

**BEHAVIORAL ECOLOGY OF CETACEANS
IN THE SOUTHERN CALIFORNIA BIGHT**

A Dissertation
by
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Submitted to the Office of Graduate and Professional Studies of
Texas A&M University
in partial fulfillment of the requirements for the degree of
DOCTOR OF PHILOSOPHY

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May 2016
Marine Biology
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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 (82,467 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.

ACKNOWLEDGEMENTS

I thank wholeheartedly and gratefully acknowledge my primary advisor Bernd Würsig for his endless support, encouragement, and humor and inspiring me with further passion to learn and teach as well as Melany Würsig for her continual smiles, acceptance and support. Thank you to my dear committee member Jane Packard for pushing me beyond my comfort zone, challenging me intellectually, providing detailed structure, guidance and positive critique and for teaching amazing classes inspired by her passion and extensive knowledge of animal behavior and conservation. Thank you to Doug Biggs and Jay Rooker for sharing their advice, encouragement and zeal for their expertise and for sharing and opening my brain and eyes to different perspectives.

A very grateful thank you to the Texas A&M University at Galveston (TAMUG) faculty and staff for their support in many aspects. This included answering all my detailed questions and guiding me through paperwork and requirements, especially Holly Richards who has always been there for me for the last 5 years with a cheerful answer and guidance.

Data were collected with U.S. Navy (Navy) funding under contract to Smultea Sciences through HDR Inc., Scripps Institute of Oceanography, or Marine Mammal Research Consultants under National Marine Fisheries permit numbers 14451, 15369 and 774-1714-09. A special thanks to Navy personnel, in particular C. Johnson, J. Bredvik, S. Hanser, R. Uyeyama, and L. Mazzuca (formerly of the Navy), for providing encouraging support and logistics for this fieldwork and analyses. Additional funding for my PhD program was provided by the Erma Lee and Luke Mooney Foundation, Seaspace Scholarship in Marine Sciences, TAMUG Marine Biology Department, and TAMUG Marine Mammal Behavioral Ecology Group.

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

the surveys and helped collect, process or manage data: K. Ampela, C. Bacon, I. Smultea-Bates, O. Smultea-Bates, J. Biondi, J. Black, C. Boerger, R. Braaten, J. Bredvik, M. Cotter, Mark Deakos, D. Engelhaupt, A. Fowler, G. Fulling, S. Garrett, C. Goertz, J.C. Grady, J. Hopkins, V. James, C. Johnson, C. Kyburg, K. Lomac MacNair, M. MacKay, L. Mazzuca, R. Merizan, J. Mobley, Jr., M. Moore, T. Norris, M. Richie, F. Robertson, and D. Steckler. A special recognition and thanks for the passion, patience, skill, and attention to safety and detail from Aspen Helicopters (C. Bartush, A. Blasingame, N. Carillo, M. Estomo, B. Hanson, S. Jones, D. Moody, I. Ufford, and K. Veatch), and to R. Throckmorton who made all the logistic arrangements.

In addition to my advisor and committee, various versions of this dissertation were edited, reviewed or improved by D. Fertl, S. Steckler, J. Hopkins, G. Campbell, S. Courbis D, K. Lomac-MacNair, L. Mazzuca, T. McDonald, D. Orbach, A. Phillips, F. Robertson, O. Smultea-Bates, I. Smultea-Bates, and D. Steckler. I am so very grateful for your time reading such long text over and over. Special thanks to Endnote Queen D. Fertl for digging up obscure references for me and encouraging me. Thank you M. Steckler for giving me some of the wisest words of wisdom that kept me going through this process of writing: "Just Do IT!" A special amazing thank you to my partner (and luck for me a computer software engineer) Dave Steckler of Entiat River Technologies who filled a needed gap in user-friendly and user-adaptable data collection and processing software. He did this by engineering and finessing Mysticetus Observation Software to meet my project needs. Mysticetus maximized the ability to collect accurate detailed data on behavior (focal individual and group follows) along with line transect density data, when there was no other software available to do this. Special thanks also to Jenelle Black for taking the time and detail to help develop a systematic Excel database that could be easily manipulated for statistical purposes, and to Mark Deakos for helping us set up various software on a Palm Pilot, iPad and iPhone before Mysticetus.

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 Areas

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 1

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. 2003; 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).

33 Time is an important factor to be considered in MPA management, a concept identified as
34 “Dynamic Ocean Management” (Maxwell et al. 2015). Spatial distribution of marine resources
35 and anthropogenic activities are likely to change with short-term oscillations as well as long-term
36 trends such as global climate change. Resources needed by a species may move outside a
37 static protected area. Alternatively, anthropogenic activities may be restricted only during certain
38 periods considered biologically important to one or more species (Mangel 2000; NRC 2001;
39 Apostolaki et al. 2002). Examples for cetaceans include Designated Critical Habitat for the
40 endangered Cook Inlet beluga whale (*Delphinapterus leucas*) in Cook Inlet, Alaska (FR 2008).
41 During the ice-free season, seismic and other activities exceeding noise criteria regulated by
42 National Marine Fisheries Service (NMFS) are prohibited within 18 km of the Susitna River
43 mouth near Anchorage, coinciding with the peak migration of important beluga fish prey (NMFS
44 2008, 2015). Off Kaikoura, New Zealand, legislative mandates exclude tourism involving humans
45 swimming with dusky dolphins during specific daily dolphin rest periods to avoid disturbing
46 dolphins during this energetically important period (Lundquist et al. 2012, 2013). In the North
47 Atlantic, Seasonal Management Areas (SMAs) for endangered North Atlantic right whales are
48 designated at this species’ southern calving grounds during winter, along the migration route
49 during spring and fall migration, and on northern feeding grounds during summer (FR 2016).
50 SMAs include restricting vessel speed to reduce the risk of vessels striking and injuring or killing
51 right whales.

52

53 For species protected under the U.S. Endangered Species Act (ESA) or the Convention on
54 International Trade in Endangered Species of Wild Fauna and Flora (CITES), management
55 typically focuses on one species of conservation concern. For example, an MPA has been
56 proposed based on critical habitat for the Chinese white dolphin (*Sousa chinensis*) in coastal
57 waters of western Taiwan (Liu et al. 2015). This single-species approach contrasts with the
58 multi-species approach recommended for MPA management (Schmiing et al 2015). However, a
59 multiple-species approach may overlook critical needs of a single species. This paradox can be
60 resolved if management for a single species also benefits multiple species in a MPA. When
61 ecological communities derive benefits from single-species protection efforts, the focal species is
62 termed an “umbrella species” (Wilcox 1984). Umbrella species are often wide-ranging with
63 relatively large space requirements that maximize benefits to other species (Groom et al. 2006).
64 For example, the northern spotted owl (*Strix occidentalis caurina*) is an umbrella species whose
65 protection benefits smaller species (e.g., invertebrates, amphibians) in the old-growth forest that
66 is the owl’s habitat (Dunk et al. 2006). Similarly, a “flagship species” is a single-species
67 conservation option based on the charismatic appeal to gain public support, thereby protecting

68 other less-charismatic species inhabiting the same area (Ducarme et al. 2013). Examples of
69 flagship species include the polar bear (*Ursus maritimus*) as well as whales and dolphins in the
70 suborder *Mysticeti* (Leader-Williams and Dublin 2000; Barney et al. 2005).

71

72 Spatio-temporal habitat management for multiple species is a relatively new overarching concept
73 for marine mammals in the face of growing anthropogenic pressures in the marine environment
74 (Weilgart 2006; Dolman and Jasny 2015). Integrated spatial and temporal data analysis of
75 marine environments is essential for effective adaptive management, particularly in cases where
76 anthropogenic activity is outside a regulatory framework, such as shipping or military training
77 activities (Fox et al. 2013). For example, buffer zones can be applied for voluntary compliance
78 with best management practices reducing exposure to specific underwater noise levels (Weilgart
79 2006). The recent designation by NMFS of Biologically Important Areas (BIA) for multiple
80 cetacean species is an example of a voluntary best management practices approach that
81 focuses on areas encompassing critical seasonal feeding, calving and/or migratory habitat for
82 cetaceans of concern (Calambokidis et al. 2015; Ferguson et al. 2015). Species-specific spatio-
83 temporal data were useful in the development of an MPA, seasonal restrictions and closures for
84 reducing ship collisions risks with the North Atlantic right whale (Garrison 2007; Conn and Silber
85 2013; Petruny et al. 2014).

