for blue and gray whales. Among the four analyzed cetacean species, calving and mating periods experience some degree of overlap based on available data. Observed larger group size with calf presence likely resulted from a combination of proximate overlapping mating and calving periods, and behavioral responses and ultimate adaptations to reduce calf predation risk. Behavioral ecology theory predicts that in habitats characterized by high predation pressure and clumped food resources, females should form groups which reduce predation risk on young and attract males to females during the mating season (Krause and Ruxton 2002; Beauchamp 2014). These factors are believed to favor larger group sizes. Larger group size presumably decreases predation risk to calves through dilution in numbers, group defense, predator confusion, etc., as summarized in various reviews for multiple species and taxa (e.g., Crook and Gartlan 1966; Fertl 1994a,b; Würsig et al. 1997; Acevedo-Gutierrez 2009).

Larger mean group size found for groups with a calf is also likely due to the close physical association and reliance of young calves on their mothers for nursing, protection, and assisted locomotion (Aguilar 2009). Among mysticetes, females with a calf do not form groups, unlike among most odontocetes (Jefferson et al. 2015). Thus, the mean group size of 3.2 for fin whale groups with a calf indicates that mother-calf pairs tended to be accompanied by at least one other non-calf whale. An accompanying fin whale may be a courting male waiting for a mating opportunity, as a small percentage of female fin whales with a calf experience estrus (Aguilar 2009; Mizroch et al. 2009). This behavior appears to be an alternative mating strategy among male humpback whales (Smultea 1991, 1994; Craig et al. 2002).

Among Risso’s dolphins, calf presence was the only variable explaining differences in group size, resulting in nearly doubling of group size with calf presence. Similarly, in the Azores, an isolated oceanic island ecosystem, Risso’s dolphin groups with calves were significantly larger than groups without a calf (Hartman et al. 2014). Again, this pattern appears to be related to at least two factors: decreased predation risk and possibly male attraction to estrus females. The latter premise is based on reported partial overlap of peak parturition and mating periods of Risso’s dolphins (Baird 2009). Bottlenose dolphin group size also doubled when calves were present. The same pattern is commonly reported for bottlenose dolphins elsewhere (Weller 1991; Bearzi et al. 1997; Vermeulen et al. 2015), including in Santa Monica Bay in the SCB (Bearzi 2005). Associated benefits of larger group sizes likely provide increased protection for young dolphins through increased vigilance (e.g., Shane et al. 1986; Fertl 1994a,b; Mann et al. 2000). Bottlenose dolphins and Risso’s dolphins may also form segregated nursery groups as reported elsewhere (e.g., Lusseau and Newman 2004; Gowans et al. 2008; Gibson and Mann 2008; Hartman et al. 2014). Group size of segregated female bottlenose dolphins with calves appears to vary with predation risk, availability of food resources, and social/mating pressure from males (Connor et al. 2000; Gibson and Mann 2008). Risso’s dolphins with calves segregate in nearshore waters while other non-calf groups prefer more offshore waters in the Azores, possibly due to shared ecological and social constraints associated with calf care (Hartman et al. 2008, 2014). Dusky dolphin females with calves off New Zealand likewise form variably sized nursery groups typically though not consistently separate from other age and sex classes (Weir et al. 2010).

Similar to Risso’s and bottlenose dolphins, common dolphin groups with a calf were over 2.5 times larger than groups without calves. Common dolphin group size also decreased across the year from about 245 individuals in winter to about 170 dolphins during fall. This pattern fits the biological trend that peak calving and mating occur in winter and early spring in the SCB, when males would be expected to join females in estrus. However, in apparent contrast to typical segregation of mothers with calves as reported for some Risso’s and bottlenose populations, common dolphin mother-calf pairs form subgroups within a larger encompassing group during the peak calving and mating seasons (Chivers et al. 2015), likely to derive group benefits discussed previously.

4.6.2 Group Cohesion: Calf Presence and Reproductive Timing

Consistent with my second hypothesis, group cohesion was closer during the calving and mating seasons for the four species with sample sizes adequate for regression analyses: fin whales, Risso's dolphins, bottlenose dolphins and common dolphins. This hypothesis was based on the premise that newborn calves remain close to their mothers during early development when they are highly dependent on their mother for survival (Norris and Dohl 1980). Cohesion was closest during Julian days coinciding with the reported peak calving and mating seasons for Risso's dolphin and bottlenose dolphin. As described above for group size, increased group cohesion during these overlapping reproductive periods may be related to males joining and closely following females in estrus during the mating season. In addition, calves swim closer to their mothers during the early development months as evidenced among other cetaceans including dusky dolphin populations off Kaikoura (Weir et al. 2010) and common bottlenose dolphins in Monkey Mia, Australia (e.g., Connor et al. 2000).

Cohesion among Risso's dolphin groups was most strongly influenced by time of day and Julian day, increasing across the day (i.e., animals closer together) but decreasing with Julian day across the calendar year. Group cohesion among Risso's dolphins also decreased with water depth. Decreased cohesion between individuals across the day and with deeper water is consistent with patterns summarized for nocturnal foraging Hawaiian spinner and Kaikoura dusky dolphin populations (Cipriano 1992; Norris et al. 1994; Würsig and Pearson 2014). During late morning through early afternoon rest periods, these spinner and dusky dolphin populations form small tight groups. However, near dawn and several hours after nocturnal offshore foraging, and again several hours before dusk, individuals of both species spread out in larger groups; near dusk, the small tight groups actively coalesce to form larger looser groups, an apparent coordinated staging before moving offshore to feed in a large aggregation (Norris et al. 1994; Würsig et al. 1997). Similarly, Risso's dolphins formed tighter groups from late morning through mid-afternoon, with looser group formations occurring later in the day when they would be expected to move offshore to forage on solitary spread-out cephalopod prey. As no observations occurred in the few hours after dawn, cohesion at that time and near dusk were unknown. However, no significant changes in group size occurred across the day, unlike reported among the aforementioned Kaikoura dusky and Hawaiian spinner dolphin populations. Differences may be related to the Risso's dolphin's approximately 200% larger body size (Jefferson et al. 2015), potentially associated with lower risk of predation. SCB Risso's dolphins also appear to be behaviorally more aggressive interspecifically and possibly intraspecifically, the latter based on opportunistic and incidental reports of their agonistic behaviors towards both smaller and larger cetaceans, including larger killer whales (Dahlheim et al. 2008), sperm whales (Smultea et al. 2014), and pilot whales (Shane 1995) within the SCB.

Similar to Risso's dolphin, Julian day significantly influenced cohesion within bottlenose dolphin groups: groups were less cohesive as the year progressed, i.e., after the reported peak calving and mating periods. Again, this pattern is hypothesized to result from tighter group spacing during the reported peak calving and mating season occurring earlier in the year during spring-summer (Urian et al. 1996; Thayer et al. 2003; Danil et al. 2010). At these times, close proximity may be needed by males to determine whether a female is in estrus and to determine sexual readiness, perhaps via taste imparted to waters (Caldwell and Caldwell 1967; Norris and Dohl 1980; Muraco 2015). Another factor likely contributing to tighter group spacing earlier vs. later in the year is that younger cetacean calves are more tightly bonded to their mothers as measured by physical spacing; this average spacing gradually increases with increasing calf age (e.g., Taber and Thomas 1982; Gibson and Mann 2008; Cartwright and Sullivan 2009). Calves consistently swim closer to their mother than other group members do to each other (Norris and Dohl 1980).

The potential biological meaning of the observed increase in group cohesion with time of day among common dolphin groups with calf presence is unclear. Groups of common dolphins with calf presence typically included multiple calves in what appeared to be segregated mother-calf subgroups, consistent with Chivers et al. (2015). Increased cohesion across the day among common dolphins may indicate increased socializing near dusk or possibly coalescing to move to other areas to feed on the Deep Scattering Layer (DSL), as documented for Hawaiian spinner dolphins and Kaikoura dusky dolphin populations (see Risso's dolphin above; e.g., Norris et al. 1994; Würsig et al. 1997; Würsig and Pearson 2014). Huddling behavior and close cohesion is commonly associated with socializing delphinids (e.g., Norris and Dohl 1980; Norris et al. 1994; Würsig and Würsig 2010).

4.6.3 Diurnal Activity Patterns of Nocturnal Foragers

Diurnal behavioral patterns of Risso's dolphins and common dolphins were generally consistent with my third hypothesis that rest/slow travel by these two reported nighttime-foraging species peaks during midday, while faster travel peaks in the morning and late afternoon. For both species, rest/slow travel was more common during morning through midday, while faster travel was more common in early morning or late afternoon. This is consistent with studies indicating that increasing hunger is linked to increased locomotion (e.g., speed and turning angles) and increased inter-individual distances (Wieser et al. 1988). Similarly, Henderson (2010) found that common dolphins in the SCB increased their speed of travel across the day, with a morning peak in slow travel with occasional foraging. From combined visual and acoustic behavioral data, Henderson (2010) concluded that common dolphins fed predominantly at night, presumably on the DSL. The combined studies indicate that common dolphin and Risso's dolphin behavioral patterns reflect those of other delphinids that feed at night on the DSL, most notably the Hawaiian spinner dolphin (Norris et al. 1994; Benoit-Bird and Au 2003) and Kaikoura dusky dolphin populations (Benoit-Bird et al. 2004; Vaughn et al. 2007; Würsig et al. 2007, 2010). During early morning, the latter two species return from offshore nocturnal foraging on DSL prey in deeper waters to shallow, more protected coastal waters. Here, they transition over several hours from initially elevated activity state levels to rest mode. As the afternoon progresses, the dolphins transition back over several hours into higher-level activity. This includes increasing group sizes and coalescing into a large group before heading offshore again to feed in deep waters. However, I did not find that group size changed by time of day for Risso's and common dolphins.

I made no observations of Risso's and common dolphin behavior near dawn and dusk to confirm a parallel pattern to Hawaiian spinner and Kaikoura dusky dolphins (effort typically did not occur within 2-3 h of sunrise or sunset to avoid low-light conditions limiting observer visibility). I hypothesize that had I collected data during early morning, I would have similarly seen increasing levels of rest/slow travel since I found this behavior peaked at midday. During early morning (6:00-9:00), Henderson (2010) found that common dolphin behavior in the SCB was similar to mid-morning, with slow travel at its peak. These observations are consistent with the aforementioned Hawaiian spinner and Kaikoura dusky dolphin populations. Furthermore, combined studies indicate that fastest movement occurs near dusk, culminating in offshore foraging expeditions, given shared similarities in habitats and nighttime DSL foraging strategies with other delphinids. Increasing speed of movement across the day for Risso's dolphins is consistent with their apparent crepuscular and nocturnal foraging habits in the SCB (Henderson 2010; Soldevilla et al. 2011; G. Schorr, unpubl. data). The increased activity levels in late afternoon that I found for common and Risso's dolphins is consistent with the social facilitation hypothesis described by Markowitz et al. (2004) for Kaikoura dusky dolphins. In the latter situation, and among Hawaiian spinner dolphins, leaping and faster moving behavior are believed to cue individuals and small groups to coalesce into a large loose aggregation and move offshore again to feed at night, in a safer formation of higher diluted numbers (Norris and Dohl 1980; Norris et al. 1994; Heithaus and Dill 2009; Würsig 2009).

The observed peak in resting during morning and midday for common and Risso's dolphins is presumably important energetically. Rest allows individuals to restore high energy expended during apparent crepuscular and nocturnal feeding on DSL prey. Notably, changes in group size or heading were rarely observed during rest/slow travel among 51 focal group sessions on SCB Risso's dolphin lasting up to 1 h (mean duration 21.6 min, Standard Deviation [SD]=12.9 min; Smultea and Bacon 2012).

Henderson (2010) found that common dolphins off north San Clemente Island moved inshore (east) in the mornings and offshore (west) in late afternoon. Smultea and Bacon (2012) using data from my study found that common dolphin heading was related to bottom depth: as depth increased, dolphins were more likely to be headed northeast than northwest, southeast, or southwest (SW). Further analyses of my data may indicate diurnal trends in heading, but I did not examine this relationship herein.

4.7 Conclusion

Calf presence, time of day, and Julian day were important factors influencing group size, group cohesion, and behavioral state among fin whales, Risso's dolphins, bottlenose dolphins and common dolphins in the SCB study area. Calf presence was the most consistent variable explaining increased group size. Decreased group cohesion was correlated with temporal factors coinciding with the peak calving and/or mating seasons for all three delphinid species and the fin whale. Risso's and common dolphin behavioral activity levels and states fluctuated predictably across the day, with rest peaking near midday and higher activity behaviors peaking during early morning and late afternoon, closer to nocturnal foraging periods. These diurnal behavioral patterns were similar to patterns described in studies of both species in the SCB and other nocturnally foraging delphinids. Mid-afternoon thus appears to be an important rest period for both Risso's and common dolphins in the SCB. An unexpected result was that slope aspect consistently influenced only the gray whale and is hypothesized to serve as a migration cue.

Findings demonstrate that behavior and group characteristics were influenced by factors that may be useful for potential spatiotemporal management relative to anthropogenic activities and sensitive biological periods documented among the four SCB cetacean species. Mating, calving and/or foraging/feeding activities of fin whales and Risso's, bottlenose and common dolphins in the SCB overlap areas used for military training exercises across the year in the SCB (DoN 2008a,b). The few behavioral response studies that have been conducted on Risso's dolphins suggest sensitivity to anthropogenic disturbance by tourism vessels. For example, midday resting behavior by Risso's dolphins was disrupted with increased whalewatching activity as observed from shore in the Azores (Visser et al. 2011). Common dolphins may also respond to mid-frequency active sonar in the SCB, though the naturally high variability in their behavior requires a large sample size to differentiate natural and anthropogenic effects (Henderson et al. 2014b). Although long-term population and health impacts of anthropogenic disturbance are uncertain, chronic and cumulative long-term disturbance can lead to impacts of concern. These include displacement and disruption of behaviors important for survival, potentially resulting in decreased animal energy reserves and increased stress levels (NRC 2005; Southall et al. 2007; Ellison et al. 2012).

Important biological periods for cetaceans with respect to results of this study in the SCB include (1) summer-fall peak feeding and early winter socializing periods for fin whales, (2) reported winter/spring calving and mating periods for Risso's, bottlenose, and common dolphins, and (3) morning/midday resting periods exhibited by Risso's and common dolphins. Spatio-temporal management measures have not been previously implemented in the SCB for cetaceans. Results of this systematic study conducted over a five-year period from 2008-2012 and focused on the relatively fine management scale of the SCB identify temporal windows that may be more important than others in terms of biological function and sensitivity. Information on such temporal windows may assist in species-specific adaptive management and monitoring of cetaceans in the SCB and elsewhere. Future work could consider integration of this information across species to identify overlapping periods of temporal biological sensitivity relative to overlapping temporal and spatial windows of anthropogenic activity. Further research on potential geographical and species variation in biologically sensitive periods merits further investigation in other areas where anthropogenic activities are of concern to cetaceans.

CHAPTER V

SUMMARY

5.1 Summary of Findings

Cetaceans exhibited inter- and intra-specific differences in habitat selection, group size, group cohesion, and behavioral state based on sighting data collected during aerial surveys conducted in the SCB during 2008-2013. This behavioral ecology perspective contributes to an integrated database facilitating a science-based approach to adaptive management of anthropogenic activities in the SCB.

5.1.1 Chapter II: Spatial Factors

This study focused on systematically mapping and predicting cetacean habitat use relative to behavior and the spatial distribution and availability of resources. This approach was possible through the use of newly developed survey software and application of statistical RSF analysis to the marine environment, allowing accuracy in a manner not previously attempted at the relatively small scale of the SCB study area. Animal distribution and behavior reflect responses to the availability and distribution of resources needed for survival relative to predation risk (Elith and Leathwick 2009; Beauchamp 2014). Spatial distribution of resources is important to understand for basic and applied species management, as it reveals how animals are distributed in space relative to those resources. RSFs were used to relate habitat choice to functional behavioral states that are important for species survival and reproduction. RSF modeling assumed equal access by animals to the study area and compared probability of habitat use based on the ratio of eight environmental explanatory variables (Table 2-2) at sighting locations relative to availability of those variables at randomly selected points in the study area. The resulting probability of habitat parameter use relative to parameter availability was plotted on a map of the study area to identify high-probability habitat by geographical reference. Final models based on data collected during 15 aerial surveys in 2008-2012 indicated that fin whales, gray whales, Risso's dolphins, and bottlenose dolphins selected specific habitat parameters and locations at significantly ($p<0.05$) higher probability relative to availability in the study area as summarized in Table 5-1. Larger sample sizes may show a significant trend for gray whales in known offshore migration corridors as a form of shelter from predation, consistent with the Ford and Reeves (2008) model for this species.

Although it was beyond the scope of this study, a systematic approach to analyzing the spatial overlap of species would contribute to adaptive management of the SCB region. Software such as “Marxan” were useful for implementation of a multi-species and multi-use ecosystem approach in the Azores (Schmiing et al. 2015). Separation of “fisheries related” scenarios and “biodiversity” scenarios was key to the success of this approach. Lessons have been learned from the use of collaborative decision support software in implementation of the California Marine Life Protection Act (Cravens 2016). The SCB region and cetaceans were not included in previous initiatives under this policy (Fox et al. 2013). Although Naval training exercises may be under public scrutiny, many other natural and anthropogenic changes in the region should be considered in the scientific interpretation of the meaning of data generated by ongoing monitoring efforts.

5.1.2 Chapter III: Focal Species

The two largest whale species in the SCB (blue, fin) are also listed as endangered. This raises the question of whether they might serve as “umbrella species”, whose protection might also benefit the smaller species in the region. However, it is important to know to what extent their social behavior differs from the smaller species. This study focused on group size and cohesion.

I developed and tested a model (the Smultea model) expanding and combining socioecological models developed for ungulates and cetaceans inhabiting open environments. This Smultea model predicted that in open semi-pelagic and pelagic waters, as cetacean species body size increases, overall mean group size decreases, groups become less cohesive (i.e. individuals are spaced farther apart), and individuals are more likely to occur alone. The Smultea model drew from socioecological models predicting relationships between body size, group size, home range, and/or resource predictability and availability for ungulates inhabiting open African savannah (Jarman 1974), and delphinids (Gowans et al. 2008) and mysticetes (Ford and Reeves 2008) inhabiting semi-pelagic and pelagic waters. These models are based on the premise that in open habitats, food resources are clumped and relatively unpredictable in space and time, and predation risk is high. In response to these ecological pressures, smaller species should form larger groups to reduce predation risk through the benefits of dilution, enhanced predator detection, and increased predator confusion, etc. (Beauchamp 2014).