86

87 Effective marine spatial planning and adaptive management require species-specific spatio-
88 temporal data that identify when, how often, and why certain habitats are used by each species
89 relative to critical biological functions (e.g., nursing, feeding), as animals may be more sensitive
90 to disturbance during certain periods or behaviors (Dolman 2007; Brilot et al. 2012; Basille et al.
91 2013). There is increasing evidence across vertebrate taxonomic groups that species, location,
92 animal activity (i.e., behavioral) state (e.g., feeding, migrating), and reproductive status (e.g.,
93 presence of young) affect individual response levels to anthropogenic activities (e.g., Brilot et al.
94 2012; Basille et al. 2013; Robertson et al. 2013). However, behavioral patterns (e.g., foraging,
95 group size, social structure, habitat selection) vary spatiotemporally within and across
96 populations and geographical regions in response to resource availability and predation risk
97 (e.g., Gittleman 1989; Sterelny 2007; Kappeler et al. 2013).

98 Closely related species inhabiting the same environment are predicted to adapt distribution,
99 group size, and social structure to dynamically changing time (diel, seasonal) and space
100 gradients (e.g., ephemeral patchiness, habitat distribution) that affect resource availability (e.g.,
101 food, cover, mates), while still minimizing predation risk (e.g., Parrish and Edelstein-Keshet
102 1999; Beauchamp 2014, Ch 7). Predation pressure in particular is considered one of the

103 strongest factors shaping the behavioral ecology of prey species (Norris and Schilt 1988; Kie
104 1999; Beauchamp 2014). Thus, identification of species-specific differences in behavioral
105 ecology and factors influencing these differences are needed for effective conservation and
106 adaptive management. Species-specific spatio-temporal data should be collected at a scale
107 appropriate in the specific area of concern to appropriately interpret impacts and identify
108 management measures (Meentemeyer and Box 1987; Wiens 1989).

109 **1.1 Cetacean Behavioral Ecology Models**

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

116

117 The resulting social structure represents tradeoffs between group size, intra-group competition,
118 and predation risk. For example, in structurally complex coastal and inland waters where
119 predation risk is usually low and where food resources are predictable but limited, Gowans et al.
120 (2008) predict that delphinid species should be resident and form small, relatively stable social
121 groups (<10 dolphins), facilitating male sequestering of females for breeding. Example species
122 include island-associated spinner dolphins (*Stenella longirostris*) and inshore bottlenose dolphins
123 (*Tursiops* sp.). Gowans et al. (2008) compared the latter social grouping to African antelopes
124 inhabiting structurally complex forests that provide reduced risk of predation. In contrast,
125 Gowans et al. (2008) equated delphinids inhabiting deep oceanic waters (including the
126 continental shelf and slope), such as short-beaked common dolphins, with large-bodied ungulate
127 antelopes of the open African savannah. For both taxa, they suggested that living in large groups
128 of ~100-1,000+ individuals may be the only anti-predator strategy possible in open habitat,
129 where food patches are generally unpredictable and widely spaced, requiring individuals to travel
130 long distances to forage.

131

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

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

144

145 A number of delphinid studies have since shown patterns consistent with the Gowans et al.
146 (2008) predictive framework. In shallow coastal waters characterized by relatively high structural
147 complexity (e.g., vegetation, embayments), small delphinid groups form some stable
148 associations and exhibit residency, presumably reflecting more predictable and localized prey
149 availability. These include the Guiana dolphin (*Sotalia guianensis*), Commerson's dolphin
150 (*Cephalorhynchus commersoni*), and Australian snubfin dolphin (*Orcaella heinsohni*) (Santos et
151 al. 2010; Coscarella et al. 2011; Parra et al. 2011).

152

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

164

165 Among mysticete (baleen) whales, Ford and Reeves (2008) suggested that as body size and
166 swim speed ability increase, predation risk decreases. They proposed that mysticetes have
167 evolved divergent anti-predator strategies reflected by differences in body size, morphology and
168 habitat selection: Balaenoptera (e.g., blue and fin whales) inhabiting primarily open pelagic
169 waters have large streamlined bodies, and minimize predation by individually out fleeing killer
170 whale (*Orcinus orca*) predators. In contrast, other mysticete genera (e.g., gray and bowhead
171 whales, *Balaena mysticetus*) tend to have shorter, more robust bodies with slower swimming
172 capability and are better suited for avoiding predators by seeking refuge in more structurally

173 complex coastal waters (e.g., shallow depth, ice, kelp beds) or fighting off predators individually
174 or in groups (Ford and Reeves 2008). In both strategies, Ford and Reeves (2008) concluded that
175 one reason large mysticetes may have evolved large body size and/or fast swimming ability is to
176 minimize predation risk by killer whales. Ford and Reeves (2008) suggested that fast-swimming
177 balaenopterids require fast long chases by and risk of injury to predatory killer whales, traits that
178 have evolved as a predator deterrent compared to preying on smaller-bodied cetaceans.

179

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

198

1.2 Statement of the Problem

199 The Southern California Bight (SCB) in the North Pacific Ocean off San Diego and Los Angeles,
200 California, is characterized by relatively high levels of anthropogenic activities, including
201 commercial shipping, military exercises, whalewatching, commercial and recreational fishing,
202 and chemical runoff (DoN 2008a,b; Redfern et al. 2013; Calambokidis et al. 2015). These
203 activities overlap with some of the highest densities and diversity of marine mammals attracted
204 to the SCB by high biological productivity that peaks during spring and fall (Carretta et al. 2000;
205 Forney et al. 2012; Jefferson et al. 2014a). The Navy conducts military training exercises
206 involving large ships, submarines, sonar, and underwater detonations within the Southern
207 California Range Complex (SOCAL Range Complex; DoN 2008a,b, 2010, 2012) bounded by the

208 SCB (Fig. 1-1). To address growing concerns over potential impacts of these activities on marine
209 mammals, there is a need to describe and monitor the density, habitat use, and behavior of
210 marine mammal species on the scale of the SCB (DoN 2010, 2011, 2012). Data are needed in
211 sufficient sample sizes to be statistically valid and of appropriate duration to address naturally
212 occurring environmental variability. Successful species management requires identification of
213 biologically important habitat and temporal periods associated with behavior essential to species
214 survival (e.g., birthing, breeding and feeding areas, migration). Knowing such information allows
215 managers to develop spatio-temporal measures to effectively manage and enumerate impacts of
216 anthropogenic activities on species of concern, and to monitor and evaluate effectiveness of
217 protective measures.

218

219 Although an MPA network has been developed for other regions of California (Airamé et al.
220 2003; Botsford et al. 2014, Saarman et al. 2013), the viability of a spatiotemporal management
221 approach has not yet been applied for cetaceans in the SCB (Fox et al. 2013). Efforts to
222 systematically identify important species-specific habitat and sensitive biological periods on the
223 scale of the SCB are generally lacking or problematic (Mills et al. 2015). Although BIAs have
224 been identified for fin whales off southern California (Calambokidis et al. 2015), BIAs have no
225 accompanying regulatory implications. There is a need to identify important habitats and
226 sensitive biological periods for SCB cetacean species, given increasing anthropogenic activities.

227

228 Relatively little is known about the site-specific behavioral ecology of the approximately 19
229 cetacean species regularly inhabiting deep waters of the SCB, with the exception of blue whales
230 (Calambokidis et al. 2007; Goldbogen et al. 2011; Lomac-MacNair and Smultea 2016). At the
231 time of this study, data on the density and behavior of marine mammals were outdated, lacked
232 systematic rigor, and/or were collected at much coarser or more localized scales than the SCB
233 (Smultea and Jefferson 2014). Over the last 30+ years, previous studies in the region have
234 focused primarily on population counts and predicting distribution and density of marine
235 mammals relative to biotic and abiotic habitat factors on a much larger geographical scale. For
236 example, multi-year vessel surveys involving widely spaced (>100 km) transect lines were
237 conducted in the U.S. Exclusive Economic Zone extending 370 km (200 nm) offshore of the U.S.
238 west coast, and within the California Current Ecosystem (CCE) extending along the length of
239 California (e.g., Carretta et al. 2000; Becker et al. 2010; Campbell et al. 2015). More recently,
240 SCB studies have focused on diving, movement or feeding behavior of beaked whales, and fin
241 and blue whales based largely on tagging data (Falcone and Schorr 2014; Goldbogen et al.
242 2015; Mate et al. 2015). The latter studies have included behavioral responses of blue whales to

243 military mid-frequency active (MFA) sonar noise (Melcon et al. 2012; Goldbogen et al. 2013).
244 Henderson (2010, 2012) conducted focal group behavioral studies of cetaceans from a
245 stationary platform north of San Clemente Island during fall of 2006-2008 using both visual and
246 passive acoustic monitoring. Few other studies have considered the social context of cetacean
247 behaviors (e.g., group size, composition, cohesion) that are known to affect cetacean behavioral
248 ecology (e.g., common bottlenose dolphin, Shane et al. 1986; gray whale, Poole 1984; Risso's
249 dolphin, Hartman et al. 2008). Furthermore, past studies were conducted primarily during
250 summer and fall, resulting in a data gap during winter and spring.

251 *1.2.1 Background*

252 In 2009, the Navy developed a Marine Species Monitoring Plan (MSMP) for the
253 SOCAL Range Complex to monitor potential effects of military training activities on SCB marine
254 mammals as required under the U.S. Marine Mammal Protection Act and ESA (DoN 2009). In
255 2010 (DoN 2010), an associated Integrated Comprehensive Monitoring Plan (ICMP) was
256 developed to implement adaptive management and monitoring measures as new data become
257 available. As part of the MSMP in the SOCAL Range Complex, I designed an aerial survey study
258 to identify inter-specific relationships between cetacean habitat use, behavioral state, and group
259 and environmental characteristics. The goal was to quantitatively identify important habitat and
260 sensitive biological periods to provide a baseline against which to compare potential baselines
261 shifts. Fig. 1-2 shows the systematic transect lines and the locations and names of bathymetric
262 and topographic geographical locations in the study area mentioned in this dissertation. The
263 study was planned to span a five-year period to address natural environmental variability. All
264 survey effort conducted in the study area during the 2008-2013 survey period is shown in Fig. 1-
265 3.

266
267 It is expensive to repeatedly access deep waters, and therefore group behavioral data on
268 cetacean species in deep (>200 m) waters in the SCB and elsewhere are relatively sparse.
269 Available information has primarily been collected from vessels (e.g., Shane 1995; Falcone et al.
270 2009), individually tagged animals (Baird et al. 2006; Falcone and Schorr 2014; Mate et al.
271 2015), a limited number of aircraft-based studies (Richardson et al. 1985; Würsig et al. 1985;
272 Smultea and Würsig 1995), an offshore stationary platform (Henderson 2010, Henderson et al.
273 2014a,b), and more recently video recordings and photos from unmanned autonomous aircraft
274 (currently limited by short observation durations, expense, and/or special permitting; Durban et
275 al. 2015; Koski et al. 2015). Each of these approaches presents different perspectives,
276 advantages and disadvantages (Dawson et al. 2008).

277

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

290

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

301

1.2.2 *Study Species: Ecology and Life History*

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

312 associate with coastal and adjacent slope waters near San Clemente and Santa Catalina
313 islands.

314 **1.3 Chapter Organization, Study Questions and Goals**

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

324 *1.3.1 Chapter I*

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

333 *1.3.2 Chapter II*

334 Chapter II entitled *Modeling Cetacean Habitat Selection* applies Resource Selection Function
335 (RSF) analysis (Manly et al. 1993, 2010) to identify high-probability selection of environmental
336 parameters for four cetacean species as a function of behavioral state relative to eight static
337 habitat parameters. Static habitat parameters were chosen to facilitate geo-referencing and
338 prioritization of habitat relative to decisions on the relatively fine management scale of the SCB.
339 RSF is unique from other habitat-use analyses as it compares the ratio of environmental
340 variables selected by a species to the availability of those variables in a given area. For
341 example, in my study, habitat parameters associated with sighting locations were compared with
342 habitat variables associated with >35,000 randomly selected points in the study area. Thus, an
343 RSF estimates “selection” (i.e., “preference”) rather than “use” by quantifying the ratio between
344 which habitat variables are used versus available to animals. Separate RSF models were run for

345 different behavioral states to determine the role of behavioral state in habitat selection and to
346 evaluate the relative functional importance of habitat to cetacean species. The overarching
347 question and goal of this chapter are identified below.

348

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

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

353 **Target Journal:** Marine Ecology Progress Series

354

1.3.3 Chapter III

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

366

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

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

372 **Target Journal:** Behavioral Ecology and Sociobiology

373

1.3.4 Chapter IV

374 Chapter IV entitled *Spatiotemporal Behavioral Patterns of Cetaceans in the Southern California*
375 *Bight* uses first-observed sighting data of cetaceans to examine how the response variables
376 behavioral state, group size, and group cohesion are affected by social, temporal, and
377 environmental factors. The eight explanatory variables examined include calf presence, time of
378 day, day of the year (i.e., Julian day), season, water depth, distance from shore, slope, and

379 slope-face aspect. Resulting patterns across species may reflect varying reproductive phase,
380 resource availability and adaptations to predation risk. This information is important in identifying
381 species-specific and biologically sensitive temporal periods. Observed natural variations in group
382 size, group cohesion and behavioral state should be considered when differentiating potential
383 effects of increasing anthropogenic activities of concern in the SCB. Three related overarching
384 study questions are addressed in this chapter:

385

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

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

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

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

396 **Target Journal:** Behavioral Ecology and Sociobiology

397

1.3.5 Chapter V

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

405 **1.4 Ecological Gradients of Cetaceans Relative to Existing Models**

406 Life history traits and related ecological gradients for each of the six cetacean species addressed
407 herein are summarized below and in detail in Appendix A to position results in a meaningful
408 biological context, using data from the SCB as available. Table 1-1 focuses on documented and
409 predicted ecological and social parameters for the cetacean study species relative to the
410 Gowans et al. (2008) model for delphinids and the Ford and Reeves (2008) model for
411 mysticetes, as discussed above. The blue whale, fin whale, Risso's dolphin and common dolphin
412 spp. inhabit primarily semi-pelagic and deep open waters, foraging along slopes on spatially

413 clumped food resources. The gray whale migrates through the SCB primarily close to the
414 mainland coast and to a lesser extent offshore migratory corridors through the Channel Islands.
415 The remaining apparent island-associated ecotype of bottlenose dolphin appears to closely
416 associate with coastal and adjacent slope waters near San Clemente and Santa Catalina
417 islands.

418

CHAPTER 2

419

MODELING CETACEAN HABITAT USING BEHAVIOR

420

2.1 Synopsis

421 The role of behavioral state in cetacean habitat selection was examined relative to eight
422 environmental variables in deep (>200 m) waters of the Southern California Bight (SCB) from
423 2008-2012. Fifteen aerial transect surveys totaling 18,831 km of systematic effort were
424 conducted. Resource Selection Function (RSF) models predicted relative probability of
425 occurrence by contrasting environmental characteristics at cetacean locations with random point
426 locations. Analyses involved 59 endangered fin whale, 40 gray whale, 134 Risso's dolphin, and
427 31 bottlenose dolphin groups. Each species model was fit for up to three behavioral states (mill,
428 rest/slow travel, medium/fast travel) and all behaviors pooled. Behavioral state influenced habitat
429 use, and some regions and features were selected for important biological functions (foraging,
430 resting) at higher rates than expected based on availability of those features. Fin whales were
431 most likely to display rapid travel over deep flat basins, while rest/slow travel was associated
432 more frequently than expected with nearshore waters including islands. Migrating gray whale
433 habitat use probability decreased east to west from the mainland coast, with rapid travel
434 predicted to occur along the San Clemente Island shoreline. Risso's dolphins were most likely to
435 display rapid travel near San Clemente Island and the mainland coast. Bottlenose dolphins were
436 closely affiliated with shallow nearshore waters particularly of Santa Catalina Island for all
437 behaviors (including foraging, feeding, and calf nurturing). Results improve understanding of how
438 behavioral state influences habitat selection of little-studied offshore cetaceans. Such knowledge
439 is useful to identify potential opportunities for spatiotemporal management relative to sensitive
440 areas and periods for cetaceans. Data provide an important 5-year baseline for little-known
441 species to compare potential future changes in habitat selection patterns, assisting in
442 conservation and management decisions in a relatively high-anthropogenic use area.