My Smultea model built on the aforementioned ungulate, mysticete and delphinid socioecological models by additionally considering the roles of group cohesion and cetacean body size in semi-pelagic and pelagic environments. Study results from data collected during 18 aerial surveys in

2008-2013 supported Smultea model predictions, when mysticetes were considered separately from odontocetes. Species body size was inversely related to group size and group cohesion, and positively related to frequency of lone animals among the three examined mysticetes and three delphinid odontocete groups, respectively. Blue whales (largest body size) were most frequently found alone ($p<0.05$), while gray whales had significantly ($p<0.05$) larger mean group size, were less likely to occur alone, and were more cohesive than blue and fin whale groups. The same pattern was found among delphinids; the largest-sized Risso's dolphin and the slightly smaller-sized bottlenose dolphin occurred in significantly ($p<0.05$) smaller and less cohesive groups than the smaller-sized common dolphin spp. (Table 1.2).

Smultea model and results were consistent with hypotheses proposed originally by Jarman (1974) for ungulates and by Ford and Reeves (2008) for mysticetes that species with larger body sizes have smaller group sizes and are more likely to occur alone. The open environment leads to species-specific ecological trade-offs through various combinations of group size, cohesions, body size, and prey specialization/foraging strategy. For example, larger-sized prey (e.g., blue and fin whales) are more costly to predators because they require higher predator energy expenditure and risk of injury to successfully pursue and kill, and they sink quickly (i.e. less time to consume the body near the surface) compared to the smaller and more rotund gray and right whales (Ford and Reeves 2008). The latter factors are hypothesized to reduce the likelihood that large-bodied cetaceans will be attacked by predatory killer whales and perhaps sharks (Ford and Reeves 2008; Weller 2009; Beauchamp 2014). Thus, cetaceans with larger body sizes should be able to survive in smaller group sizes than smaller-sized cetaceans in oceanic waters. My results also agreed with Ford and Reeves' (2008) hypothesis that the robust but shorter-bodied gray whale should occur in larger mean group sizes than blue and fin whales in open waters, and should seek refuge (from predation) close to more structurally complex shorelines. Similarly, Gygax (2002b) tested a model examining the evolution of group size in dolphins and porpoises and found that species was the most influential variable affecting differences in group size. Findings also supported my prediction that smaller-sized cetacean species would swim closer together. This prediction was based on the hypothesis that increased cohesion improves sensory integration, including coordinated defense and food finding and capturing abilities among schooling fish and dolphins (Norris and Schilt 1988). In contrast, larger cetaceans should form smaller groups based on an increased ability to successfully fight off or flee from predators (Ford and Reeves 2008) combined with increased food needs required to sustain a larger body.

Observations of semi-pelagic Risso’s dolphins, coastal and semi-pelagic island-associated bottlenose dolphins, and semi-pelagic/pelagic common dolphin spp. fit the Gowans et al. (2008) model as well as the Smultea model. The Risso’s dolphin and bottlenose dolphin were found in medium-sized groups (>10-100) while common dolphin spp. occurred in large-sized groups (>100). This is consistent with the larger body size of the Risso’s dolphin and bottlenose dolphin compared to the common dolphin spp. (Table 1.2). Group cohesion was also significantly ($p<0.05$) higher for the smaller-sized common dolphins than the Risso’s dolphin and bottlenose dolphin.

Based on study results and other integrated studies (e.g., Falcone and Schorr 2012, 2013, 2014; Calambokidis et al. 2015), waters near San Clemente and Santa Catalina islands and the mainland coast provide important habitat for fin whales. The latter areas overlap areas used for summer-fall feeding/socializing blue whales, as well as migrating gray whales, Risso’s dolphins, bottlenose dolphins and common dolphins. By focusing attention on the fin and blue whales as flagship species popular with the general public, other species may benefit from fin and blue whale directed spatiotemporal management efforts and research.

5.1.3 Chapter IV: Temporal Factors

To the extent that reproductive cycles, prey distribution and predation risk vary over time, I predicted species-specific behavior would change over diel and seasonal cycles. To address these questions, I conducted multiple regression analyses using three response variables (group size, group cohesion, and behavioral state) considering eight environmental and group composition explanatory variables (Table 2-2). Results based on 2008-2012 aerial survey data were consistent with the first prediction that group size was significantly ($p<0.05$) larger with calf presence for the fin whale, Risso’s dolphin, bottlenose dolphin and common dolphin. In all four taxa calving and mating periods show some degree of overlap based on available data, consistent with correlations between mammalian body size and reproductive events (e.g., Gittleman and Thompson 1988). Larger group size with calf presence is hypothesized to reduce calf predation risk (Norris and Dohl 1980; Hartman et al. 2014). This is consistent with behavioral ecology theory that in open habitats, some females form groups to reduce predation risk on newborn young, and males are attracted to females during the mating season (Davies et al. 2012, Ch. 2, 7 and 9). These factors favor overall larger group sizes.

I also tested the prediction that groups are more cohesive (i.e., individuals are closer together on average) during the calving and mating seasons. My results supported this prediction: among fin whales, Risso’s dolphins, and common dolphins, group cohesion was tighter during the expected peak calving and mating seasons. These results were consistent with studies indicating that newborn cetacean calves remain close to their mothers during early development when they are dependent on milk, protection, and assisted locomotion from their mother (Norris and Dohl 1980; Weir et al. 2010). Cohesion was closest during Julian days coinciding with the expected peak calving and mating seasons for the bottlenose dolphin and Risso’s dolphin. The biological meaning of this pattern may be related to males joining and closely following females in estrus during the mating season, and young calves swimming closer to their mothers as described for numerous cetacean ontogeny studies (e.g., Taber and Thomas 1982; Weir et al. 2010; Orbach et al. 2014).

My final temporal prediction was that rest/slow travel should peak during midday while faster travel should peak in the early morning and late afternoon for nighttime foraging odontocetes. Behavioral state regression modeling for the Risso’s and common dolphins were generally consistent with this prediction. For both species, rest/slow travel was more common than faster travel during late morning through midday, while faster travel was more common than rest/slow travel in early morning or late afternoon. This contrasting pattern in activity levels is supported by studies indicating that increasing hunger is linked to greater locomotion (e.g., speed and turning angles) and larger inter-individual distances (Wieser et al. 1988). I also found that group size and cohesion increased across the day for Risso’s dolphins, but only group cohesion increased diurnally for common dolphins. Spatiotemporal behavioral patterns for Risso’s and common dolphins reflected those of other delphinids that feed at night on the DSL, most notably the Hawaiian spinner dolphin and the Kaikoura dusky dolphin populations. During early morning, the latter two species return from offshore nocturnal foraging forays on DSL prey in deeper waters to shallow, more protected coastal waters where they transition over several hours from initially elevated activity state levels to rest mode (Norris et al. 1994; Dahood and Benoit-Bird 2010; Vaughn et al. 2010). As the afternoon progresses, the dolphins transition over several hours into higher-level activity again.

5.2 Conclusion and Implications

From a basic science perspective, this study contributed to testing models based on a conceptual framework of behavioral ecology. Knowledge of cetacean habitat use relative to biologically important behaviors and time periods is a prerequisite to effectively manage and monitor impacts of anthropogenic activities. Study results provide localized information for the period from 2008-2013 that may be useful for spatio-temporal management of cetaceans and human-related activities in the SCB. Study data contribute to meeting adaptive management goals of the Navy’s

MSMP and ICMP by providing spatio-temporal occurrence and behavioral information on cetaceans within the Navy's SOCAL Range Complex (DoN 2009, 2010, 2011). New software systems (Mysticetus™) made it possible to systematically collect data over a 5-year period tailored to the relatively fine scale of the SCB and the Navy's SOCAL Range Complex. Sophisticated statistical analyses (RSF) facilitated mapping of species-specific behaviors relative to habitat selection. High-probability locations associated with important biological activities and periods were predicted for fin whales, gray whales, Risso's dolphins, bottlenose dolphins, and common dolphin spp. The SCB region is of public concern because shipping has injured and killed cetaceans, cetaceans have died and become entangled in fishing gear, and MFA sonar has been shown to behaviorally disturb some cetaceans in the SCB (Melcon et al. 2012; DeRuiter et al. 2013; Goldbogen et al. 2013; Henderson et al. 2014b). MFA sonar has been implicated with cetacean injury and death in regions outside the SCB (Jepson et al. 2003; Cox et al. 2006). Due to plans for continued and increased use as a military training range, the SCB is designated for long-term monitoring of marine mammals, as required under the ESA and Marine Mammal Protection Act (MMPA) (DoN 2008a, 2011, 2015; NMFS 2015).

One of the most effective strategies to minimize and mitigate repetitive anthropogenic effects in marine and terrestrial ecosystems involves spatiotemporal-based management measures (Daly and Harrison 2012; Dolman and Jasny 2015). Synthesis of species-specific habitat and temporal behavioral patterns could be useful for adjustments of human-related activities in the SCB, particularly for endangered fin and blue whales. There are certain periods of the year and day when some cetacean species are in higher numbers or engaged in behaviors considered to be more sensitive to anthropogenic disturbance (e.g., resting, feeding) than others. Important locations and periods relative to study results are summarized in Table 5-2 and illustrated in Fig. 2-1 through 2-4. The future challenge in assessing impacts of anthropogenic activities will be to implement study protocols involving sample sizes and statistical analyses sufficiently sensitive to differentiate anthropogenic versus naturally induced changes in cetacean distribution and behavior, given that results herein clearly indicate that multiple socioecological and environmental variables interact to influence species-specific cetacean habitat use and behavior in the SCB.

Results demonstrate that behavioral data shown to be indices of stress and anthropogenic disturbance, including displacement and interruption of behavioral activity (e.g., nursing, socializing, group cohesion, mother-calf behavior) can be collected systematically and quantitatively from a small circling aircraft covering relatively inaccessible deep water areas of the SCB. This aerial perspective provides a unique "bird's eye" three-dimensional view in a non-intrusive manner when operating outside documented potential aircraft sound-transmission disturbance zones (Richardson et al. 1995). The aerial platform enables behavioral data collection at and below the water surface (in the SCB to approximately 20-30 m depth), facilitating extended observation and video recording periods of intricate details on inter-animal spacing, orientations and physical interactions that are difficult to obtain from the typically lower-vantage points or further distances available from vessel- and shore-based platforms (e.g., Würsig et al. 1984; Lomac MacNair and Smultea 2016; Durban et al. 2015).

5.3 Future Research Recommendations

Baseline results from this five-year study revealed further questions and provided insight into future research useful for science-based adaptive management relative to growing public concern over impacts of anthropogenic activities on cetaceans within the SCB. Results identified spatiotemporally important areas (selected at higher rates of probability than expected) for four of the most commonly seen cetacean species in the SCB, two of which are listed as endangered (blue, fin). Obtaining a larger sample size for the endangered blue whale sufficient to conduct RSF modeling of preferred habitat characteristics, and conducting similar RSF modeling for common dolphins (ideally separating out short- and long-beaked common dolphins) within the study area would fill species research gaps. Collection of genetic photo-identification data from the apparent island ecotype of bottlenose dolphins that may be resident to Santa Catalina and San Clemente Islands would help determine if this population is genetically distinct from other “offshore” ecotypes. For example, recent studies found that the California coastal ecotype is genetically distinct from offshore bottlenose dolphins, but sample sizes were too small to assess differences among offshore ecotypes (Lowther-Thieleking et al. 2015). This information is relevant to evaluating levels of anthropogenic impact (i.e., number of “takes”) for separate species stocks as required by NMFS.

Another area of research that may contribute to a better understanding of cetacean occurrence and habitat use in the SCB and meets Navy MSMP and ICMP strategic goals is determining lengths of times cetaceans remain within the SCB, particularly endangered species and those that occur there year-round. There is currently very little information on whether these animals are the same individuals across hours and days. This information is needed to address strategic management goals identified in the Navy’s MSMP and ICMP (DoN 2010, 2011, 2012) to understand how often and how long individuals may be exposed to Navy sonar and underwater detonations in the SCB. Because this study and others show that most cetacean species are social in the SCB, especially delphinids, a subsample of tagged animals should be followed using non-intrusive platforms capable of collecting detailed social and behavioral data (e.g., social interactions and cohesion, group composition, calf presence), since they have been shown to affect behavior and habitat selection. Examples include using autonomous unmanned vehicles such as remotely operated hexacopters equipped with high-resolution video (Durban et al. 2015), or conducting focal group follows from shore or from small aircraft at distances that do not disturb animals under observation.

There is also a need to determine how prey and dynamic oceanographic factors (e.g., SST, currents) influence relative small-scale use of the SCB by cetacean species. Such information is needed to differentiate naturally occurring changes from potential anthropogenic activities. I am currently working with NMFS-affiliated scientists with Navy funding to re-examine data collected during this study to assess if densities of species with adequate sample sizes (e.g., likely fin whale, common dolphin spp., Risso's dolphin) are influenced by these bottom-up factors. Further, given inter-seasonal, inter-annual and inter-decadal changes in oceanographic conditions off California (e.g., Becker et al. 2010; Campbell et al. 2015), it is important to continue long-term multi-platform monitoring in the SCB to detect potential changes in habitat-use and behavior patterns while also monitoring multiple sources of potential anthropogenic disturbance (e.g., commercial shipping, tourism, fishing, offshore oil and gas development, and military activities).

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APPENDIX A

TABLES AND FIGURES

A.1. Chapter I Introduction

Table 1-1. Ecological gradients of cetacean study species in the Southern California Bight relative to parameters addressed in the Jarman (1974) ungulate, the Ford and Reeves (2008) mysticete whale, and Gowans et al. (2008) delphinid (dolphin) socioecological predictive framework models.

Model parameter	Blue whale[1]	Fin whale[2]	Gray whale[3]	Risso's dolphin[4]	Common bottlenose dolphin[5]	Common dolphin spp.[6]
Habitat	Open pelagic, semi-pelagic slopes	Open pelagic, semi-pelagic slopes	Coastal shallow	Semi-pelagic slopes	Island coasts	Open pelagic, semi-pelagic slopes
Typical reported group size	Small (1-2)	Small (1-2)	Small (2-3)	Medium (15-20)	Medium (15-25)	Large (>100)
Home range size	Large (migratory)	Large (migratory)	Large (migratory)	Medium?	Small?	Medium?
Dominant prey	Krill	Krill, small schooling fishes	N/A (benthic amphipods-SCB feeding unlikely)	Squid, mesopelagic fishes	Opportunistic: medium/small fishes, squid	Squid, small schooling fishes
Prey distribution	Clumped, unpredictable, widely spread	Clumped, unpredictable, widely spread	N/A in SCB	Individual, some clumped, DSL predictable	Individual resident, clumped DSL predictable	Clumped, unpredictable, widely spread, DSL predictable
Temporal Changes in Food	Peak summer-fall	Peak summer-fall	N/A in SCB (opportunistic	Squid spawn shallow waters summer?	Unknown	Schooling fish peak summer-fall; squid

Model parameter	Blue whale[1]	Fin whale[2]	Gray whale[3]	Risso's dolphin[4]	Common bottlenose dolphin[5]	Common dolphin spp.[6]
			?)			spawn shallow water summer?
Diurnal Changes in Food	DSL: closer to surface at night	DSL: closer to surface at night	None known	DSL: closer to surface at night	Unknown	DSL: closer to surface at night
Predation risk	Low	Low	Moderate	Moderate?	High	High
Predation response	Flee individually	Flee individually	Seek refuge, fight, coordinated group defense	Form group	Form group, seek refuge?	Form large group
Breeding/social strategy	Males compete for females?	Males compete for females?	Promiscuous	Promiscuous? Male groups defend areas used by females? Age/sex segregation, some long-term associations	Promiscuous, fission-fusion?, some long-term associations	Promiscuous, fission-fusion, mother-calf subgroups
Mean body length	23.7	21.7	13.5	3.0	2.4	1.9
Predicted relative cohesion	Low	Moderate	High	Moderate	Moderate	High
Predicted group size	Single, small	Small	Small-medium	Medium	Medium	Large

SCB=Southern California Bight; DSL=Deep Scattering Layer

[1] Sears and Perrin 2009; Jefferson et al. 2014a, 2015

[2] Calambokidis et al. 2015

[3] Rice and Wolman 1971; Wolman 1985; Poole 1984; Rugh et al. 2001, 2005

[4] Kruse et al. 1999; Shane 1990; Baird 2009; Bearzi et al. 2010; Hartman et al. 2008. 2015; G. Campbell, Texas A&M University, personal communication

[5] Norris and Prescott 1961; Henderson 2010; Carretta et al. 2015 (newborn calves seen year-round in coastal ecotype, possible peak spring-summer per stranding data)

[6] Evans 1974, 1975, 1994; Heyning and Perrin 1994; Chivers et al. 2015

Table 1-2. Comparison of life history traits of cetacean study species while in the Southern California Bight.