443

2.2 Introduction

444 Numerous studies have successfully used habitat modeling to quantitatively link habitat use to
445 ecological attributes based on the underlying premise that an animal's distribution reflects its
446 response to the environment (Barry and Elith 2006; Elith and Leathwick 2009; Becker et al.
447 2014). However, data on the underlying biological function of habitat use is often lacking,
448 especially in offshore marine environments (Hastie et al. 2004; Becker et al. 2014). Information
449 on spatial use of habitat resources is needed for applied species management, as it indicates

450 how individuals are distributed in space relative to those resources. With such knowledge,
451 effective management and monitoring can be developed to minimize impacts to species of
452 concern (Hooker et al. 1999; Cañadas et al. 2002; Redfern et al. 2013), including modification of
453 human activities in time or space relative to sensitive biological periods and locations (Lusseau
454 and Bejder 2007; Halpern et al. 2013; Dolman and Jasny 2015).

455

456 Resource selection function (RSF) analyses have been applied to identify terrestrial animal
457 habitat use, including anthropogenic effects from oil and gas exploration, construction, tourism,
458 and climate change (e.g., Manly et al. 1993, 2010; McDonald and McDonald 2002; Sawyer et al.
459 2006). The RSF method assumes that resources (e.g., food items, cover types, or any
460 quantifiable habitat characteristic) important to individuals are used disproportionately to
461 availability, and numerically compares the availability of attributes throughout a study area to
462 those associated with animal locations (Johnson 1980; Manly et al. 2010). In marine
463 ecosystems, RSFs have been used to identify preferred habitat attributes of marine mammals
464 and subsequent changes induced by anthropogenic disturbance among endangered polar bears
465 (*Ursus maritimus*; Amstrup et al. 2001; Durner et al. 2009), Pacific walrus (*Rosmarus divergens*;
466 Jay et al. 2014), endangered Cook Inlet beluga whales (*Delphinapterus leucas*; Goetz et al.
467 2007), Hector's dolphins (*Cephalorhynchus hectori*; Bräger et al. 2003), bottlenose dolphins
468 (Fortuna 2006), and dugongs (*Dugong dugon*; Sheppard et al. 2010). The tools afforded by the
469 RSF method have enabled managers to successfully identify preferred habitat, adverse effects,
470 and viable mitigation and management opportunities, by correlating changes in habitat use with
471 changes in anthropogenic activity. However, behavioral states that can represent how preferred
472 habitats function biologically, have rarely been incorporated into habitat-modeling studies.

473

474 The SCB is encompassed by the California Current Ecosystem, one of the richest areas of year-
475 round biological productivity and diversity in the world (Dailey et al. 1993; Hayward and Venrick
476 1998). A distinct feature of the SCB is deep water close to shore characterized by alternating
477 deep (~500-2,500 m) underwater basins, 9 islands, 12 large canyons, and 18 marine basins
478 (Emery 1960; Fig. 1-2). The SCB is used by over 30 marine mammal species (Forney and
479 Barlow 1998; Campbell et al. 2015; Smultea and Jefferson 2014) as well as growing
480 anthropogenic activities of concern to these species (McDonald et al. 2006; DoN 2008b; Falcone
481 et al. 2009). Peak seasonal spring and fall plankton blooms in the SCB are linked with dynamic
482 oceanographic processes. These processes include upwelling, fronts, eddies, gyres, and mixing
483 of four different water masses along the mainland and Channel Islands coasts, seamounts, and
484 underwater canyon slopes that serve to aggregate prey consumed by many cetaceans (Hayward

485 and Venrick 1998; Mann and Lazier 2013; Munger et al. 2009). Ongoing human activities include
486 fishing, commercial shipping, recreational boating, marine tourism, oil and gas development, and
487 military operations involving mid-frequency active sonar (McDonald et al. 2006; DoN 2008b,
488 2010).

489

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

500

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

519 assist with management decisions on smaller scales such as the SCB is limited. Moreover,
520 existing data are limited to summer-fall periods.

521

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

533

2.3 Materials and Methods

534

2.3.1 Study Area and Aircraft

535 Aerial surveys were conducted in two sub-areas: the Santa Catalina Basin (8,473 km²) and the
536 San Nicolas Basin (4,180 km²) including the South of San Clemente Island area (4,903 km²)
537 (Fig. 1-1). Parallel transect lines were flown primarily along a WNW to ESE orientation generally
538 perpendicular to bathymetric contours to obtain a random sample of individuals and thereby
539 avoid biasing results if selection was associated with depth contours (Buckland et al. 2015). The
540 prescribed area was intensively surveyed by following transect lines spaced approximately 14
541 km apart between the coast and San Clemente Island in the Santa Catalina Basin, and spaced 7
542 km apart to the west in the San Nicolas Basin and South San Clemente Island (Fig. 1-2).
543 Surveys were flown at speeds of approximately 185 km hr⁻¹ and altitudes of approximately 227-
544 357 m from a small high-wing, twin-engine airplane equipped with bubble observer windows on
545 the left and ride sides of the middle seats.

546

2.3.2 Data Collection

547 Two trained biologists observed cetaceans from the middle seats of the aircraft while a
548 dedicated recorder/photographer sat in the front and/or rear seats. Basic sighting and
549 environmental data (e.g., observation effort, Beaufort sea state, visibility, glare, etc.; see
550 Jefferson et al. 2014a) were recorded using the following hardware and software. In 2008 and
551 2009 BioSpectator was used on a Palm Pilot TX or an Apple iPhone or iTouch. In 2010 and part

552 of 2011 a customized Excel spreadsheet on a Windows-based notebook computer was used.
553 During part of 2011 and all of 2012 customized observation software (Mysticetus Observation
554 Platform, Mysticetus™) was used on a notebook computer. During all surveys, a wide-area
555 augmented system-enabled Global Positioning System (GPS) was used to automatically assign
556 a time stamp, a sequential sighting number, and a GPS position. A Suunto handheld clinometer
557 was used to measure horizontal angles to sightings that were converted to a GPS position by
558 Mysticetus™.

559

560 Following the protocol of Smultea (1994), we recorded the initial sighting location and first-
561 observed group behavioral state relative to movement type/speed of travel for each sighting
562 (mill, rest/slow travel, medium/fast travel; Table 2-1). A “group” was defined as >50% of
563 individuals engaged in the same polarized behavioral state up to 100 Body Lengths (BL) apart
564 within visual range of observers (after Norris and Schilt 1988; Baird and Dill 1996; Lusseau et al.
565 2005; Table 2-1). Within observed groups, individuals were typically within 10-20 BL of each
566 other but occasionally up to 50-100 adult BL apart. For common dolphins that formed much
567 larger groups than other cetaceans (on the order of hundreds to thousands), cohesion was
568 based on distinct subgroups that met the above group definition. Species, sighting time, group
569 size, and number of calves were also recorded. Sightings were circled at radial distances of
570 approximately 500-1000 m to confirm sighting information as needed. The latter included using
571 Steiner 7 X 25 or Swarovski 10 X 32 binoculars or photo-documentation with a Canon EOS 40D
572 or 60D or Nikon D300 or D7000 DSLR camera with a 100-400 mm f/4.5-5.6 IS USM lens). High
573 Definition (HD) video was also recorded when conducting focal behavioral follows as part of a
574 separate study using a Sony Handycam HDR-XR550 or HDR-XR520 video camera.

575

2.3.3 Data Analysis

576 RSFs were developed for cetacean sighting (i.e., group) locations obtained along systematic
577 transect lines and shorter connecting lines during conditions suitable for sighting cetaceans
578 (Beaufort sea state ≤ 4 ; Jefferson et al. 2014a). For the RSF analysis, site characteristics at
579 marine mammal locations were contrasted to site characteristics at 33,177 randomly selected
580 “available” points obtained at a randomly placed systematic grid of locations within the study
581 area. However, the bottlenose dolphin was modeled only for the Santa Catalina Basin region
582 with a set of 23,455 available site points, as none were seen in the region west of this island.

583

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

587
$$\Pi(x_1, x_2, \dots, x_p) = \exp(\beta_0 + \beta_1 x_1 + \beta_2 x_2 + \dots + \beta_p x_p)$$

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

604

605 To select a final RSF model, all 127 models were fitted representing all possible combinations of
606 the eight explanatory variables. Models were run separately for all sightings and for each
607 behavioral state. Pearson correlations between all pairs of continuous variables were calculated
608 and correlations >0.6 in absolute value were not permitted to enter regression models together.
609 Each pair of categorical variables was cross-tabulated and results were examined for evidence
610 of association. If Fisher's two-sided exact test was significant ($p < 0.05$), the two variables were
611 not permitted to enter any model together. All models were ranked with Akaike's Information
612 Criterion (AIC) (Burnham and Anderson 2002) to evaluate model fit based on the log likelihood
613 and a penalty for parameter inclusion. Observations with missing values for any variables were
614 excluded from analyses.

615

616 The models associated with the minimum AIC value for each species and behavior were
617 selected as the final models. Direction (positive or negative value) of the parameter estimate
618 indicated whether the relationship between the variable and use was positively or negatively
619 correlated. Significance of the parameter estimate (i.e., testing that the parameter was
620 significantly different from zero) was computed from the corresponding t -ratio (parameters
621 estimate divided by standard error). P values < 0.05 were considered statistically significant. Final

622 RSF models were used to predict the relatively probability of selection for sub-areas within the
623 study area. The resulting predicted RSF values were illustrated on maps color-coded based on
624 five predicted classes rated from low to high relative probability of use.

625 **2.4 Results**

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

638 *2.4.1 Fin Whale*

639 Most of the 59 fin whale groups used in RSF modeling displayed medium/fast travel ($n=36$),
640 followed by rest/slow travel ($n=20$), and mill ($n=2$), with one group whose behavior was unknown
641 (Table 2-3). Due to small sample size, the two mill groups were pooled with rest/slow travel for
642 analysis. This resulted in fitting of three RSF models for fin whales: all sightings, rest/slow travel,
643 and medium/fast travel. The final RSF model for rest/slow travel contained only distance to
644 shore, but did not account for a significant amount of variation in the data ($p=0.3970$; Table 2-3).
645 For medium/fast travel, the final RSF model contained longitude ($p=0.0276$) and depth
646 ($p=0.0017$) (Table 2-3). Both variables were positively correlated with relative probability of use,
647 meaning that during medium-fast travel, fin whales used deeper eastern waters more than
648 expected relative to availability. Pooling all behaviors, fin whale habitat selection was associated
649 with four variables: latitude, longitude, depth and distance to shore (Tables 2-3 and 2-4). Latitude
650 and distance from shore were negatively correlated with relative probability of use, while
651 longitude and depth were positively correlated. Thus, assuming equal access to all parts of the
652 study area, fin whales used deeper waters as close to shore as possible in the eastern and
653 southern parts of the study area (Table 2-3).
654

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

660 *2.4.2 Gray Whale*

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

676
677 Maps of predicted relative probability of habitat use indicated that overall, gray whales selectively
678 used waters closest to the mainland coast, with probability of use decreasing with increasing
679 distance from the mainland coast (Table 2-3, Fig. 2-4). Although behavioral state was not
680 significantly related to any variable, longitude produced the best-fitting model for rest/slow travel,
681 suggesting that this behavior was relatively higher to the east along the mainland coast (Table 2-
682 3, Fig. 2-4).

683 *2.4.3 Risso's Dolphin*

684 Most of the 134 Risso's dolphin groups used in RSF modeling displayed rest/slow travel ($n=63$),
685 followed by medium/fast travel ($n=56$), or mill ($n=11$) (Table 2-3). This resulted in fitting of more
686 ($n=4$) RSF models than any other species: all sightings, rest/slow travel, medium/fast travel, and
687 mill. The final RSF model for rest/slow travel contained longitude, distance from shore, and
688 depth, although only longitude ($p=0.0149$) and distance from shore ($p=0.0084$) addressed a

689 significant amount of variation in the data (Tables 2-3 and 2-4). Longitude was positively
690 correlated with use, meaning that for rest/slow travel, Risso's dolphins used eastern areas more
691 than expected relative to availability. Distance from shore was negatively correlated with use,
692 thus for rest/slow travel, dolphins selectively used areas closer to shore (including islands) more
693 often than expected relative to availability. A positive but insignificant ($p=0.0803$) correlation was
694 also found between depth and rest/slow travel, with deeper waters associated with higher use.

695

696 The final RSF model for medium/fast travel among Risso's dolphins contained latitude, distance
697 from shore, longitude, and depth, all which accounted for a significant amount of variation in the
698 data ($p\leq 0.0378$) except depth ($p=0.1298$) (Tables 2-3 and 2-4). Latitude and shore distance were
699 negatively correlated while longitude was positively correlated with relative probability of use.

700 Thus, assuming equal access to all parts of the study area, Risso's dolphins used nearshore
701 southern and eastern waters of the study area for medium/fast travel more than expected
702 relative to availability (Fig. 2-5). Depth was negatively correlated with use (i.e., increasing
703 relative use with decreasing depth), but did not account for a significant amount of variation in
704 the data (Tables 2-3 and 2-4).

705

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

713

714 Maps of predicted relative probability of habitat selection indicated that overall, Risso's dolphins
715 selectively used waters close to San Clemente and Santa Catalina islands and the mainland
716 coast, with relatively lower than expected use in the western half of San Nicolas Basin and the
717 southcentral part of the study area (Fig. 2-5). In addition, relative probability of habitat use also
718 differed by behavior in some areas as follows. Along the northeast and east side of San
719 Clemente Island and south of Santa Catalina Island, relative probability of use was higher for
720 rest/slow travel and lower for medium/fast travel than expected, coinciding with the deep
721 Catalina Basin (~1000-1300 m) and around Emery Knoll (Figs. 1-2 and 2-5). In contrast,
722 southeast of San Clemente Island, relative probability of use for medium/fast travel was higher
723 but rest/slow travel was lower than expected (Figs. 1-2 and 2-5). The latter subarea is associated

724 with the western edge of Fortymile Bank, a moderately deep (~500-800 m) flat area that drops
725 off steeply into San Clemente Canyon to the west and Coronado Canyon to the east (Figs. 1-2
726 and 2-5). Along the mainland coast relative probability of use was similarly higher than expected
727 for mill, rest/slow travel, and medium/fast travel in the subarea approximately 10 to 40 km
728 offshore, where bottom depth ranges from about 200-800 m (Fig. 2-5).

729 *2.4.4 Bottlenose Dolphin*

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

744
745 Maps of predicted relative probability of habitat selection indicated that overall and for medium-
746 fast travel, bottlenose dolphins primarily selected nearshore waters of San Clemente Island and
747 the mainland, and few subareas near San Clemente Island associated with Emory Knoll and
748 bank edges (Figs. 1-2 and 2-6). In contrast, rest/slow travel was not significantly related to any
749 variable, although latitude produced the best-fitting model according to AIC; the resulting map of
750 predicated relative probability of habitat use suggested that bottlenose dolphins selected
751 northern waters more often than expected relative to availability (Fig. 2-6).