Trait (N hemis.)	Blue whale[1]	Fin whale[2]	Gray whale[3]	Risso's dolphin[4]	Bottlenose dolphin[5]	Common dolphin spp.[6]
Occurrence in SCB	Spring & fall migrant, feed summer-fall	Spring & fall migrant, year-round occurrence	Winter & spring migrant	Seen year round, abundance higher winter	Seen year round near islands	Seen year round, abundance higher summer
Migratory?	yes	yes, some possibly resident	yes	possibly	Island ecotype no; coastal yes	possibly
Habitat association	Slopes with upwelling	Slopes with upwelling	90% migrate <10 km from mainland coast, two offshore migration corridors in Channel Islds	Deep-water (>200m) slopes	Island and mainland coasts; coastal ecotype <1 km from mainland	Deep-water (>200 m) slopes, seamounts
Mating peak	Late fall-winter	Dec-Jan	Late Nov-early Dec	Late fall in NE Pacific	Late fall-winter, year-round?	Winter-early spring
Calving peak	Winter	Dec-Jan	Mid-Dec	Winter in NE Pacific; summer in N Atlantic	Spring-summer?	Winter-early spring
Foraging strategy	Peak feeding crepuscular, forage deeper day vs. night, individual lunge feeding	Forage deeper day vs. night, individual lunge feeding	Feed at/near bottom individually by sucking/filtering sediment	Forage in dispersed group, feed individually?	Forage during day together/feed individually?	Feed mostly at night on DSL, sometimes during day; forage together, coop. prey herding

SCB=Southern California Bight; DSL=Deep Scattering Layer

[1] Sears and Perrin 2009 (reverse sexual dimorphism; length is average for males and females northern hemisphere)

[2] Clapham et al. 1997; Mizroch et al. 2009 (reverse sexual dimorphism; length is average for males and females northern hemisphere)

[3] Rice and Wolman 1971; Wolman 1985

[4] Kruse 1989; Kruse et al. 1999; Pereira 2008; Baird 2009; Bearzi et al. 2010; Henderson 2010; Chen et al. 2011; Hartman et al. 2014

[5] Norris and Prescott 1961; Carretta et al. 2015 (newborn calves seen year-round in coastal ecotype with possible peak in spring-summer based on stranding data)

[6] Heyning and Perrin 1994; Henderson 2010; Henderson et al. 2012, 2014a,b; Chivers et al. 2015

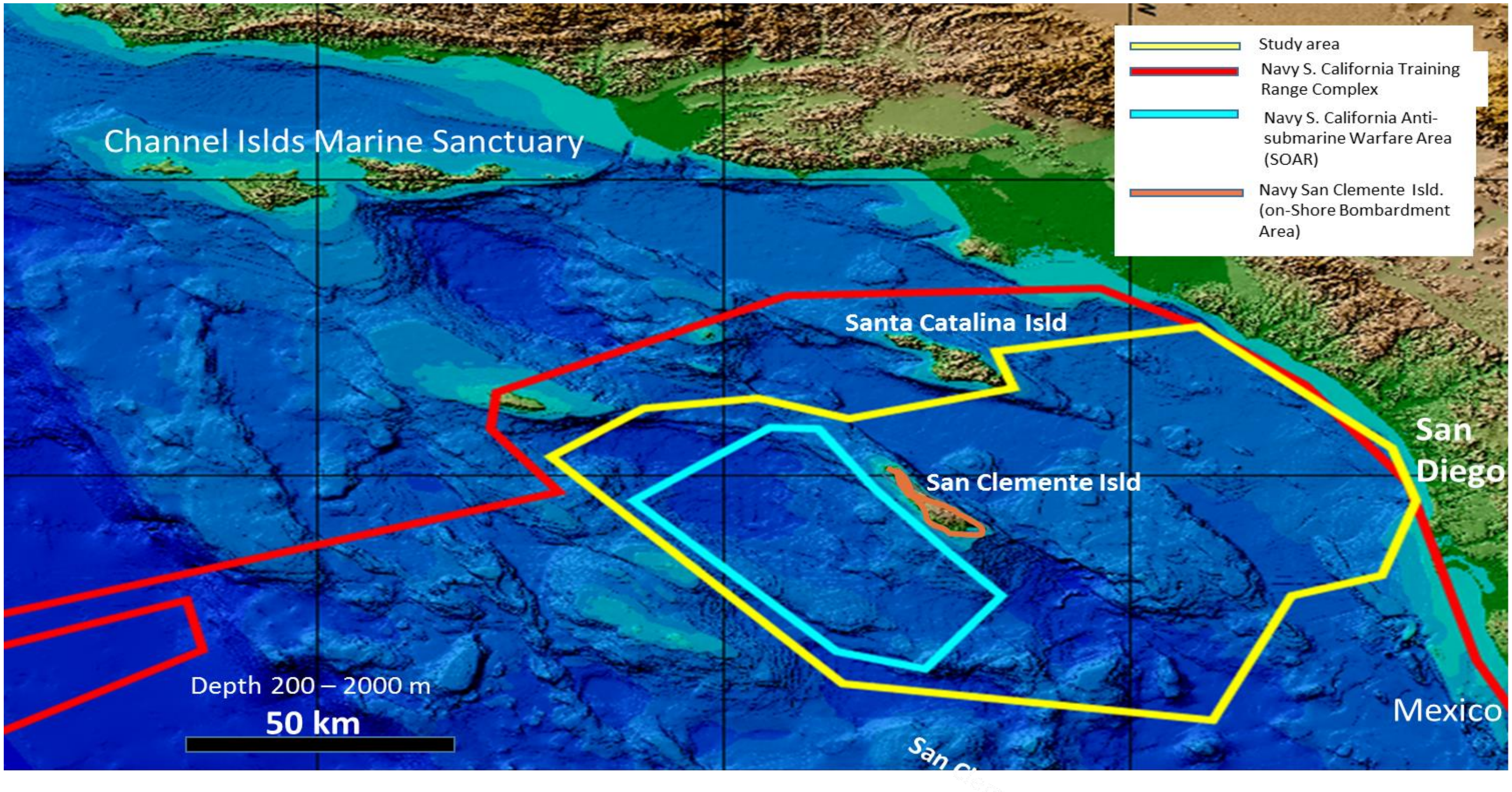


Fig. 1-1. The Southern California Bight (SCB) study area and U.S. Navy training areas (DoN 2008b).

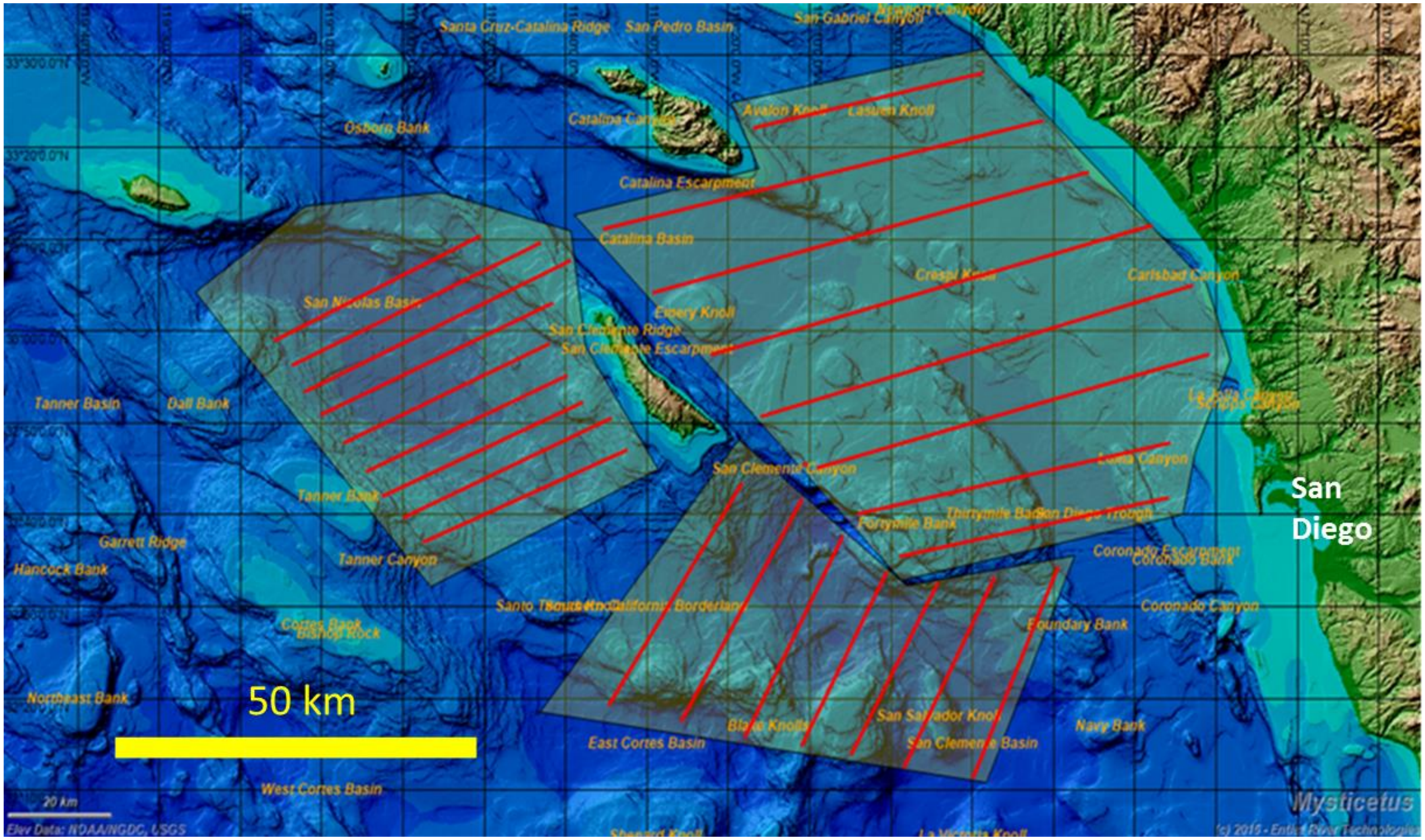


Fig. 1-2. **The aerial survey study area delineated by shaded polygons, systematic survey lines (in red), and underwater bathymetric and geographical references and locations mentioned in this dissertation.**

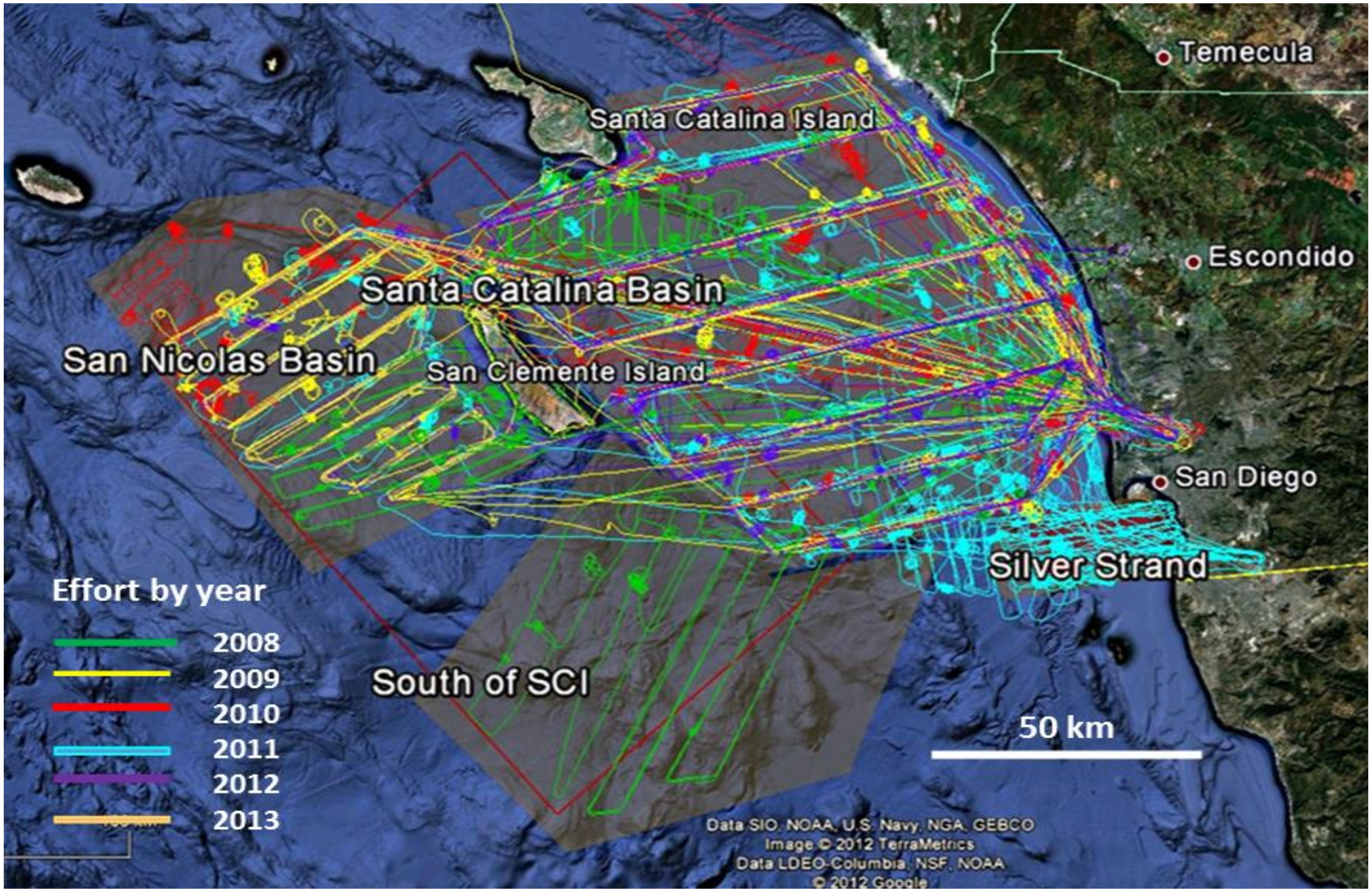


Fig. 1-3. All 2008-2013 aerial survey effort conducted in the Southern California Bight study area.

A.2. Chapter II Modeling Cetacean Habitat Using Behavior

Table 2-1. Ethogram defining behavioral states used during the study based on the activity of at least 50% of the group (Smultea 1991, 1994; Smultea and Bacon 2012).

Behavioral State	Definition
Mill	≥50% of group swimming with no obvious consistent orientation (non-directional) characterized by asynchronous headings, circling, changes in speed, and no surface activity. Includes socializing (animals touching/within 0.5 body lengths of one another) and probable foraging involving apparent searching for/chasing of prey[a].
Rest/slow travel	≥50% of group exhibiting little or no forward movement (<1 km hr^{-1}) remaining at the surface in the same location or drifting/traveling slowly with no wake; includes rest at surface
Medium/fast travel	≥50% of group swimming with an obvious consistent orientation (directional) and estimated speed ≥1 km hr^{-1} creating a wake or white water

[a] Heithaus and Dill (2009)

Table 2-2. Variables used in statistical analyses.

Variable	Type	Description	Type of Data
Response Variables			
Behavioral state	Category	Behavioral state: mill, rest/slow travel, medium/fast travel (See Table 2-1 ethogram)	Field data, including video
Group size	Count	Best estimate of group size	Field data, including photographs & video
Group cohesion	Scale	Maximum inter-individual distance between neighbors within a group based on estimated adult body lengths	Field data, including video
Explanatory Variables			**Type of Data**
Aspect	Continuous	Degrees magnetic to which the underwater slope faces; transformed via cosine and sine functions for analysis	Mysticetus*
Calf	Binomial category	At least one calf absent (0) or present (1), where calf=an animal closely accompanying another adults and ≤1/2 its body length	Field data, including photographs & video
Cos_asp, Sin_asp	Derived	Aspect transformed into cosine and sine	WEST, Inc., biostatisticians calculated
Season	Category	Cold-water (November-April) or warm-water season (May-October) (cold=0, warm=1) (after Carretta et al. 2000)	Derived from field data
Shore distance	Continuous	Closest distance to shore from sighting location in kilometers	Mysticetus™*
Slope	Continuous	Degrees of an underwater slope calculated as the maximum, three-dimensional rise over the run	Mysticetus™*

Table 2-2 Continued

Variable	Type	Description	Type of Data
Subregion	Binomial category	Study Area subregion relative to direction from San Clemente Island (E =east=0, W=west=1). E consisted of the San Nicolas Basin east of San Clemente Island; W included the Santa Catalina Basin, Silver Strand, and the subregion South of San Clemente Island (the latter two subregions were combined with Santa Catalina Basin because they were rarely sampled) (Figure1-2)	Derived from field data using Mysticetus™*
Time of day	Continuous	Time in minutes since sunrise in San Diego, CA	Derived from field data
Time of year	Scale	Julian day number (1=January 1, each year)	Derived from field data
Water depth	Continuous	Seafloor (bottom) bathymetric water depth in meters, positive-valued	Mysticetus™*

*Mysticetus™ Geographic Information Systems (GIS) used the following databases to determine the values of these variables for sighting locations: Depth, Slope, Aspect, Distance from Shore - NOAA National Geophysical Data Center - Digital Elevation Models (DEM):
Locations near-shore: San Diego, CA, Tsunami Inundation project, 1/3 arc-second DEM http://www.ngdc.noaa.gov/dem/squareCellGrid/download/3543
Locations outside the 1/3 arc-second DEM: U.S. Coastal Relief Model, Southern California (region 6), 3 arc-second DEM
http://www.ngdc.noaa.gov/mgg/coastal/grddas06/grddas06.htm

Table 2-3. RSF model variables used to predict the relative probability of selection for four cetacean species by behavioral state in the Southern California Bight. Positive effect indicates variables are positively related to selection, negative effect indicates variables are negatively related to selection.[1]

Species	Behavioral state	No. groups	Variable	Effect	p-value (*italics*= ≤0.05)
Fin whale	All	59	Latitude	–	*0.0413*
			Longitude	+	0.0517
			Depth	+	*0.0053*
			Shore Distance	+	*0.0359*
	Rest/slow travel	22	Shore Distance	–	0.3970
	Medium/fast travel	36	Longitude	+	*0.0276*
			Depth	+	*0.0017*
Gray whale	All	40	Longitude	+	*0.0074*
	Rest/slow travel (pooled with 1 mill behavior)	19	Longitude	+	0.0639
			Aspect North	–	0.0958
	Medium/fast* travel	21	Longitude	+	0.1630
			Shore distance	–	0.1480
Risso's dolphin	All	134	Latitude	-	*0.0190*
			Longitude	+	*0.001*
			Shore distance	-	*0.0006*
	Mill	14	Longitude	+	0.2370
	Rest/slow travel	63	Longitude	+	*0.0149*
			Shore distance	-	*0.0084*
			Depth	+	0.0803
	Med/fast travel	56	Latitude	-	*0.0192*
			Longitude	+	*0.0259*
			Shore distance	-	*0.0378*
Bottlenose dolphin	All	31	Depth	-	0.1298
			Latitude	+	0.0579
			Depth	-	*0.0003*
			Shore distance	-	*0.0201*
	Rest/slow travel (pooled with 1 mill behavior)	12	Latitude	-	*0.0378*
	Med/fast travel	19	Longitude	-	*0.0302*
			Depth	-	*0.0003*
			Shore distance	-	*0.0419*

Table 2-4. Three highest-ranked models among 127 models fitted to estimate Resource Selection Function of four cetacean species in the Southern California Bight.