752 **2.5 Discussion**

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

757

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

770 2.5.1 *Fin Whale*

771 During medium/fast travel, fin whales selected deep (1000-2000 m), southern, and eastern parts
772 of the study area with higher relative probability than other areas. Rest/slow travel and faster
773 travel are believed to serve different biological functions. Rest/slow travel is associated with
774 resting, feeding, and socializing while medium/fast travel is typically associated with directed
775 point-to-point movement. Mate et al. (2015) reported that four blue whales tagged in the SCB for
776 a median of 19.4 days exhibited primarily slow and fast behavioral states based on analysis of
777 dive and GPS data. Slow behavior presumably involved feeding based on deeper dives
778 occurring within a small (median 1.5 km²) area for <1 – 13.3 h, with most foraging dives during
779 daytime (Mate et al. 2015). Similarly, fin whales spent most of their time in relatively small areas
780 engaged in rest/slow travel presumed to involve feeding and foraging based on data from 53 fin
781 whales satellite-tagged for a median duration of 20 days in the SCB in 2008-2014 (Falcone and
782 Schorr 2014). During my study, rest/slow travel also included open-mouthed lunge feeding,
783 logging at the surface, and apparent courting similar to humpback whales *Megaptera*
784 *novaeangliae* based on video recordings. In contrast, Mate et al. (2015) reported that fast
785 behavior involved point-to-point movement with few turns and was consequently associated with
786 traveling and migrating rather than feeding. Likewise, medium/fast travel was associated with
787 directed point-to-point movement, with minimal changes in heading based on fin whales video
788 recorded for 10-60+ minutes (min) (Smultea unpublished data).

789
790 Higher relative probability of use of deep waters by fin whales during medium/fast travel (when
791 feeding is unlikely) is consistent with expected low densities of prey in deep areas with low
792 bathymetric relief. The deepest parts of our study area were predominately flat basins west of

793 San Clemente Island and southeast relatively near shore. Fin whale prey (small invertebrates
794 and schooling fish) are less likely to concentrate in such areas given the lack of bathymetric
795 features associated with high upwelling and biological productivity that aggregate them
796 (Hayward and Vernick 1998; Schoenherr 1991; Fiedler et al. 1998). Thus, faster travel over deep
797 waters instead likely represents transit between locally productive areas associated with feeding
798 and socializing or farther migratory destinations. In contrast, data from 56 tagged SCB fin whales
799 indicated that travel speed between estimated satellite GPS positions was faster over shallow
800 vs. deep water (Falcone and Schorr 2014). Ground-truthing of fin whale speed and headings
801 relative to behavioral states such as feeding/ foraging and point-to-point traveling are needed to
802 further clarify differences across studies in the SCB.

803

804 Overall, during 2008–2012, RSF modeling indicated highest relative probability of fin whale use
805 in deep waters of the San Nicolas Basin and the San Diego Trough in the southeastern SCB.
806 The fin whale was the only cetacean species with relative high probability of use of the San
807 Nicolas Basin west of San Clemente Island, consistent with previous studies off southern
808 California (e.g., Falcone and Schorr 2014; Jefferson et al. 2014a; Calambokidis et al. 2015). The
809 Cuvier's beaked whale is the only other cetacean species within the SCB exhibiting high affinity
810 to the San Nicolas Basin (Falcone et al. 2009). Relatively high use of the San Nicolas Basin by
811 fin whales is consistent with estimated fin whale densities being over three times higher there
812 than the Santa Catalina Basin during both the cold- and warm-water periods in 2008–2013
813 (Jefferson et al. 2014a). Similarly, Falcone and Schorr's (2014) tagging results showed extensive
814 fin whale use of the northern San Nicolas Basin in 2008–2014. However, they also reported high
815 use of the northern Santa Catalina Basin in contrast to my results indicating relatively highest
816 use of the southeastern Santa Catalina Basin. Differences may be due to spatiotemporal
817 disparities in effort and/or seasonal differences in fin whale habitat use. For example, in 2008–
818 2014, Falcone and Schorr (2014) also reported an apparent seasonal distributional shift by fin
819 whales differing from historical data. During fall and winter, fin whales apparently concentrated
820 along the mainland coast and northern Santa Catalina Basin, while during spring and summer
821 they tended to be more dispersed throughout the SCB; the northern San Nicolas Basin was used
822 year-round (Falcone and Schorr 2014; Calambokidis et al. 2015). Other cetacean surveys in the
823 California Current Ecosystem indicated that fin whale abundance and density were higher during
824 the warm-water (summer-fall) vs. the cold-water period (winter-spring) (Forney and Barlow 1998;
825 Douglas et al. 2014; Calambokidis et al. 2015). However, 2008–2012 data reported herein
826 showed that fin whale density and abundance was nearly identical during these two periods, and
827 in fact higher than historically reported SCB densities (Smultea and Jefferson 2014; Jefferson et

828 al. 2014a). The latter is consistent with the documented increase in fin whale abundance along
829 the U.S. west coast, presumably due largely to protection from whaling by the International
830 Whaling Commission since 1976 (Moore and Barlow 2011; Calambokidis et al. 2015; Jefferson
831 et al. 2015).

832 2.5.2 Gray Whale

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

842
843 Maps of predicted relative probability of habitat use suggested that gray whales were more likely
844 to select nearshore waters close to San Clemente and Santa Catalina islands in the offshore
845 migration corridor, though this prediction was not supported by a significant correlation. Sumich
846 and Show (2011) reported during winter 1988-1990 that more southbound gray whales used this
847 offshore migratory corridor and another corridor 80-90 km farther west, than the coastal
848 mainland corridor. Based on photogrammetry data, Sumich and Show (2011) suggested that
849 smaller (<11.5 m), presumably younger gray whales preferentially use the coastal migratory
850 corridor in the SCB, along with most mothers with young calves, presumably to avoid
851 documented killer whale *Orcinus orca* predation by hugging shallow waters and kelp forests
852 (Weller 2009). However, we observed four separate gray whale mother-calf pairs approximately
853 10 to 50 km from the nearest coastline, including two pairs 10 and 25 km west of San Clemente
854 Island.

855
856 There was some indication that north aspects may have been negatively correlated with relative
857 probability of use by migrating gray whales during rest/slow travel, though aspect did not account
858 for a significant amount of variation in the data ($p=0.0958$). This potential correlation may be
859 related to localized currents or other oceanographic features (e.g., upwelling, water temperature
860 changes) that influence gray whale behavior and migration movement patterns. It is possible that
861 whales use these contours for migration cues during generally east-west movements between
862 the mainland coast and outer islands in the SCB. Avoidance of predators may also influence

863 observed migratory travel-speed differences related to habitat features. The possible role of
864 aspect in relative probability of habitat use by gray whales may warrant further study.

865 *2.5.3 Risso's Dolphin*

866 Overall and during medium-fast travel, Risso's dolphins showed a clear relative preference for
867 southern and eastern nearshore waters of the study area, particularly near San Clemente island
868 and the mainland coast, where . This is consistent with other studies indicating that this species
869 inhabits deep waters over steep slopes, at least during daytime (Kruse 1989; Shane 1994; Kruse
870 et al. 1999; Carretta et al. 2000; Baird 2009; Carretta et al. 2015; Jefferson et al. 2014b, 2015).
871 However, differences emerged among habitat use when behavioral state was considered in the
872 RSF model, suggesting that different habitat features and subareas serve different biological
873 functions. Contrasting differences in behavior and habitat use were most evident along eastern
874 San Clemente Island, where the probability of rest/slow travel was highest in nearshore water
875 along steep underwater slopes. Based on daytime video recordings and field observations
876 during extended focal behavior sessions in the SCB, rest/slow travel frequently involved rest and
877 socializing characterized by tight group cohesion ($\leq 2 - 3$ adult body lengths apart), sometimes in
878 tight layers of animals, with individuals occasionally touching and crisscrossing through the
879 group (Smultea unpublished data). On one occasion, apparent mating or other socio-sexual
880 behavior was photographed close to southeastern San Clemente Island during spring (Smultea
881 unpublished data). Similarly, Shane (1995) reported that Risso's dolphins most frequently rested
882 and slow traveled up and down the coastline over a steep underwater drop off within several
883 kilometers of Santa Catalina Island. Slow daytime behavior is characteristic of night-time
884 foraging cetaceans such as spinner dolphins *Stenella longirostris* (e.g., Norris and Dohl 1980;
885 Norris et al. 1994; Benoit-Bird and Au 2003; Thorne et al. 2012), sperm whales *Physeter*
886 *macrocephalus* (Davis et al. 2007), and some regional dusky dolphin *Lagenorhynchus obscurus*
887 populations whose nighttime foraging correlates with darkness when prey associated with the
888 Deep Scattering Layer (DSL) move closer to the water surface (Benoit-Bird et al. 2004; Vaughn
889 et al. 2007; Würsig et al. 2007; Würsig Würsig and 2010). Similarly, Risso's dolphins presumably
890 feed at night on squid associated with the DSL (Leatherwood and Reeves 1983; Baird 2009;
891 Jefferson et al. 2014b, 2015).