Species	Behavioral State	Rank	Model[1/]	AIC[2/]	ΔAIC[3/]
Fin whale	All	1	Lat + Long + Depth + Dist	868.41	0
		2	Lat + Long + Depth + Aspect E + Dist	870.08	1.67
		3	Lat + Long + Depth+ Aspect N + Dist	870.22	0.15
	Rest/Slow Travel	1	Dist	371.86	0.00
		2	Lat	372.01	0.15
		3	Lat + Dist	372.12	0.11
	Medium/Fast Travel	1	Long + Depth	563.23	0.00
		2	Lat + Long + Depth	564.28	1.04
		3	Lat + Long + Depth + Dist	564.41	0.13
Gray whale	All	1	Long	618.34	0.00
		2	Long + Dist	618.42	0.08
		3	Lat + Long + Dist	619.39	0.98
	Rest/Slow Travel	1	Long + Aspect N	321.20	0.00
		2	Long	322.29	1.08
		3	Lat + Long + Aspect N	322.82	0.54
	Medium/Fast Travel	1	Long + Dist	354.81	0.00
		2	Dist	354.86	0.05
		3	Long	355.02	0.15
Risso’s dolphin	All	1	Lat + Long + Dist	1725.67	0.00
		2	Lat + Long + Slope + Dist	1727.45	1.78
		3	Lat + Long + Aspect N + Dist	1727.57	0.12
	Mill	1	Long	249.72	0.00
		2	Aspect E	249.78	0.06
		3	Depth	250.60	0.82
	Rest/slow travel	1	Long + Depth + Dist	917.54	0.00
		2	Lat + Long + Depth + Dist	918.61	1.07
		3	Long + Dist	918.74	0.13
	Medium/fast travel	1	Lat + Long + Depth + Dist	803.56	0.00
		2	Lat + Long + Dist	803.80	0.24
		3	Lat + Long + Depth + Aspect N + Dist	804.14	0.34

Table 2-4 Continued

Species	**Behavioral State**	**Rank**	**Model**[1/]	**AIC**[2/]	**ΔAIC**[3/]
Bottlenose dolphin	All	1	Long + Depth + Dist	454.64	0.00
		2	Long + Depth + Aspect N + Dist	456.30	1.66
		3	Depth + Dist	456.31	0.01
	Rest/slow travel	1	Lat	207.51	0.00
		2	Dist	207.83	0.32
		3	Depth	208.12	0.29
	Medium/fast travel	1	Long + Depth + Dist	289.83	0.00
		2	Lat + Long + Depth + Dist	290.31	0.48
		3	Long + Depth + Slope + Dist	291.26	0.95

[1] Long=longitude, Lat=latitude, Dist=closest distance from shore including islands, Aspect N=Aspect north, Aspect E=aspect east. See Table 2-2 for definitions of variables.

[2] AIC=Akaike's Information Criteria

[3] ΔAIC=difference in consecutive AIC scores

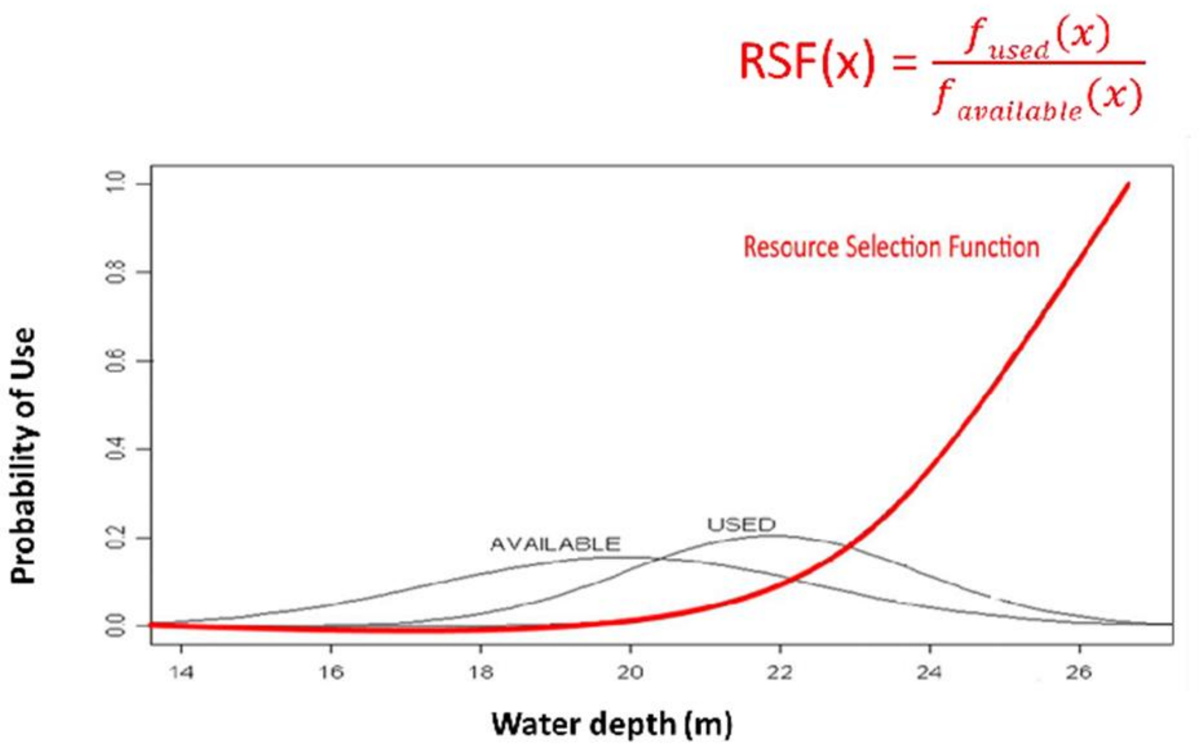


Fig. 2-1. Example graphic of a Resource Selection Function and associated equation (modified from Manly et al., 2010).

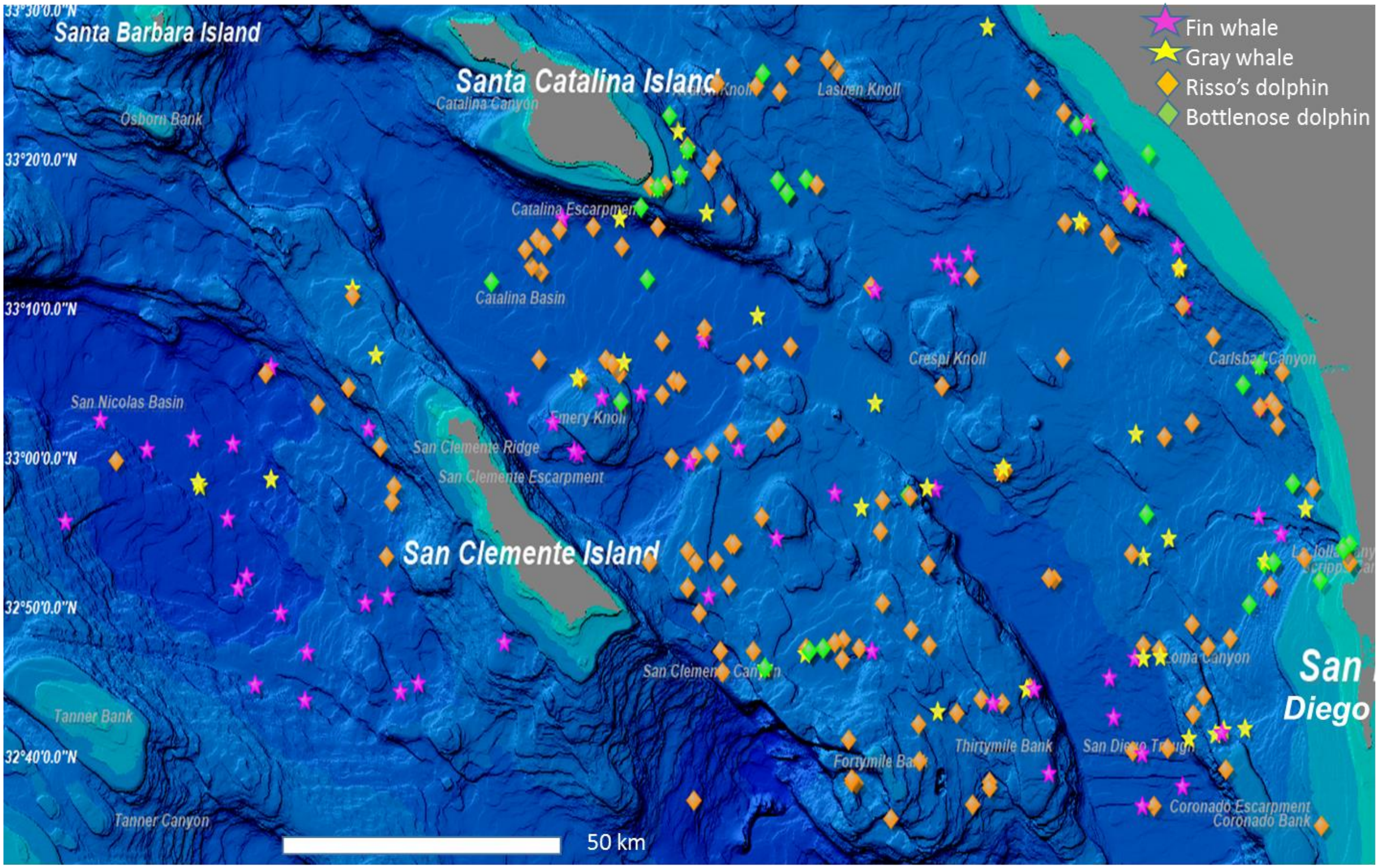
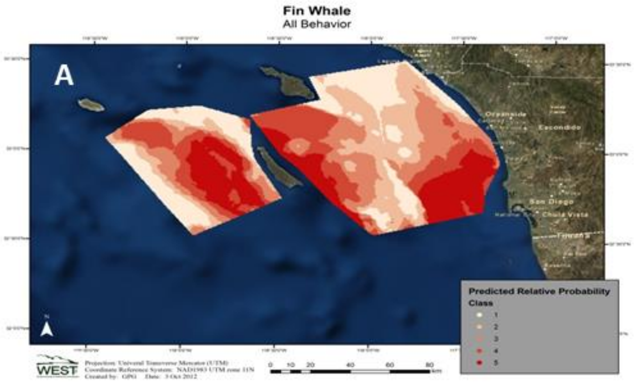
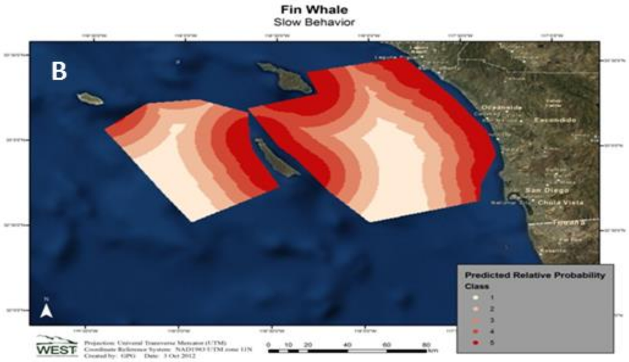


Fig. 2-2. Cetacean sightings made during systematic and connector aerial survey effort used for Resource Selection Function analyses in the Southern California Bight study area 2008-2012.





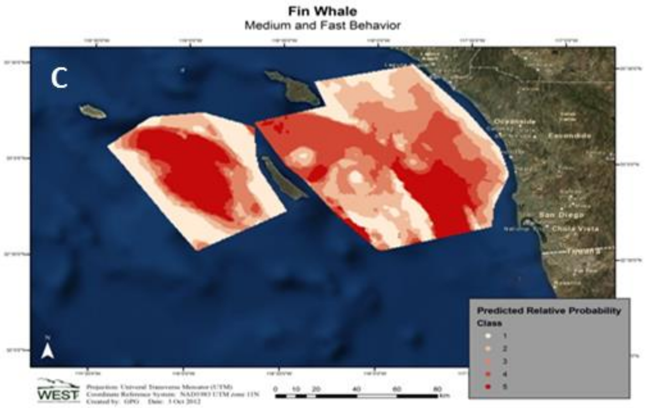


Fig. 2-3. Predicted relative probability of habitat selection for fin whale by behavioral states: A) all behavior, B) rest/slow travel, and C) medium/fast travel. Areas with highest probability of selection are represented by red; areas with lowest probability of selection are represented by white.

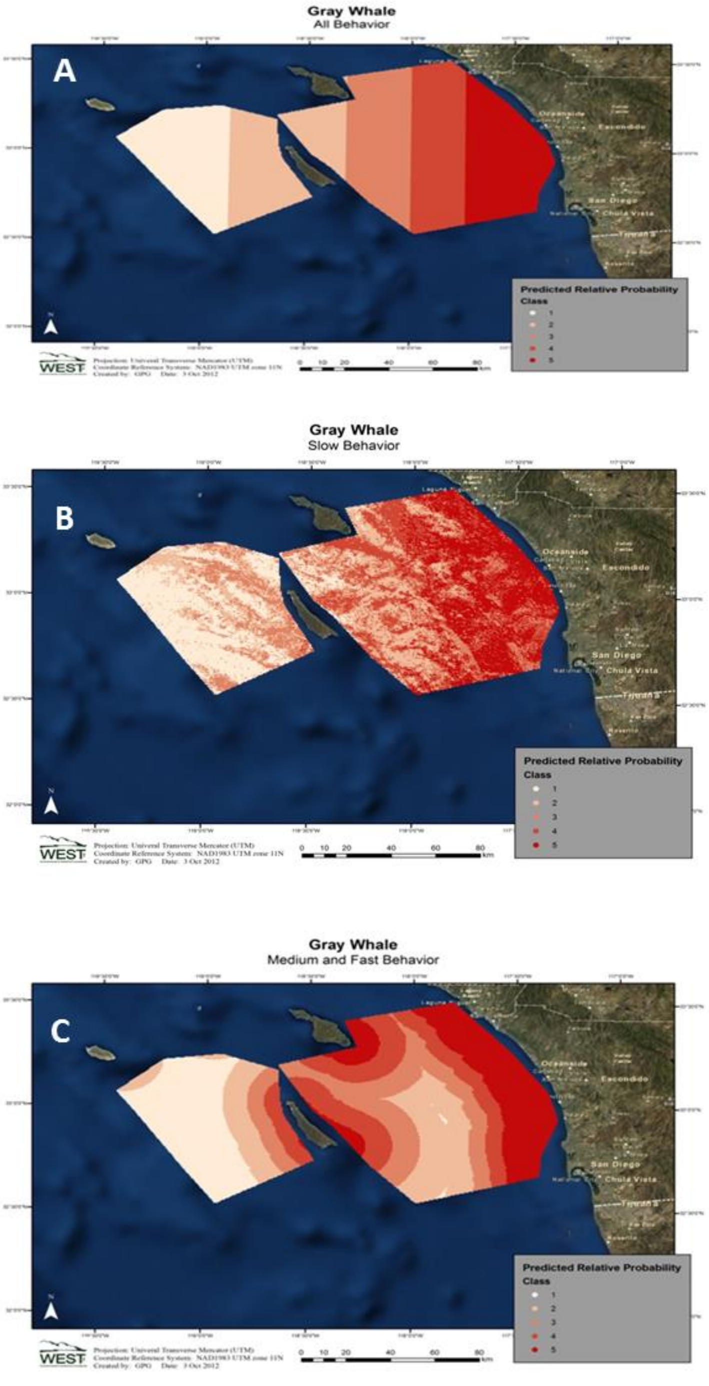


Fig. 2-4. Predicted relative probability of habitat selection for gray whale by behavioral states: A) all behavior, B) rest/slow travel, and C) medium/fast travel. Areas with highest probability of selection are represented by red; areas with lowest probability of selection are represented by white

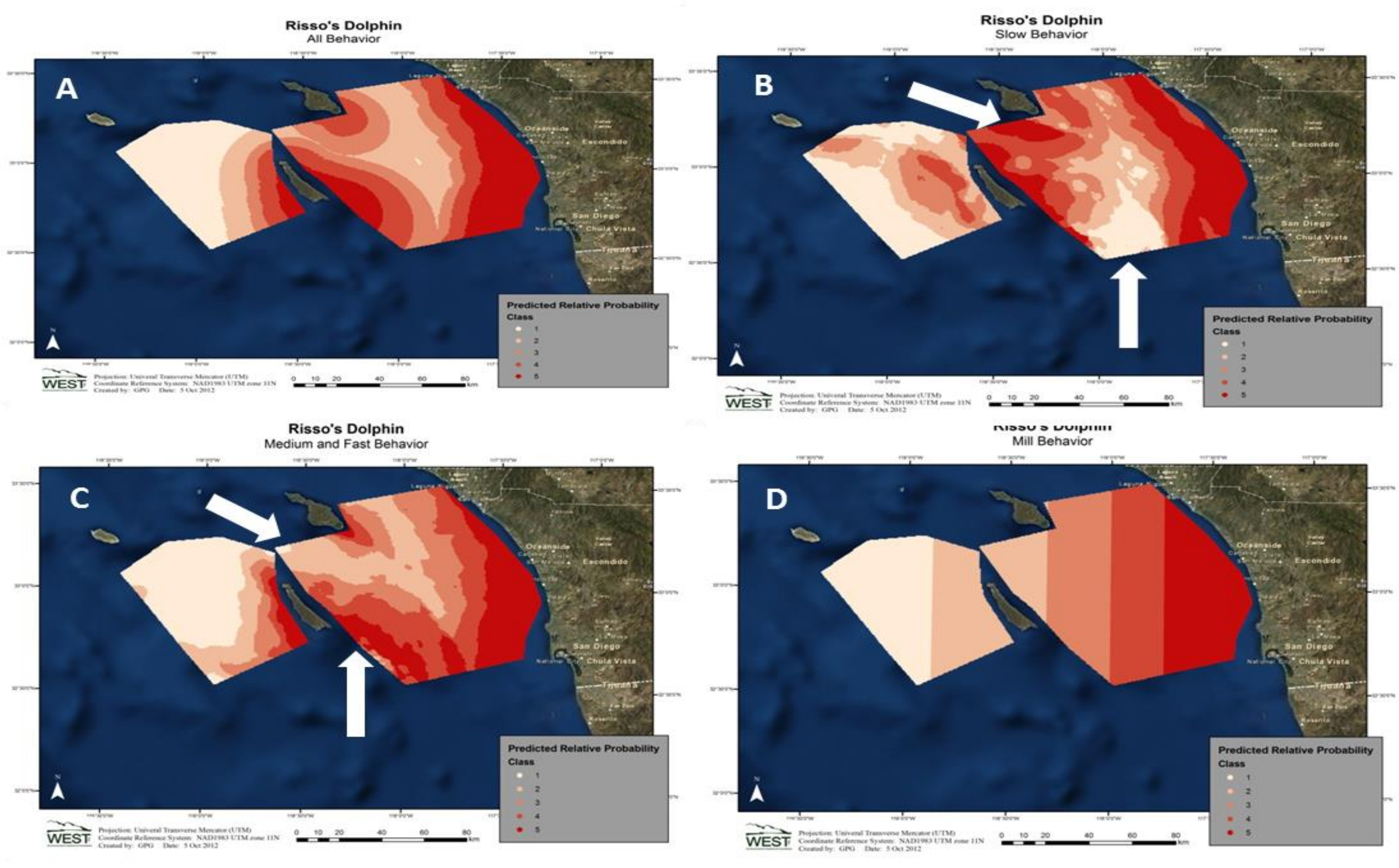


Fig. 2-5. Predicted relative probability of selection for Risso's dolphin by behavioral states: A) all behavior, B) rest/slow travel, C) medium/fast travel, and D) mill. Areas with highest probability of selection are represented by red; areas with lowest probability of selection are represented by white. Arrows highlight spatial differences between rest/slow travel and medium/fast travel.

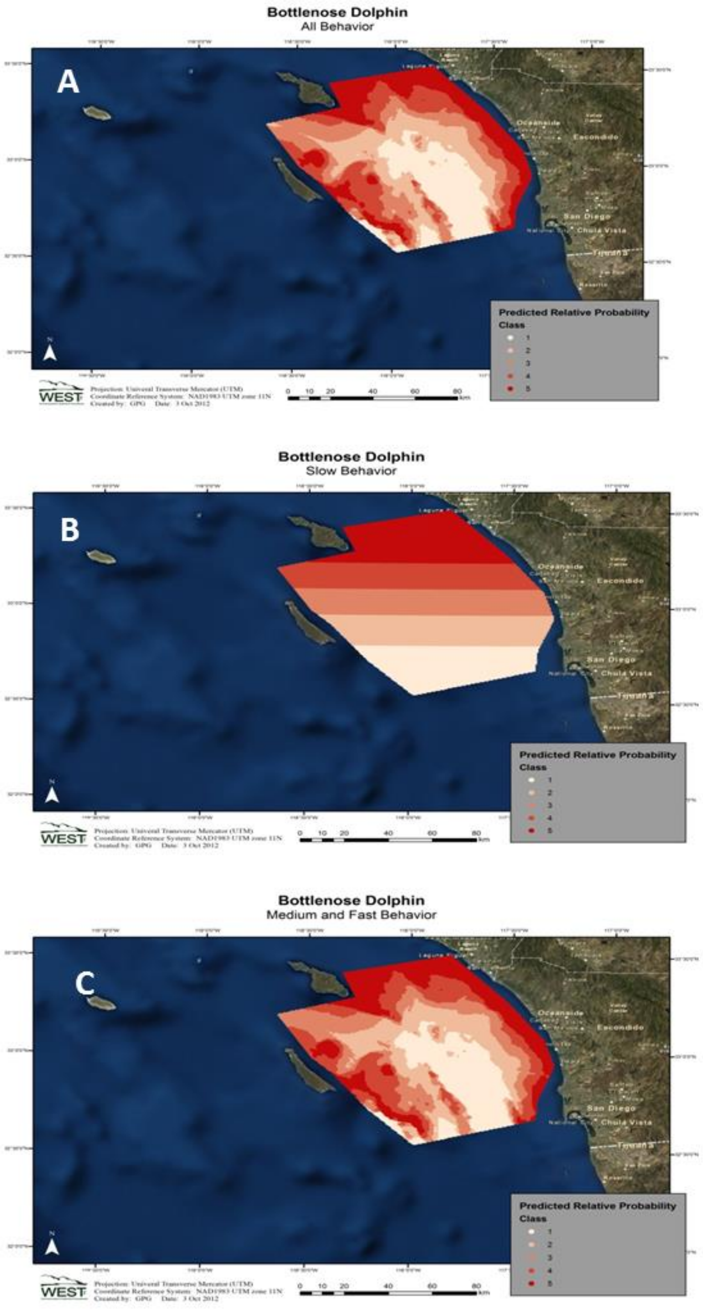


Fig. 2-6. Predicted relative probability of habitat selection for the bottlenose dolphin by behavioral states: A) all behavior, B) rest/slow travel, and C) medium/fast travel. Areas with highest probability of selection are represented by red; areas with lowest probability of selection are represented by white.

A.3. Chapter III Cetacean Body Size, Group Size, and Group Cohesion

Table 3-1. Summary statistics for observed group sizes of mysticete and odontocete species in the Southern California Bight 2008-2012. These data include those sightings where only one individual animal was observed.

Species	n	$\bar{x}$	SE	SD	Range
Mysticete					
Blue whale	66	1.6	0.14	1.1	1-6
Fin whale	130	1.7	0.08	0.9	1-7
Gray whale	68	2.1	0.17	1.4	1-9
Odontocete					
Risso’s dolphin	320	16.6	0.91	16.3	1-120
Bottlenose dolphin	107	18.3	2.10	21.7	1-150
Common dolphin sp.	362	254.9	21.47	408.5	1-2500

Table 3-2. Summary statistics for observed group cohesion, measured in maximum body lengths, for mysticete and odontocete species in the Southern California Bight 2008-2012. These data only include those sightings where group sizes were ≥2 animals.

Species	n	$\bar{x}$	SE	SD	Range
Mysticete					
Blue whale	24	12.0	2.62	12.8	0.1-40
Fin whale	62	4.9	0.82	6.4	0.5-20
Gray whale	40	1.7	0.52	3.3	0.1-20
Odontocete					
Risso’s dolphin	294	7.7	0.74	12.8	0.1-100
Bottlenose dolphin	97	5.2	0.81	9.9	0.5-55
Common dolphin sp.	359	5.32	0.28	5.3	0.5-50

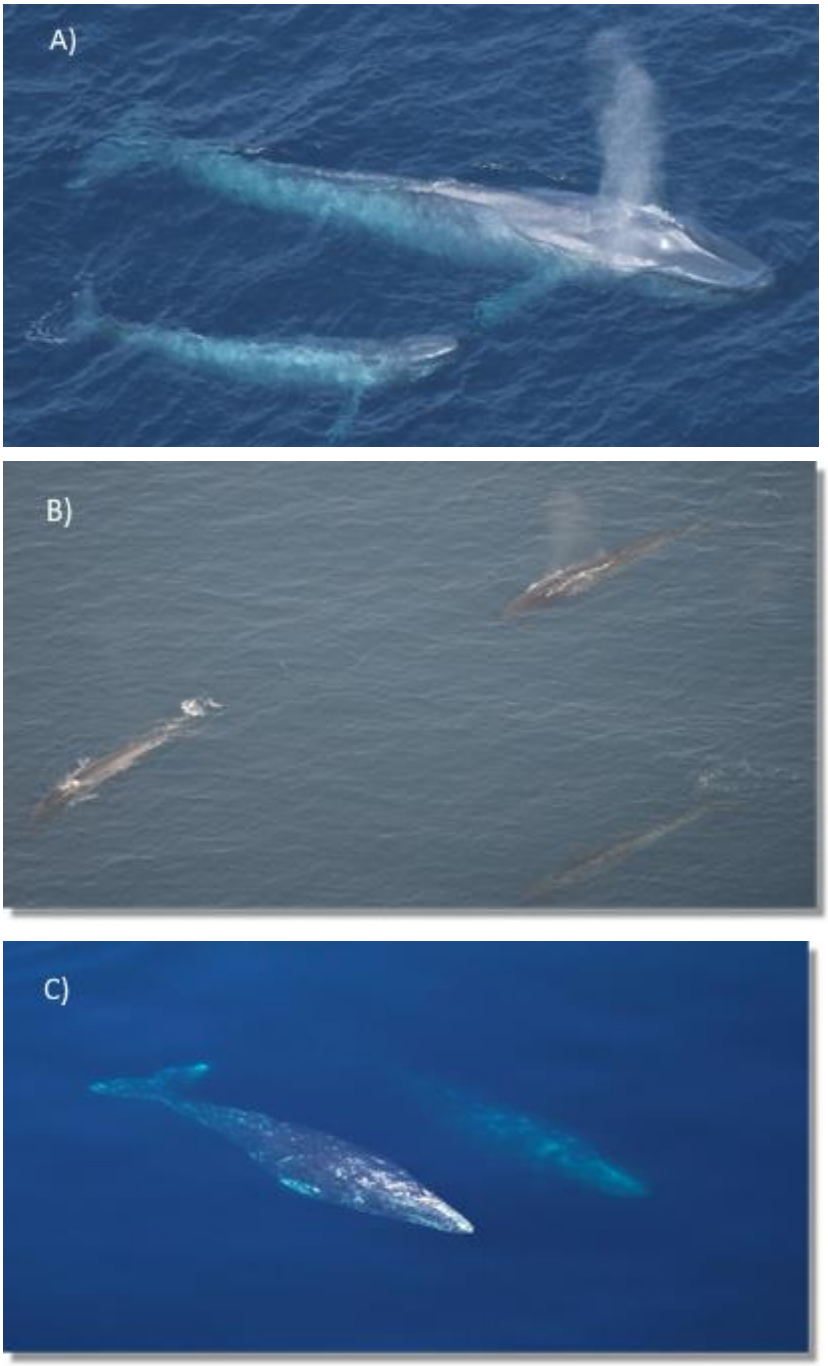


Fig. 3-1. Photographs of A) a mother and calf blue whale, B) three fin whales, and C) two gray whales showing variation in group cohesion based on maximum distance between nearest neighbors estimated in adult species body length. Photographs taken by D. Steckler, B. Würsig, and B. Würsig, respectively, under NMFS permit 14451.

Fig. 3-2. Photographs of A) Risso's dolphins, B) bottlenose dolphins, and C) common dolphins showing variation in group cohesion based on maximum distance between nearest neighbors estimated in adult species body length. Photographs taken by L. Mazzuca, A. Henry (NMFS/NOAA website), and B. Würsig, respectively, under NMFS permit 14451.

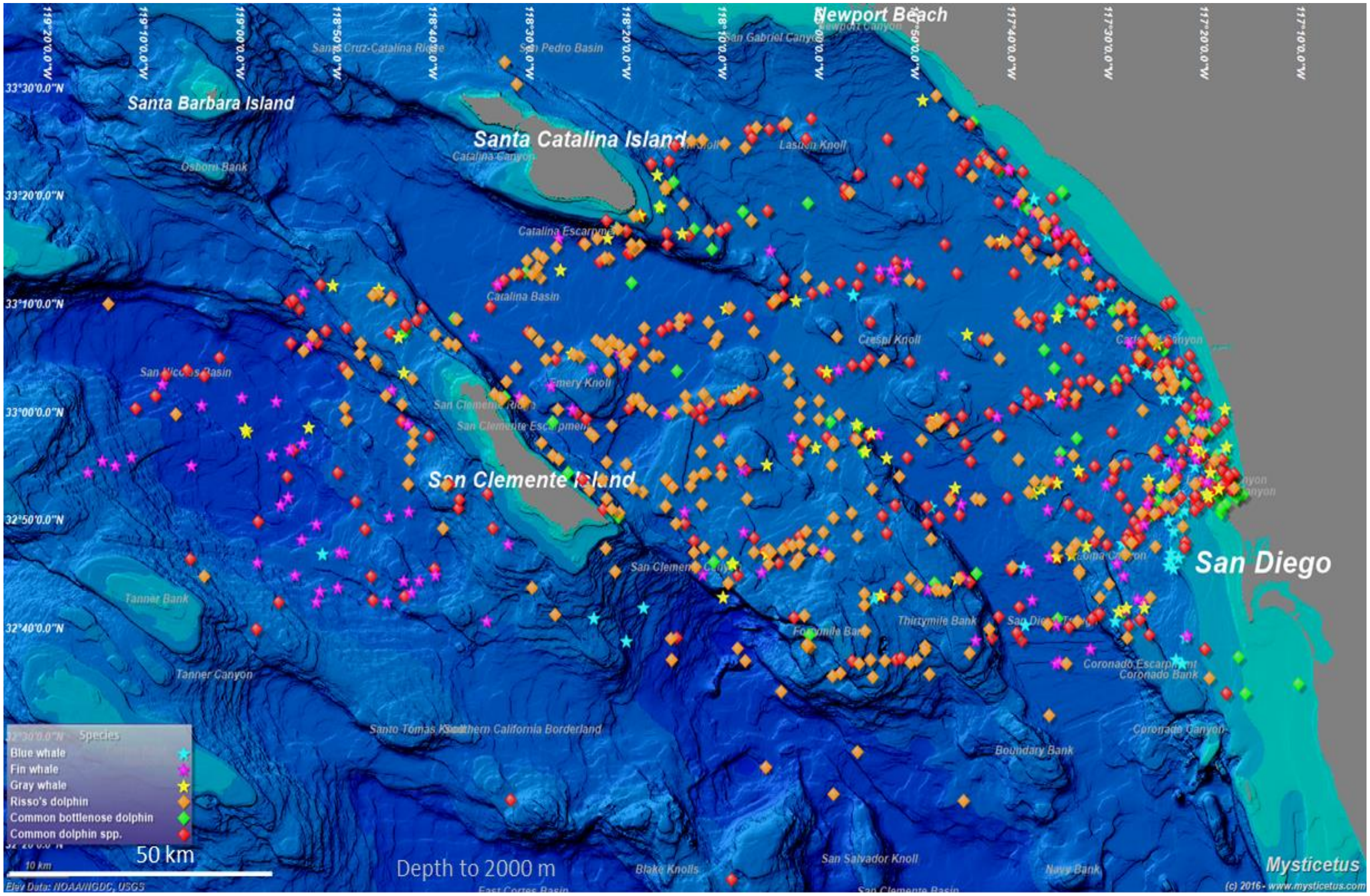


Fig. 3-3. All cetacean sightings made during the 2008-2013 aerial surveys in the Southern California Bight study area.

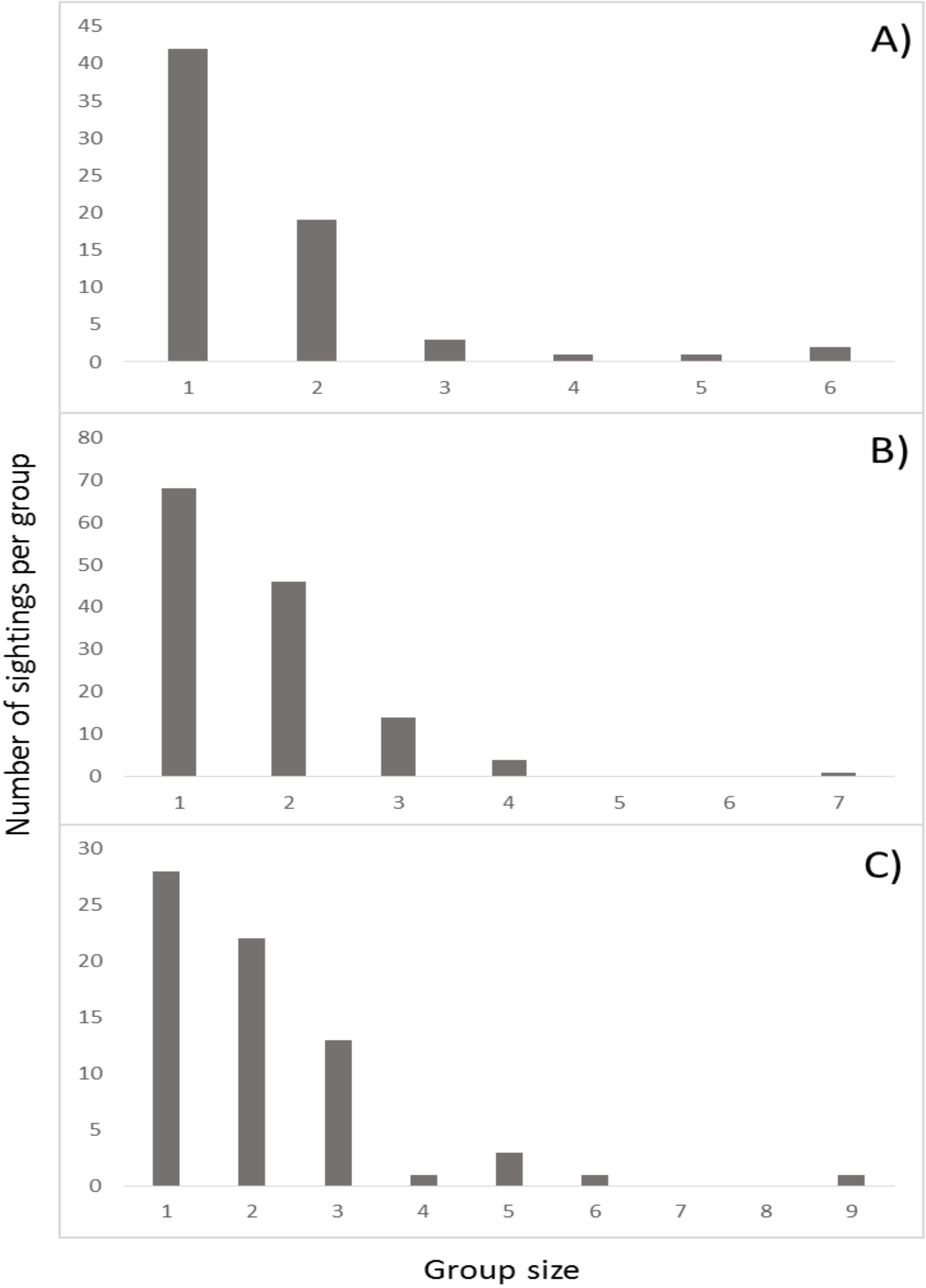


Fig. 3-4. Distribution frequency by group size of A) blue whale, B) fin whale, and C) gray whale based on aerial survey data in the Southern California Bight 2008-2013.