892

893 In contrast to rest/slow travel over deep nearshore water, medium/fast travel among Risso's
894 dolphins was strongly associated with shallower nearshore water. This medium/fast travel may
895 represent directed point-to-point movement foraging and searching for prey as exhibited by
896 Southern Resident killer whales (Heimlich-Boran 1988). Alternatively, Risso's dolphins fast
897 traveling over shallower water may be the most efficient way to cross less-productive habitat to

898 reach deeper steep drop-offs in coastal areas used for daytime resting/socializing. Similarly,
899 near dusk, Hawaiian spinner dolphins (Norris and Dohl 1980; Norris et al. 1994) and dusky
900 dolphins off Kaikoura, New Zealand (Benoit-Bird et al. 2004; Vaughn et al. 2007; Würsig et al.
901 2007; Würsig Würsig and 2010), must travel fast directly to offshore nighttime feeding
902 areas to prey on DSL fishes and squid; near dawn, dolphins return at fast travel to coastal
903 waters to rest and socialize much of the day. However, unlike spinner dolphins and dusky
904 dolphins, Risso's dolphins may forage at night over habitat similar to that used for daytime
905 resting and socializing. In the SCB, tagged Risso's dolphins made deep foraging dives primarily
906 at night over steep coastal drop offs, with deepest dives occurring near dusk and dawn (Schorr,
907 unpubl. data). Apparent foraging was observed and video recorded just three times, always over
908 a steep underwater drop off, during over 18 daytime hours (h) of conducting focal observations
909 of 51 Risso's dolphin groups (mean duration of 22 min; Smultea unpublished data). Individuals
910 or pairs of foraging Risso's dolphins sprinted a short (~25 - 50 m) distance then dove steeply and
911 rapidly, surfacing 1-2 min later, with several northern right whale dolphins *Lissodelphis borealis*
912 following behind in some instances. Risso's dolphins may also employ an alternative foraging
913 strategy of kleptoparasitism. SCB Risso's dolphins were video recorded harassing and charging
914 sperm whales, with northern right whale dolphins following closely, and hypothesized this was to
915 induce sperm whales to regurgitate squid parts (Smultea et al. 2014). In summary, during
916 daytime, Risso's dolphins in the SCB preferred nearshore waters near San Clemente and Santa
917 Catalina islands and the mainland over steep underwater drop offs for essential resting,
918 socializing, and young-rearing, with a trend for rest/slow travel to occur over deeper water than
919 medium/fast travel.

920 *2.5.4 Bottlenose Dolphin*

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

929
930 Regardless of behavior, all three RSF models indicated that bottlenose dolphins selectively used
931 nearshore shallower waters more than expected based on availability, assuming equal access to
932 all parts of the study area. These preferences corresponded with coastal waters of Santa

933 Catalina Island, the mainland, and subareas off eastern San Clemente Island (Fig. 2-6). This
934 pattern is generally consistent with the coastal common bottlenose dolphin worldwide (Jefferson
935 et al. 2015). Small, vessel-based photo-identification studies suggest that some individual
936 bottlenose dolphins demonstrate long-term site fidelity to both San Clemente and Santa Catalina
937 islands (Campbell, unpubl. data). However, sightings are generally more common near Santa
938 Catalina Island (Shane 1995; Campbell et al. 2010, 2011).

939

940 For medium-fast travel, western nearshore shallow waters of Santa Catalina Basin were
941 positively correlated with high relative probability of use by bottlenose dolphins. Rest/slow travel
942 and faster travel likely are associated with different biological functions. Shane (1994) indicated
943 that fast traveling individuals near Santa Catalina Island were likely foraging. Similarly, Heimlich-
944 Boran (1998) reported that killer whales in the San Juan Islands travel rapidly while foraging.
945 Faster travel in deeper waters could also be related to fast transit between feeding or other
946 areas. In contrast, winter behavioral studies of bottlenose dolphins near Santa Catalina Island in
947 1983-1991 reported that rest/slow travel was typically associated with socializing (i.e., touching,
948 orienting towards one another) and active feeding (diving repeatedly in one area, facing in
949 varying directions when surfacing; Shane 1994). Similarly, mill and rest/slow travel during our
950 2008-2013 aerial surveys often included socializing and probable feeding (individuals criss-
951 crossing while performing short dives) based on extended focal follows recorded on video
952 (Smultea unpublished data).

953

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

962

2.6 Conclusions

963 Behavioral state was related to habitat use of fin whales, gray whales, Risso's dolphins, and
964 bottlenose dolphins in deep waters of the SCB. RSF modeling showed that some subareas and
965 environmental features were selected proportionally more frequently than available in the study
966 area, assuming equal access to all parts of the study area. However, the fundamental behavioral
967 functions of these preferences remain poorly understood. Point-sampling protocol used to gather

968 behavioral state data was commonly limited to relatively short (~10-30 sec) periods with animals
969 observable at or near the water surface from the aircraft (to an estimated depth of 20-30 m).
970 However, the plane circled back to confirm species, group size for ≥ 5 -60+ min during ~19% of all
971 sightings, and 52% of large whale sightings. Another caveat is that it was unknown what animals
972 were doing while diving beyond view. However, SCB satellite tagging results (Falcone and
973 Schorr 2014; Mate et al. 2015) are consistent with the premise that rest/slow travel (including
974 mill) is more likely to include feeding than fast travel. Detailed analysis of the over 50 h of
975 behavioral data collected from our circling aircraft with HD video may further elucidate the
976 functional importance of behavioral states relative to differential habitat use.

977

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

988

989 In summary, results provide a better understanding of how behavioral state influences habitat
990 selection of little-studied offshore cetaceans, illustrating the complexity of differentiating naturally
991 occurring behavioral variability from potential anthropogenic disturbance of cetaceans in the
992 SCB. Findings are useful for adaptive management relative to concerns regarding increasing
993 anthropogenic activities. For example, some areas of relative high probability of use for
994 important cetacean behaviors (e.g., resting, feeding, foraging) overlap with areas used regularly
995 for military training activities involving Mid-frequency Active (MFA) sonar (DoN 2008b, 2011,
996 2014). While this study provides an important five-year baseline, further research is needed to
997 refine cetacean habitat use relative to critical behaviors and periods, and to monitor potential
998 changes in habitat usage and species viability in the face of climate change and growing
999 anthropogenic activities.

1000

CHAPTER 3

1001

CETACEAN BODY SIZE, GROUP SIZE AND GROUP COHESION

1002

3.1 Synopsis

1003 In open environments, prey are hypothesized to reduce predation risk through increased body
1004 size, group size, or tighter group cohesion. Cetacean group size and spacing change in
1005 response to natural and human-related factors (e.g., predators, behavior, noise exposure, close
1006 vessel approaches). A comparative approach was used to test the prediction that as cetacean
1007 species body size increases, group size decreases, cohesion decreases, and individuals are
1008 more likely to occur alone. Sighting data were collected in the Southern California Bight (SCB)
1009 from 2008-2013 during 18 one-week-long aerial surveys totaling 82,502 km of observations
1010 along systematic transect and other effort. Point-sampling protocol was used to document the
1011 first-observed group cohesion (i.e., maximum nearest-neighbor distance estimated in adult Body
1012 Lengths [BL]) of cetacean sightings. Non-parametric statistical analyses were used to examine
1013 relationships between group size, cohesion and body length (using as a proxy). A total of 66
1014 blue whale, 130 fin whale, 68 gray whale groups, 320 Risso's dolphin, 107 bottlenose dolphin,
1015 and 362 common dolphin spp. groups were observed. Among each taxonomic group, as body
1016 size increased, group size decreased, group cohesion decreased (i.e., individuals were spaced
1017 farther apart), and individuals were more likely to be alone. Differences in the same habitat may
1018 reflect evolutionary adaptations to predation risk and food resource availability, as predicted by
1019 terrestrial mammal group-living patterns. Larger group size benefits may include reduced
1020 predation pressure and improved prey detection/mate access, at the risk of increased resource
1021 competition.