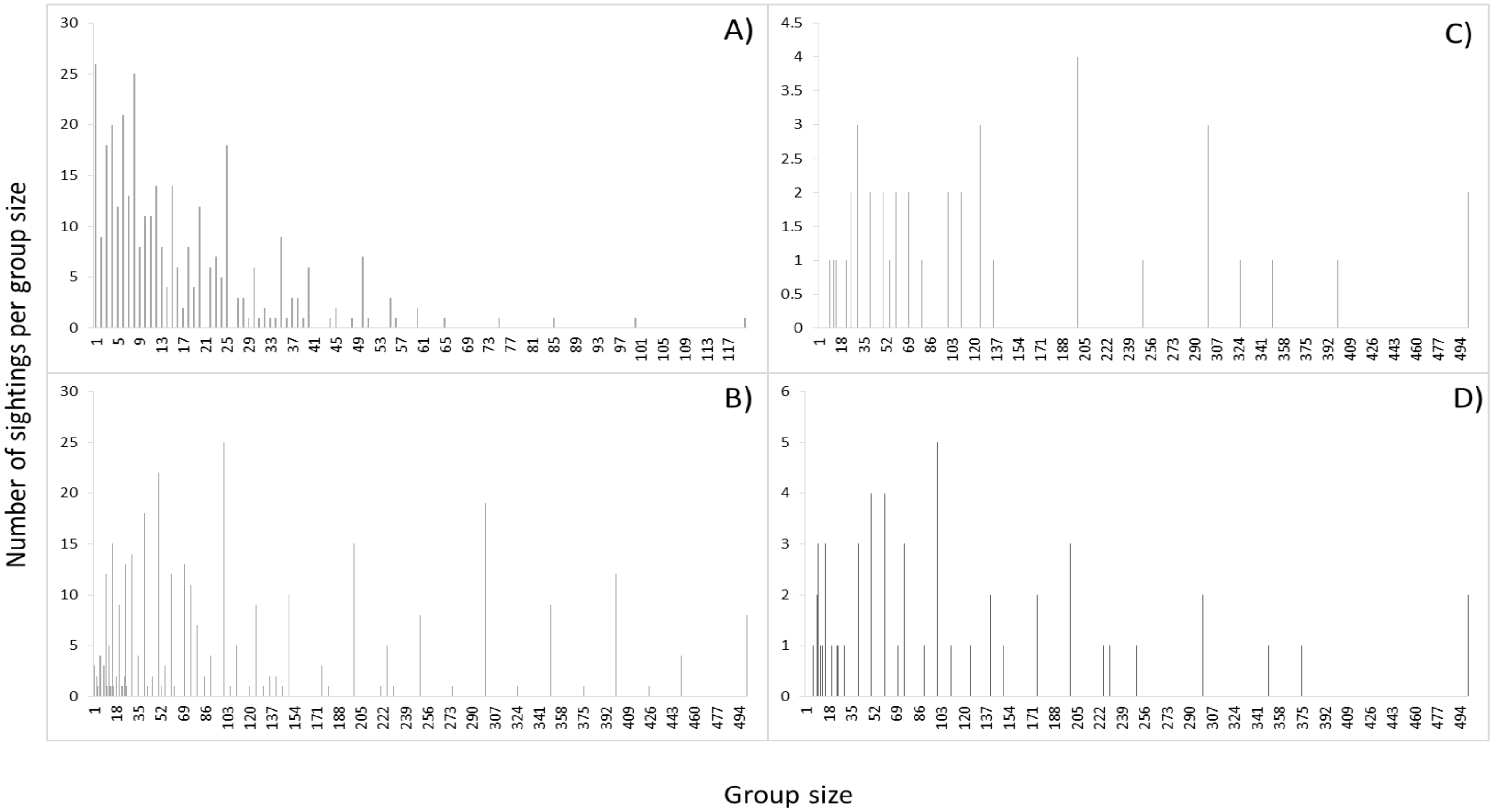


Fig. 3-5. Distribution frequency by group size of A) Risso's dolphin, B) common dolphin spp., C) long-beaked common dolphin, and D) short-beaked common dolphin based on aerial survey data in the Southern California Bight 2008-2013. For all common dolphin spp. and long-beaked common dolphin, group sizes of up to 2500 animals were occasionally seen, while group sizes of short-beaked common dolphins up to 2300 animals were ccasionally seen; the x-axes for these dolphin species have been shortened for display scale purposes

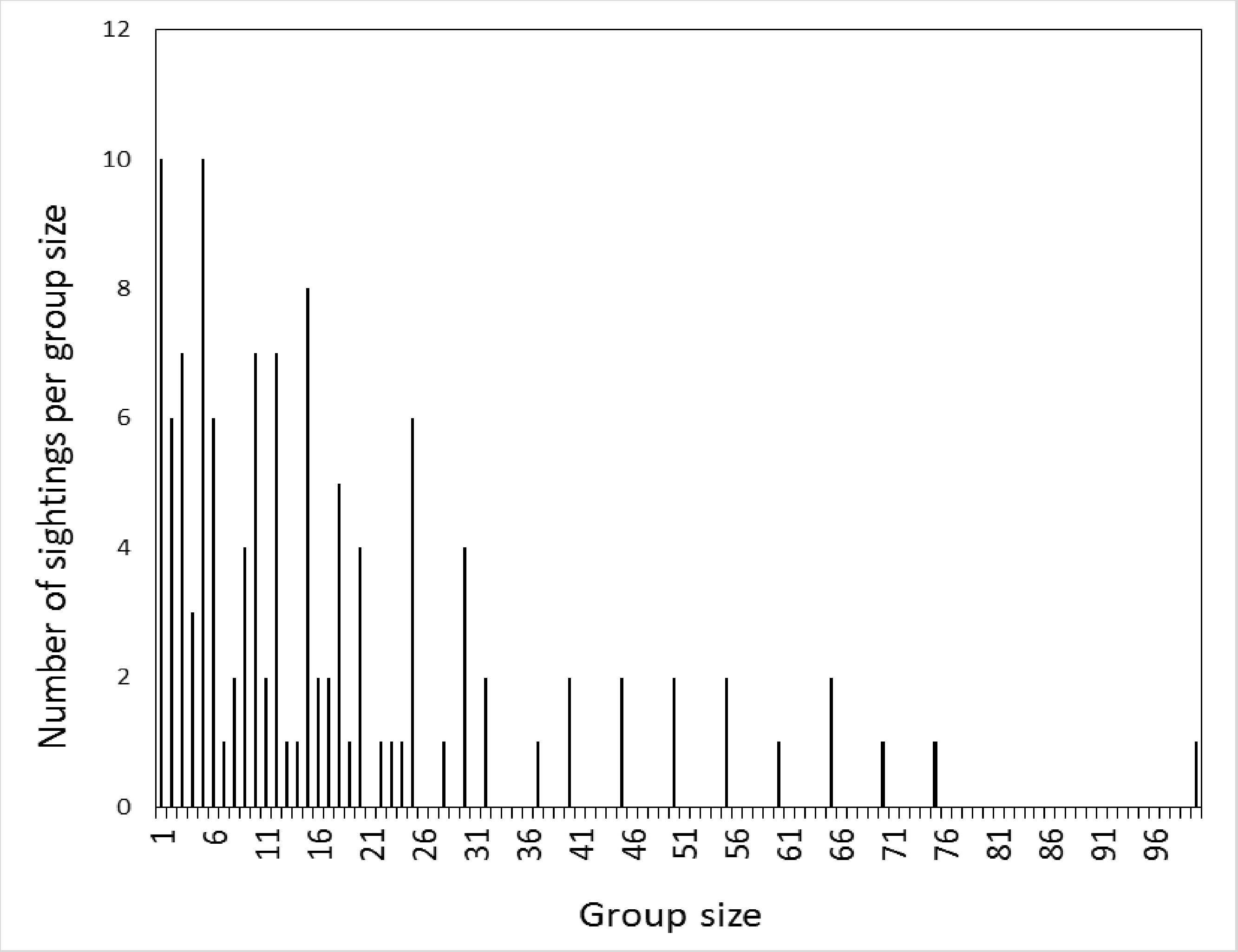


Fig. 3-6. Distribution frequency by group size of common bottlenose dolphins.

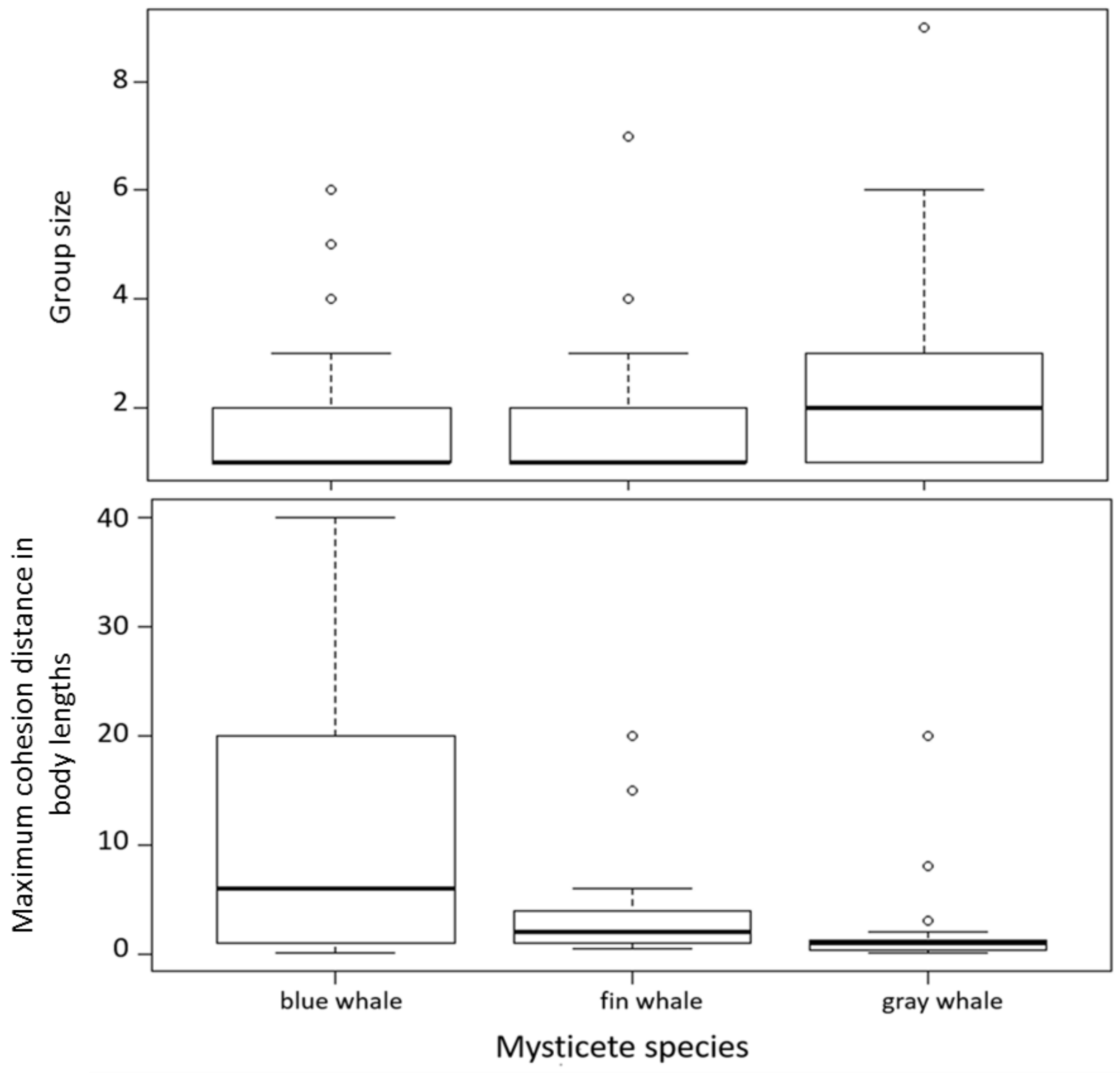


Fig. 3-7. Box plot of median group size and median maximum group cohesion distance of three mysticete whale species. The bottom and top of the box represent the first (Q1) and third quartiles (Q3), and the band inside the box is the median The upper whisker outside the box is Q3+1.5*Interquartile Range (IQR), and the lower whisker is Q1-1.5*IQR. Data points outside the hash marks are outliers.

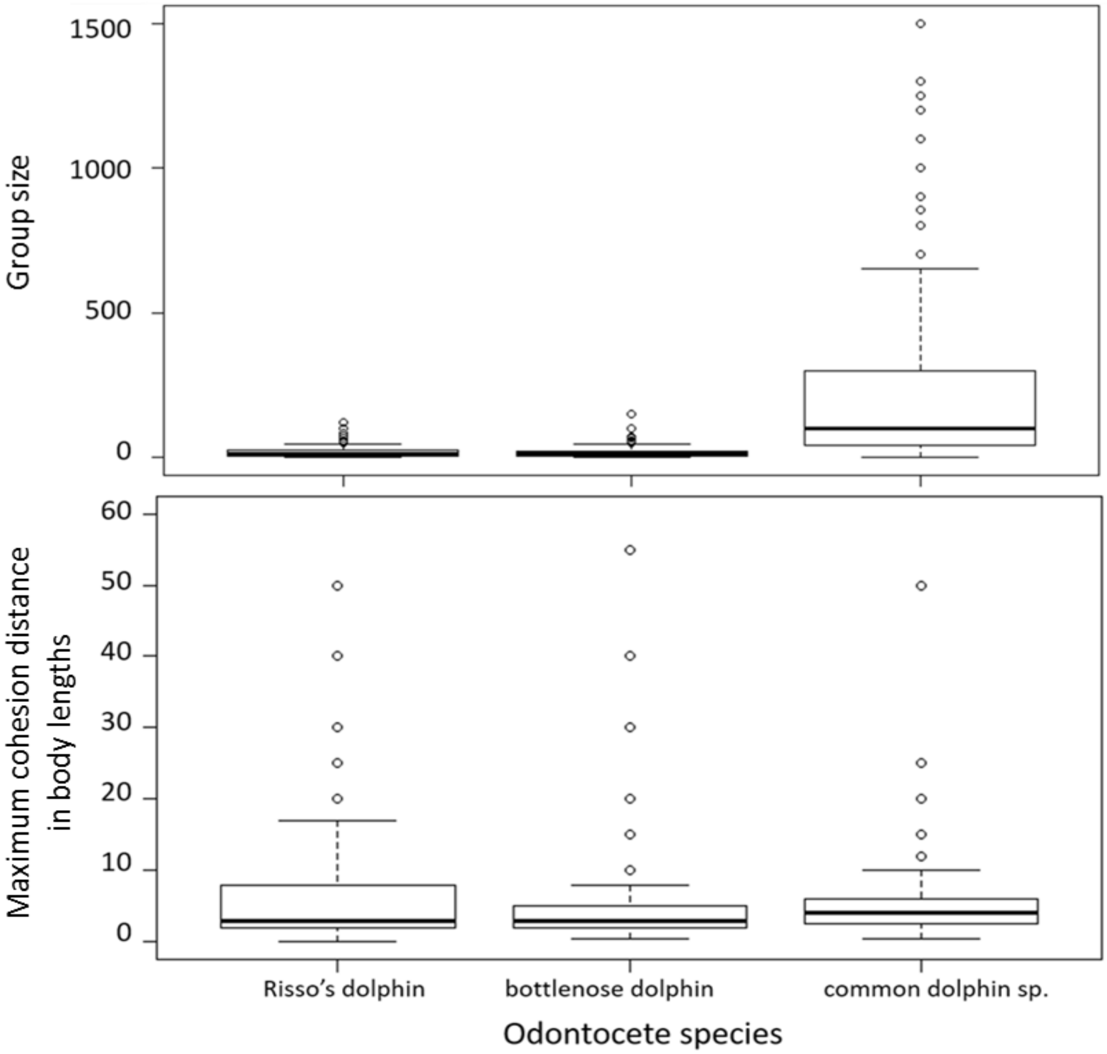


Fig. 3-8. Box plot of median group size and median maximum group cohesion distance (in body lengths) by three delphinid species groupings. See previous boxplot figure for definitions.

A.4. Chapter IV Influences on Cetacean Behavior, Group Size and Cohesion, Southern California

Table 4-1. Top three multinomial logistic regression models and AIC values for blue whale, fin whale, and gray whale response variables for data collection.

Species	**Response variable**	**Model rank**	**Model**	**AIC**	**Δ AIC**	**AIC weight**
Blue whale	Behavioral state	1	Slope	88.66	0.00	0.1916
		2	Depth	88.88	0.22	0.1717
		3	Julian day	89.12	0.47	0.1516
	Group size	1	Depth, Julian day	145.35	0.00	0.2023
		2	Julian day	145.57	0.22	0.1816
		3	Julian day, aspect, aspect	146.73	1.38	0.1015
	Group cohesion	1	Slope	69.67	0.00	0.1664
		2	Slope, time of day	70.14	0.47	0.1317
		3	Time of day	70.71	1.04	0.0989
Fin whale	Behavioral state	1	Julian day, shore distance	147.09	0.00	0.3541
		2	Other species, Julian day, shore distance	148.47	1.37	0.1784
		3	Julian day, time of day, shore distance	149.41	2.32	0.1111
	Group size	1	Calf, time of day	291.45	0.00	0.2414
		2	Calf	292.53	1.09	0.1403
		3	Calf, time of day, shore distance	293.03	1.58	0.1095
	Cohesion	1	Calf, subregion	160.97	0.00	0.1646
		2	Calf, season	161.50	0.53	0.1263
		3	Calf, season, depth	161.54	0.57	0.1241
Gray whale	Behavioral state	1	Aspect, aspect	101.31	0.00	0.1999
		2	Subregion, aspect, aspect	102.28	0.97	0.1229
		3	Calf	102.53	1.22	0.1086
	Group size	1	Subregion, aspect, aspect	253.39	0.00	0.1840
		2	Subregion, slope index, aspect, aspect	254.10	0.72	0.1286
		3	Subregion	254.11	0.73	0.1279
	Cohesion	1	Subregion, Julian day, aspect, aspect	109.24	0.00	0.1638
		2	Subregion, slope index, Julian day, aspect	109.67	0.43	0.1324

Table 4-2. Summary statistics and odds ratios for the top-ranked blue whale models by response variable.

Response variable	Parameter	Estimate	Std error	L95 CI[1/]	U95 CI	Odds ratio[2/]
Behavior-mill	Intercept	-2.0987	0.5829	-3.2411	-0.9562	
	Slope	0.0783	0.0509	-0.0214	0.1781	2.191
Behavior-rest/slow travel	Intercept	-1.2989	0.4454	-2.1719	-0.4259	
	Slope	0.0554	0.0481	-0.0389	0.1498	1.741
Group size	Intercept	-0.50121	0.61001	-1.72979	0.65687	
	Depth	-0.00061	0.00043	-0.00151	0.00018	
	Julian day	0.00672	0.00304	0.00081	0.01271	
Cohesion	Intercept	1.3647	0.4404	0.4310	2.2983	
	Slope	0.0342	0.0312	-0.0319	0.1004	

[1] CI=Confidence Interval

[2] Odds ratio for 100 days

Table 4-3. Summary statistics and odds ratios for the top-ranked fin whale models by response variable.

Response variable	Parameter	Estimate	Std error	L95 CI[1/]	U95 CI	Odds ratio[2/]
Behavior-mill	Intercept	0.9422	1.2454	-1.4987	3.3831	
	Julian day	-0.0044	0.0055	-0.0150	0.0063	0.651
	Shore distance	-0.1614	0.0697	-0.2981	-0.0248	0.202
Behavior-rest/slow travel	Intercept	1.5175	0.7328	0.0813	2.9537	
	Julian day	-0.0149	0.0046	-0.0239	-0.0060	0.221
	Shore distance	-0.0252	0.0213	-0.0669	0.0166	0.782
Group size	Intercept	0.8746	0.2206	0.4309	1.2963	
	Calf	0.6737	0.2430	0.1650	1.1228	
	Time of day	-0.0008	0.0005	-0.0017	0.0001	
Cohesion	Intercept	0.9091	0.1803	0.5469	1.2712	
	Calf	-0.8810	0.4574	-1.7997	0.0377	
	Subregion	0.6678	0.3157	0.0337	1.3019	
Northwest	Intercept	-0.2292	0.3692	-0.9528	0.4944	
	Slope	0.0742	0.0583	-0.0401	0.1885	2.101
Southeast	Intercept	-0.0171	0.4158	-0.8320	0.7978	
	Slope	-0.1126	0.1132	-0.3345	0.1092	0.321
Southwest	Intercept	0.5629	0.3524	-0.1279	1.2537	
	Slope	-0.0880	0.0848	-0.2543	0.0782	0.411

[1] CI=Confidence Interval

[2] Odds ratio for 100 days

Table 4-4. Top three multinomial logistic regression models and AIC values for Risso's dolphin, common bottlenose dolphin, and common dolphin spp. by response variables.

Species	Response variable	Model rank	Model	AIC	∆ AIC	AIC weight
Risso's dolphin	Behavioral state	1	Julian day, time of day, shore distance	491.81	0.00	0.1903
		2	Julian day, shore distance	491.91	0.10	0.1811
		3	Calf, Julian day, shore distance	492.82	1.01	0.1147
	Group size	1	Calf, other species, Julian day	2082.00	0.00	0.2321
		2	Calf, other species, slope, Julian day	2083.07	1.06	0.1364
		3	Calf, other species, depth, Julian day	2083.17	1.17	0.1294
	Cohesion	1	Depth, Julian day, time of day	652.19	0.00	0.3027
		2	Slope, depth, Julian day, time of day	653.81	1.62	0.1346
		3	Other species, depth, Julian day, time of day	654.17	1.98	0.1124
Common bottlenose dolphin	Behavioral state	1	depth, Julian day, time of day, aspect, aspect	154.53	0.00	0.2321
		2	Slope, depth, Julian day, time of day, aspect, aspect	155.02	0.49	0.1816
		3	Depth, Julian day, aspect, aspect	155.31	0.78	0.1570
	Group size	1	Calf	719.77	0.00	0.2381
		2	Calf, season	720.89	1.12	0.1362
		3	Calf, shore distance	721.27	1.50	0.1127
	Group cohesion	1	Julian day, time of day, shore distance	218.51	0.00	0.3154
		2	Slope, Julian day, time of day, shore distance	219.66	1.15	0.1776
		3	Julian day, time of day	220.95	2.44	0.0929
Common dolphin spp.	Behavioral state	1	Season, subregion	803.91	0.00	0.4560
		2	Other species, season, subregion	805.50	1.59	0.2058
		3	Calf, season, subregion	807.34	3.43	0.0821
	Group size	1	Calf, Julian day, aspect, aspect	6981.47	0.00	0.2234
		2	Calf, slope, Julian day, aspect, aspect	6982.48	1.01	0.1349
		3	Calf, Julian day, shore distance, aspect, aspect	6982.66	1.19	0.1235
	Cohesion	1	Calf, time of day	1059.65	0.00	0.1905
		2	Calf, depth, time of day, shore distance	1060.28	0.63	0.1388
		3	Calf, time of day, shore distance	1060.56	0.91	0.1207

Table 4-5. Summary statistics and odds ratios for the top-ranked Risso’s dolphin models by response variable.

Response variable	Parameter	Estimate	Std error	L95	U95	Odds ratio
Behavior-mill	Intercept	-2.1866	0.8994	-3.9493	-0.4238	
	Julian day	0.0052	0.0028	-0.0003	0.0106	1.671 [1/]
	Time of day	-0.0012	0.0012	-0.0036	0.0012	0.932 [2/]
	Shore distance	0.0331	0.0133	0.0071	0.0591	1.393 [3/]
Behavior–rest/slow travel	Intercept	2.8055	0.6080	1.6139	3.9971	
	Julian day	-0.0129	0.0026	-0.0180	-0.0078	0.281
	Time of day	-0.0020	0.0010	-0.0040	0.0000	0.892
	Shore distance	-0.0174	0.0109	-0.0388	0.0040	0.843
Group size	Intercept	2.3718	0.1124	2.1627	2.5854	
	Calf presence	0.5155	0.1511	0.2284	0.8214	
	Other spp. presence	0.5638	0.2386	0.1184	1.0670	
	Julian day	0.0024	0.0007	0.0011	0.0037	
Group cohesion	Intercept	1.31000	0.29581	0.72714	1.89286	
	Depth_m	0.00042	0.00019	0.00004	0.00080	
	Julian day	0.00313	0.00100	0.00116	0.00509	
	Time of Day	-0.00169	0.00042	-0.00252	-0.00087	

[1] Odds ratio for 100 days

[2] Odds ratio for 60 minutes

[3] Odds ratio for 10 kilometers

Table 4-6. Summary statistics and odds ratios for the top-ranked bottlenose dolphin models by response variable.

Response variable	Parameter	Estimate	Std error	L95 CI	U95 CI	Odds ratio
Behavior-Mill	Intercept	-2.3042	1.1161	-4.4917	-0.1168	
	Depth_m	-0.0001	0.0011	-0.0023	0.0022	0.991
	Julian day	0.0109	0.0051	0.0009	0.0209	2.962
	Time of Day	-0.0038	0.0026	-0.0088	0.0012	0.803
	Cos_asp	1.2410	0.6594	-0.0515	2.5334	
	Sin_asp	-1.9531	0.8461	-3.6114	-0.2949	
Behavior-rest/slow travel	Intercept	-2.4078	1.0225	-4.4119	-0.4037	
	Depth_m	0.0027	0.0009	0.0009	0.0046	1.321
	Julian Day	-0.0090	0.0061	-0.0211	0.0030	0.412
	Time of day	0.0023	0.0020	-0.0061	0.0062	1.153
	Cos_asp	1.2076	0.4661	0.2941	2.1212	
	Sin_asp	-0.3965	0.4653	-1.3084	0.5154	
Group size	Intercept	2.8122	0.1097	2.6037	3.0342	
	Calf	0.8428	0.3432	0.2202	1.5804	
Group cohesion	Intercept	1.6910	0.3523	0.9888	2.3932	
	Julian day	0.0037	0.0017	0.0003	0.0072	
	Time of day	-0.0019	0.0007	-0.0033	-0.0004	
	Shore distance	-0.0208	0.0100	-0.0408	-0.0009	

Table 4-7. Summary statistics and odds ratios for the top-ranked common dolphin spp. model by response variable.

Response Variable	Parameter	Estimate	Std error	L95 CI	U95 CI	Odds ratio
Behavior-rest/slow travel	Intercept	-3.4391	0.4390	-4.2995	-2.5788	
	Season	-0.0555	0.5345	-1.1032	0.9921	0.95
	Subregion	1.4220	0.5388	0.3660	2.4781	4.15

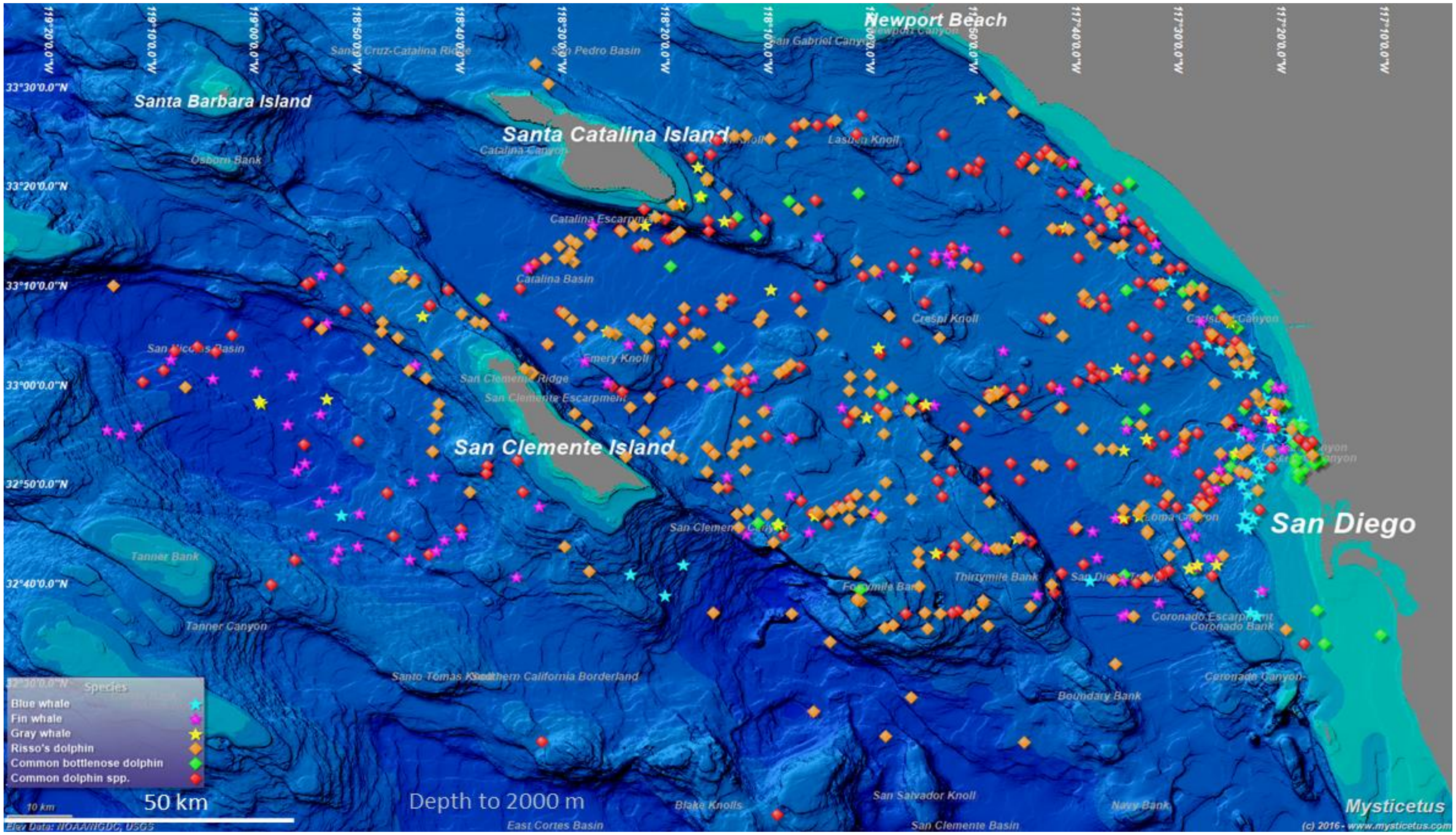


Fig. 4-1. All cetacean sightings made during aerial surveys in the Southern California Bight study area 2008-2012.

A.5. Chapter V Summary

Table 5-1. Summary of study questions and results by chapter.[1/]

Chapter/Question	Answer Based on Results	Interpretation
Ch II/Q1: How do cetacean species in the SCB select habitat relative to availability and to behavioral state?	(1) Fin whale: during medium/fast travel, relative probability of habitat use highest ($p<0.05$) for deep water (>1000 m) in San Nicolas Basin and San Diego Trough. Rest/slow travel (e.g., socializing, presumed foraging/feeding) not significantly related to any variable, although shore distance produced best fitting model per AIC.	(1) During transit between feeding areas/migration, select deeper waters
	(2) Gray whale (migrating): relative probability of habitat use decreased E to W (i.e. highest near mainland coast; $p<0.05$). No other significantly related variables, although N aspect produced best fitting model per AIC, with relative use lower ($p=0.0958$) than other aspect orientations.	(2) Possible avoidance north-facing slopes related to migration cue
	(3) Risso's dolphin: relative probability of habitat use highest ($p<0.05$) near SCI and mainland. During rest/slow travel, highest ($p<0.05$) relative use in nearshore water E of SCI, south of Santa Catalina Island, along mainland coast. During medium/fast travel, highest ($p<0.05$) relative use near and SE of SCI and along mainland coast.	(3) Select nearshore to reduce predation near feed/forage slope areas; for rest/social prefer N/NE SCI; during fast travel (transit, forage) prefer SE SCI near slope
	(4) Bottlenose dolphin: not seen W of SCI; relative probability of habitat use highest ($p<0.05$) nearshore shallow water; during medium/fast travel, highest ($p<0.05$) relative use shallow nearshore Santa Catalina Island, N mainland coast, small scattered areas near E SCI.	(4) overall prefer area E of SCI, Santa Catalina Island nearshore shallow reduce predation, rest/ socialize, forage/feed; fast travel SE SCI forage/transit
Ch III/Q2: Does social behavior, as indicated by group size and group cohesion, differ among cetacean species in the SCB?	Yes: Larger-body size (proxy for species) mysticetes and odontocetes had larger, less-cohesive groups, individuals more likely to be alone. Blue whale (largest body)/fin whale smaller mean group size and looser group cohesion than smaller gray whale ($p<0.05$); blue whale more likely to occur alone than fin/gray whale ($p<0.05$). Larger body-size Risso's/bottlenose dolphin had smaller, less-cohesive groups than smaller common dolphin (smallest relative body size; $p<0.05$). Common dolphin less likely ($p<0.05$) to occur alone than Risso's/ bottlenose dolphin.	Larger body size=reduced predation risk/less social, higher energy need=less social

Table 5-1 Continued

Chapter/Question	Answer Based on Results	Interpretation
Ch IV/Q3.1: Does calf presence influence group size and cohesion of cetacean species in the SCB?	Yes: Groups with calves larger and more cohesive than groups without calves among fin whales, Risso's dolphins, bottlenose dolphins, common dolphins ($p<0.05$).	Larger group size/tighter cohesion to reduce predation risk to calves
Ch IV/Q3.2: Are group size and group cohesion influenced by species and Julian day as related to the calving and mating seasons?	Yes: Groups with calves larger and more cohesive during expected peak calving/mating seasons among fin whales, Risso's dolphins, bottlenose dolphins, common dolphins ($p<0.05$)	Larger group size/higher cohesion coincides with peak calving/breeding
Ch IV/Q3.3: Are group size, group cohesion, and behavioral state among presumed nocturnal feeding delphinid species influenced by time of day as related to nocturnal prey behavior?	Yes: Risso's and common dolphin group size increased and groups more cohesive across day with peak in rest/slow travel midday ($p>0.05$)	Most active early morning late afternoon just after/before crepuscular/nocturnal feeding on DSL, similar to Hawaiian spinner and Kaikoura/New Zealand dusky dolphins

[1/] AIC=Akaike's Information Criterion, E=east, W=west, N=north, SE=southeast, SCI=San Clemente Island

Table 5-2. High probability habitat locations and peak periods of biological use based on study results and literature review for six cetacean species in the Southern California Bight.[1,2]

Species	ESA Status[3]	High-Probability Habitat[4]	Peak Biological Use Period[4]
All six species	Includes ESA-listed fin & blue whale	Overlap across species in coastal mainland, SCI & SCaI waters	Jul-Sep (peak blue & fin whale feeding); Mar-Apr (delphinid peak calving/mating & gray whale mother/calf north migration)
Blue whale	Endangered	Slope waters (variable)	Summer-fall peak feeding
Fin whale	Endangered	SNB; deep coastal SCI, SCaI & mainland waters	Summer-fall peak feeding
Gray whale	n/a	coastal mainland, SCI, & SCaI waters	Dec-March peak south migration; April-July peak mother-calf migration
Risso's dolphin	n/a	Coastal SCI & mainland waters , especially E/SE SCI coast	Winter peak calving/mating
Bottlenose dolphin	n/a	Coastal SCaI, SCI & mainland waters	Spring peak calving/mating
Common dolphin spp.[5]	n/a	Slope waters	Winter-spring peak calving/mating

[1] Evans 1974, 1975, 1994; Poole 1984; Urian et al. 1996; Forney and Barlow 1998; Carretta et al. 2000; Thayer et al. 2003; Rugh et al. 2005; Oleson et al. 2007a,b; Baird 2009; Sears and Perrin 2009; Becker 2007; Becker et al. 2010, 2012, 2014; Danil et al. 2010; Campbell et al. 2010, 2011; Falcone and Schorr 2011, 2012, 2013, 2014; Sumich and Show 2011; Forney et al. 2012; Douglas et al. 2014; Jefferson et al. 2014a,b, 2015; Smultea and Jefferson 2014; Calambokidis et al. 2015; Campbell et al. 2015; Carretta et al. 2015; Chivers et al. 2015; Lomac-MacNair and Smultea 2016

[2] See summary of species life history in Appendix A

[3] ESA=U.S. Endangered Species Act

[4] SCI=San Clemente Island, SCaI=Santa Catalina Island, SNB=San Nicolas Basin. E/SE=east-southeast

[3] Common dolphin spp.= short- and long-beaked common dolphins

APPENDIX B

LIFE HISTORY SUMMARY OF CETACEAN SPECIES

B.1. Blue Whale

Blue whales in the SCB belong to the Eastern Pacific Stock that feeds during summer-fall from the Gulf of Alaska to California, and subsequently migrates south to overwinter in tropical waters off Mexico, in the Gulf of California (Calambokidis et al. 1990; Reilly and Thayer 1990; Sears et. al 2014) and off Central America (Costa Rica and Nicaragua, Mate et al. 1999). Blue whales inhabit the SCB biannually during spring and fall migrations, with some animals remaining to feed primarily during summer-fall, peaking from July through September (Larkman and Veit 1998; Oleson et al. 2007a,b; Calambokidis et al. 2015; Lomac-MacNair and Smultea 2016). Blue whale peak presence in feeding areas has been shown to occur several months after peak chlorophyll-a concentrations (Burtenshaw et al. 2004). Predictive modeling of blue whale density relative to environmental factors in the California Current ecosystem (CCE) indicates their seasonal presence is linked with seasonal changes in SST based on decades of survey data (e.g., Becker et al. 2010). Foraging occurs in waters characterized by steep bathymetric relief (e.g., the continental shelf edge, island edges, seamounts) that tend to concentrate invertebrate prey downstream from core upwelling areas (Fiedler et al. 1998; Schoenherr 1991). Blue whales are considered selective consumers, typically feeding at depths of 100 to 200 m nearly exclusively on dense subsurface layers of *Euphausia pacifica* and *Thysanoessa spinifera* associated with the Deep Scattering Layer (DSL, consisting of a stratified, dense organism-rich layer such as zooplankton and fishes that undergoes a daily vertical migration closer to the surface at night; Allaby 2004) (Fiedler et al. 1998; Sears and Perrin 2009). Shallower dives typically occur during darkness when prey move closer to the surface (Sears and Perrin 2009). Feeding blue whales typically swim at 3-6 km/hr while traveling individuals swim faster at 5-35 km/hr (Sears and Perrin 2009).

Given their oceanic tendencies and low population numbers, blue whale social and group dynamics (e.g., courting, breeding, nursing, calving) are poorly understood. However, they are known to produce geographically specific calls at very low frequencies. Available data indicate that blue whales tend to occur alone or in pairs, and social associations are believed to be short term (Sears and Perrin 2009). Stable pairings were documented for periods of up to 1 h during focal studies conducted during a separate aspect of this study (Lomac-MacNair and Smultea 2016, Smultea unpublished data). While some females exhibit site fidelity to nursing grounds in the Gulf of California, birthing has never been documented. Sears et al. (2014) hypothesized that female blue whales calve in open pelagic water, subsequently moving to coastal waters as calves mature. This is contrary to other baleen whales including gray, humpback and South and North Atlantic right whales that aggregate each winter on coastal calving grounds (e.g., Herman and Tavolga 1980; Sears et al. 2014).

Mating occurs from late fall through winter, coinciding with peak calling rates including in the SCB (Wiggins et al. 2005; Sears and Perrin 2009). Birthing to a single calf occurs from fall through winter and calves are weaned near the age of 6–7 months (Sears and Perrin 2009). In the Gulf of Saint Lawrence during summer-fall, female-male pairings have been documented, sometimes for as long as five weeks (Sears and Perrin 2009). When such a pair is approached by a third blue or even a fin whale, vigorous surface-active behaviors that involve high-speed chasing, splashing, breaching and porpoising out of the water for typically 7–25 min (Sears and Perrin 2009). Blue whales in the eastern North Pacific produce relatively simple but long-duration, low-frequency (16 Hertz [Hz] songs throughout the year, known as Type A and B calls (Stafford et al. 2001). These songs are produced by males (primarily lone males) and are believed to be associated with reproduction (Oleson et al. 2007a,b). In the SCB, blue whale B songs were found to peak crepuscularly (Oleson et al. 2007b). Killer whales regularly attack blues whales as 25% of individuals in the Gulf of Mexico had killer whale teeth rake marks on their tails (Sears and Perrin 2009).

B.2. Fin Whale

Fin whales belonging to the Northeast Pacific Stock occur year-round in the SCB (Douglas et al. 2014; Jefferson et al. 2014a; Smultea and Jefferson 2014). Although some individuals inhabit the SCB for multiple days, months and years, it is unknown if any remain year-round (Falcone and Schorr 2014). Other fin whales have been sighted as they migrate southward through the SCB during fall and again as they pass northward in late spring (Forney et al. 2012; Calambokidis et al. 2015). Highest densities are in late summer/early fall during high zooplankton and fish densities associated with seasonal upwellings (Forney et al. 2012; Douglas et al. 2014; Calambokidis et al. 2015). Water depth and SST have been the most useful broad-scale environmental predictors for the CCE using predictive habitat-density modeling and summer-fall data (Forney 2000; Barlow et al. 2009; Becker et al. 2010). Data prior to 2008 suggest that during summer-fall, SCB fin whales may move shoreward west of San Clemente Island to coastal waters further out in winter-spring (Douglas et al. 2014; Falcone and Schorr 2014; Calambokidis et al. 2015). However, this trend was not apparent during SCB aerial surveys in 2008-2012 (Jefferson et al. 2014a). Fin whales in the SCB prey primarily upon krill and small schooling fish such as herring and sardines (Calambokidis et al. 2015; Jefferson et al. 2015).

Virtually nothing is known about fin whale social behavior including courting, breeding, nursing and intra- and inter-specific competition for food (Aguilar 2009). However, fin whales are hypothesized to likely exhibit physical competition between multiple males vying to monopolize a female rather than sperm competition based on testes size (Lockyer 1984). Courting and mating behaviors have similarly been documented to sometimes occur during migration periods among humpback, gray, and bowhead (*Balaena mysticetus*) whales (Nerini et al. 1984; Würsig et al. 1985; Jones and Swartz 2009).

B.3. Gray Whale

Gray whales of the Northeastern Pacific Stock migrate through the SCB twice a year between more northern feeding grounds ranging from northern California to Alaska and southern winter calving/breeding grounds off Mexico (Rice and Wolman 1971; Jones et al. 1984; Jones and Swartz 2009; Jefferson et al. 2015). Southbound animals pass through the SCB from October–March, peaking in December–March; they return northward with newborn calves, moving through the SCB from late January–July, peaking in April July (Rice and Wolman 1971; Swartz 1986; Rugh et al. 2001, 2005). Courting and mating among California gray whales appears to occur throughout the year (Norris and Dohl 1980). The vast majority of migrating animals remain within 10 km of the mainland coast, and were presumably outside the study area; however, some individuals in the SCB travel offshore and migrate through the Channel Islands including near San Clemente Island and Santa Catalina Island, within the study area (Daily et al. 1993; Sumich and Show 2011; see Chapter II).

B.4. Risso’s Dolphin

Risso’s dolphins in the SCB belong to the California/Oregon/Washington Stock inhabiting shelf, slope and offshore waters from the SCB to Washington (Carretta et al. 2015), preferring waters 400–1000 m deep (Baird 2009). In the SCB, the abundance of Risso’s dolphins has increased over the last 50 years (Jefferson et al. 2015). Risso’s dolphins were considered relatively rare (e.g., Shane 1995; Forney and Barlow 1998; Carretta et al. 2000; Smultea and Jefferson 2014), but they now are the second-most common cetacean species in the SCB, occurring year-round in relatively high numbers (Smultea and Jefferson 2014; Jefferson et al. 2014a). Historically, the species’ abundance and distribution was assumed to vary seasonally. Lowest numbers were reported during the SCB’s November–April cold-water season, with highest numbers during the

May–October warm-water season (Green et al. 1992; Forney et al. 2012; Becker et al. 2012). However, from 2008-2012, Jefferson et al. (2014a) reported seasonal trends opposite to these earlier reports. Soldevilla et al. (2010) found that Risso's dolphin echolocation activity peaked in the SCB during fall. Seasonal and yearly variability is likely influenced by ENSOs and decadal oscillations (Forney et al. 2012; Becker et al. 2012; Campbell et al. 2015). Water depth has been the only useful predictive environmental parameter for this species using complex in-situ and predictive habitat-density modeling for broad-scale data collected in the CCE over multiple years (Becker et al. 2010).

The social, reproductive, feeding, and diving behavior of Risso's dolphins are little known, given their preference for abrupt underwater slopes typically found in offshore waters. Most information on reproduction and feeding comes from dead Risso's dolphins hunted during drive fisheries (i.e. where dolphins are herded into small bays against shorelines) (Amano and Miyazaki 2004), and research studies in areas where steep slopes and/or currents meet land producing upwelling and accompanying high biological productivity. The latter includes Monterey Bay (Kruse et al. 1999), the Azores (Hartman et al. 2008, 2014, 2015; Visser et al. 2011), and the SCB (Shane 1994, 1995; Campbell et al. 2011; Falcone and Schorr 2014). The species' lack of functional teeth similar to known cetacean squid-eaters (Jefferson et al. 2015), combined with limited stomach content, and diurnally observed feeding behavioral data suggest that this species feeds predominantly at night on squid (e.g., Baird 2009; Bearzi et al. 2010; Jefferson et al. 2015; Soldevilla et al. 2011). Recent tagging data revealed that their deep foraging dives peak crepuscularly (G. Schorr unpubl. data). Risso's dolphins in the SCB may also exhibit alternative foraging strategies including kleptoparasitism (Smultea et al. 2014). Cockroft et al. (1993) reported that Risso's dolphins off South Africa feed predominantly on solitary cephalopod species that tend to be distributed widely, evenly and solitarily. Shane (1995) observed Risso's dolphins feeding on spawning squid near San Clemente Island. Typical group sizes for Risso's dolphins in the CCE and SCB range from 10-50 individuals (Forney and Barlow 1998; Baird 2009; Jefferson et al. 2014a,b).

Peak calving in the eastern Pacific appears to occur during winter (Baird 2009, Jefferson et al. 2015). Based on an estimated gestation period of 13–14 months (Baird 2009), mating correspondingly peaks in late fall. Both sexes display extensive apparent intra-specific teeth raking scars that are not found on newborn calves (Baird 2009). Hartman et al. (2008) found that the most heavily scarred animals are mature males based on photo-identification and sexing studies in the Azores. The latter studies reported strong site fidelity for some individuals, segregation by small groups of females with calves or lone female-calf pairs, and some relatively stable associations between mature males and between mature females (Hartman et al. 2008, 2014, 2015). Hartman et al. (2008, 2015) suggested that relatively stable male social associations or “clusters” may be alliances that benefit from improved mating access to females through physical coercion and cooperative breeding opportunities for males that take turns mating, as documented among male bottlenose dolphins (Connor et al. 2000). Hartman et al. (2008, 2015) based their hypothesis on observations of a known Risso’s dolphin male mating with a known female in front of four social-cluster members and a number of consistently high association indices among several groups of males. Perrin and Reilly (1984) inferred that Risso’s dolphins may be characterized by a multi-male breeding system based on relative testes size. Hartman et al. (2008, 2015) further hypothesized that such a system would be consistent with high competition among males to breed with females, suggesting that males may form maritories. A similar stratified social organization occurs among spinner dolphins associated with isolated tropical atolls (Karczmarski et al. 2005). However, stable associations may not be a unilateral species characteristic. The latter social system may be a result of the relatively isolated habitat and relatively insulted breeding population in the Azores, since it has not been previously reported among Risso’s dolphins, but remains to be investigated elsewhere. The latter social system appears intermediate to the fission-fusion and matrilineal society models applied to many odontocetes (Würsig and Würsig 1980; Norris and Dohl 1980; Connor et al. 2000).

B.5. Common Bottlenose Dolphin

Common bottlenose dolphins are generally split worldwide into coastal and offshore populations (Hansen 1990; Carretta et al. 1998; Defran and Weller 1999; Wells and Scott 2009). In the SCB, morphology (Walker 1981), photo-identification (Campbell et al. 2011) and genetics (Lowther 2006) provide evidence that bottlenose dolphins occur in two distinct stocks: a coastal stock of approximately 450 individuals inhabiting waters within 1 km of the mainland coast (Defran and Weller 1999; Dudzik et al. 2006) and an offshore stock of 3,000 individuals inhabiting offshore waters from a few km off the mainland coast to deep pelagic waters (Caretta et al. 2009). It is hypothesized that the offshore stock of bottlenose dolphins may be further divided into inshore/island-associated animals occurring near the Channel Islands and pelagic animals occurring in deep offshore waters (Shane 1994; Carretta et al. 2000; Campbell et al. 2011; Smultea and Jefferson 2014). However, the combined evidence remains inconclusive as to whether bottlenose dolphins on the offshore continental shelf and/or near islands in the SCB are distinct from those inhabiting pelagic waters. Recent photo-identification data indicate that the island ecotype displays some degree of site fidelity as well as interchange between Catalina and San Clemente islands: the same individuals were frequently resighted during survey periods ranging from 5-14 days (Campbell et al. 2011).

Bottlenose dolphins are considered opportunistic feeders, though most prey consist of a variety of fish and squid species; some individuals in the same population express specific prey preferences (Barros and Odell 1990; Wells and Scott 2009). Calving has been reported year-round in this species, though peaks occur in spring-summer (Urian et al. 1996; Thayer et al. 2003). In captivity, females are spontaneous sporadic ovulators, though male testosterone levels remain high year-round (Wells and Scott 2009). Data on calving and breeding periods specific to the SCB are not available (DoN 2008a). However, newborn calves have been observed year-round in mainland coastal waters off southern California (D. Weller, NMFS-SWFSC, personal communication in DoN 2008a). SCB stranding data suggest that calving peaks May to September (Danil et al. 2010). During the SCB aerial surveys, 84% of all groups with calf presence were seen during January-May (uncorrected for effort), with only two groups containing a calf during June-November. Differences in peak calf sightings may reflect differences between offshore and coastal populations. Gestation lasts about 12 months, and calves may remain with their mothers for 3-6 years (Wells and Scott 1999). Sharks (Wells and Scott 1999) and killer whales attack and prey upon bottlenose dolphins based on body scarring patterns (Jefferson et al. 1991).

B.6. Common Dolphins

Two species of sympatric common dolphins, the short- and long-beaked species, inhabit primarily deep offshore waters of the SCB (Carretta et al. 2015). Due to the inherent difficulty in distinguishing them at sea, they historically have been considered the same species until the mid-1990s (Jefferson et al. 2014a). Some authors have reported that they occur in distinct species-specific groups (e.g., Evans 1975; Bearzi 2005), while others have reported seeing them in mixed groups (Hill and Barlow 1992; G. Campbell, Texas A&M University, personal communication). Via photograph examination by a species expert (T. Jefferson), only 23% (17% short-beaked and 6% long-beaked common dolphin*)* of the 191 examined sightings were confirmed to species. Species confirmation was based on one or at most a few individuals in large groups of hundreds to thousands of individuals, given the limited camera and lens technology at the time relative to the 310–m flight altitude. The two species were pooled for analyses. Historically, short-beaked dolphins have outnumbered long-beaked common dolphins in the SCB. Results of a 2009 survey indicated a 1:1 ratio in the SCB (Carretta et al. 2015). Both species have been consistently reported as the most common cetacean species in the SCB since the 1950s (Smultea and Jefferson 2014). The most recent abundance estimate for the study area is 8,520 short-beaked and 3,314 long-beaked common dolphins during the May-October warm-water season; the November-April cold-water season estimates were nearly twice as high at about 15,955 short-beaked and 6,440 long-beaked common dolphins (based on pro-rating of 80% of the unidentified common dolphins; Jefferson et al. 2014a).

In the SCB, common dolphins are strongly associated with areas of steep bathymetric relief where their preferred prey tend to concentrate (Evans 1974, 1975; Reilly and Fiedler 1994; Becker et al. 2010). Forney and Barlow (1998) report historical changes in abundance in the SCB potentially related to inshore-offshore and/or north/south movements associated with changes in oceanographic conditions, most evidently sea surface temperature. Predictive density habitat-modeling conducted for hundreds of sightings throughout the CCE indicate that common dolphin density is most closely linked with large seasonal changes in sea surface temperatures (Forney and Barlow 1998; Becker et al. 2010). Short-beaked common dolphins in the SCB are considered opportunistic feeders, with prey choice related to the availability and catchability of the most abundant prey (Evans 1975, 1994). Based on stomach content analyses, short-beaked common dolphins in the SCB consume a variety of prey, all of which are associated primarily with pelagic mesopelagic waters and the DSL (e.g., fishes and squid) or epipelagic waters (e.g., opalescent inshore squid (*Doryteuthis opalescen*), and small schooling fishes such as small scombroids and clupeoids ; Evans 1994; Pusineri et al. 2007). Anchovies (*Engraulis mordax*) comprised 62% of all identified prey reported by Evans (1975). In comparison, others have reported that squid (family *Gonatidae* and *Loliga opalescens*) and Pacific whiting (*Merluccius productus*) were the most commonly consumed prey species (Fitch and Brownell 1968; Schwartz et al. 1992). Anchovies in particular are strongly associated with escarpments and submarine canyons characterized by biologically productive upwelling in the SCB (Mais 1974; Hui 1979). Common dolphin foraging dives are reported to reach 200 m, and prey diet varies seasonally and regionally with prey distribution and abundance (Evans 1994; Perrin 2009).

Little is known about the social or reproductive systems of common dolphins. Murphy et al. (2005) proposed that they practice a promiscuous breeding system characterized by sperm competition based on relatively large testes and sexual dimorphism. Gestation is estimated to last about 10-12 months, with weaning occurring when the calf is about 5-6 months old (Murphy and Rogan 2006; Danil and Chivers 2007; Perrin 2009). Based on 2009 data from the eastern North Pacific, Chivers et al. (2015) concluded peak calving occurs in winter among short-beaked common dolphins, and in early spring for long-beaked common dolphins. Perryman and Lynn (1993) found that most short-beaked common dolphin births off southern California and Baja California occurred from January-June, although some calves were born throughout the year. Evans (1975, 1994) hypothesized that these large groups include subgroups of ~20-30 individuals that may be closely related. Chivers et al. (2015) reported that calves were observed in 100 of 109 groups, though visual observations from the aircraft indicated calves tended to be randomly clustered together within larger encompassing schools in the eastern North Pacific Ocean. Chivers et al. (2015) notes the resemblance of this group structure to other studies of schools of small delphinids (e.g., Norris and Dohl 1980; Weir et al. 2010), further suggesting that differences occur in behavioral sensitivity among the two species (e.g., differences in swim depth, school shape, sensitivity to the overflying aircraft).