1022

1023 Key words: cetacean, blue whale, fin whale, Risso's dolphin, predation, cohesion

1024

3.2 Introduction

1025 In open environments where predation risk is high, prey are hypothesized to reduce such risk
1026 through increased body size, group size, and/or tighter group cohesion (e.g., Krebs and Davies
1027 1997, Ch 2; Ramakrishnan and Coss 2001; Davies et al. 2012). Species body size, group size
1028 and group cohesion are thought to represent adaptive trade-offs between the costs and benefits
1029 of group living. Large body size requires increased energy costs while large group size increases
1030 intra-specific competition for resources. Each strategy is commonly considered an adaptive
1031 response to predation pressure in open habitats lacking cover from predators, due to the dilution

1032 effect and other anti-predator benefits attributed to group formation (e.g., Jarman 1974; Norris
1033 and Dohl 1980; Gowans et al. 2008). Sociality and huddling are thought to reduce predation risk
1034 through predator confusion and improved sensory integration that enhances information transfer
1035 regarding predator detection (Norris and Dohl 1980; Kie 1999; Hebblewhite and Pletscher 2002).

1036

1037 Given the costs and benefits to forming groups, behavioral ecology theory predicts that group
1038 size should reflect surrounding environmental pressures, resulting in an optimal group size
1039 relative to body size (Jarman 1974; Wittenberger 1980; Owen-Smith 1988). A classic example of
1040 evolutionary tradeoffs between larger body size or larger group size is illustrated by comparative
1041 studies of African ungulates in open savannah habitat characterized by high predation risk.
1042 Jarman (1974) reported that in the open African savannah, as ungulate body size increases,
1043 group size decreases. This inverse relationship is believed to be a functional tradeoff between
1044 increased energy needs of larger body size leading to increased home ranges or seasonal
1045 migrations with decreased risk of predation. At the extreme, the energy required for carnivore
1046 predators to kill and consume an Eland buffalo (*Taurotragus oryx*) or giraffe (*Giraffa*
1047 *camelopardalis*) is presumably higher (due to the potential of predator injury relative to strength
1048 of the prey) than to kill an antelope such as an impala (*Aepyceros melampus*) that is over one-
1049 third smaller (Davies et al. 2012, Ch 2). The anti-predator behavior of the impala relies more on
1050 larger group sizes and the dilution and predator confusion effects. In open habitats, trade-offs
1051 between increasing group size and decreasing body size are predicted to follow a continuum.

1052

1053 Group cohesion patterns may also follow a continuum as a function of tradeoffs between
1054 ecological pressures. Pitcher (1983) proposed the elective group size concept, assuming that
1055 distance between individuals within a group is a functional trade-off between the benefits and
1056 costs of living in a group. For example, animals tend to increase cohesion when frightened or
1057 after feeding, but disperse when hungry and foraging (Romey 1997; Krause and Ruxton 2002;
1058 Würsig and Pearson 2014). In the open ocean, small schooling fishes such as herring and
1059 anchovy occur in large, tightly spaced schools of highly synchronized individuals (e.g., Norris
1060 and Dohl 1980). Tighter spacing and density changes in motion between individuals induce the
1061 “dilution effect” and the “confusion effect”, decreasing predation risk (e.g., Scott-Samuel et al.
1062 2015). Tight cohesion and coordinated movement are also beneficial by reducing energy
1063 expenditure due to “drafting” (Marras et al. 2015). In contrast, the much larger bluefin tuna occur
1064 in smaller, less-cohesive groups presumably related to increased body size resulting in reduced
1065 predation pressure (Newlands and Porcelli 2008). Group cohesion is further influenced by
1066 behavioral and physiological motivation and perceived threat. If threatened, many species

1067 increase group cohesion. In contrast, the same individuals may spread out to forage and feed in
1068 areas where predation risk is perceived to be lower or the benefits (e.g., high prey density,
1069 increased mating opportunities) appear to outweigh the risk of predation (Frid and Dill 2002).

1070

1071 Following the group formation theory of behavioral ecology, small-sized odontocetes inhabiting
1072 open-ocean habitat form relatively large, tightly spaced groups (in the hundreds to thousands) as
1073 perhaps the only way to minimize predation in a seascape void of hiding structures (Norris and
1074 Schilt 1988; Norris and Dohl 1980; Gowans et al. 2008). This behavior appears to be viable as
1075 long as sufficient resources can be found to support the group (Acevedo-Gutierrez 2009).
1076 Among such odontocetes, group size is also hypothesized to be positively correlated with
1077 relatively large home ranges and patchy yet dense food sources, such as small schooling fish
1078 (Gowans et al. 2008). Odontocete feeding efficiency on fish schools is increased through
1079 cooperation among group members to corral and take turns consuming the fish (Würsig and
1080 Würsig 1980; Benoit-Bird and Au 2009; Vaughn-Hirshorn et al. 2013). Success of cooperative
1081 feeding strategies is hypothesized to rely on intraspecific communications to orchestrate and
1082 finely tune spacing and coordination between individuals (Norris and Schilt 1988). For example,
1083 killer whales, spinner dolphins, common dolphins, dusky dolphins and pilot whales spread out
1084 laterally while foraging to maximize prey detection, and then decrease individual spacing while
1085 feeding and resting, the latter to minimize predation (Norris and Dohl 1980; Gowans et al. 2008;
1086 Henderson 2010; Würsig and Pearson 2014).

1087

1088 Based on behavioral ecology theory and terrestrial and marine studies, species adapt to the
1089 same environment in different ways, while adaptations may differ between populations of the
1090 same species in different environments across invertebrates, amphibians, fishes, birds,
1091 terrestrial carnivores, and cetaceans (e.g., Würsig and Würsig 1980; Basolo and Wagner 2004;
1092 Hoare et al. 2004). The optimal adaptive balance between body size, group size, and group
1093 cohesion relative to resource availability and predation pressure may vary across a continuum.
1094 Additional variation is predicted to occur relative to local, diurnal, seasonal, and geographical
1095 variations in resource availability and predation risk. Group size and morphology among the
1096 same species of odontocetes can vary regionally and temporally depending on site-specific
1097 ecological conditions including habitat complexity, distribution and abundance of preferred prey,
1098 predation pressure, and behavioral state (e.g., Perrin et al. 1999; Henderson 2010; Würsig and
1099 Pearson 2014). Studies of various fishes and terrestrial mammals suggest that in open habitats
1100 where predation risk is high, group size and body size are larger and group cohesion is tighter.
1101 Larger group size of dolphins in open waters has been hypothesized to be linked to increased

1102 predation pressure (Norris and Schilt 1988; Gyax 2002a; Gowans et al. 2008). Dusky dolphin
1103 populations inhabiting three distinct marine habitats exhibit different foraging and social
1104 strategies related to variations in availability of prey, habitat, and predation risk, with larger group
1105 sizes found in more open habitats, and small stable group formation where predation risk is low
1106 (Würsig and Pearson 2014). A review of limited empirical studies and general trends in the
1107 degree of habitat complexity (i.e., openness) and home range have led to a framework predicting
1108 that delphinid group size and home range increase with habitat openness; however, this
1109 framework remains to be empirically tested across more cetacean species (Gowans et al. 2008).

1110

1111 Group size and group cohesion often increase or sometimes decrease (i.e., disaffiliation,
1112 individuals fleeing) in response not only to predators but also apparent threatening
1113 anthropogenic stimuli such as vehicles, vessels, helicopters, human hunters and tourism (e.g.,
1114 Frid and Dill 2002; elk *Cervus elaphus*, Hebblewhite and Pletscher 2002; bottlenose dolphins,
1115 Smultea and Würsig 1995; sperm whales, Smultea et al. 2004, 2014). Frid and Dill (2002)
1116 reviewed numerous animal taxa and situations and concluded that reactions to predators and
1117 non-lethal disturbance stimuli have similar negative costs: a reduction in time spent in critical
1118 behavioral functions (e.g., parental care, feeding, mating) that can lead to decreased fitness and
1119 reproductive success if chronic or repetitive. However, as group size varies inter- and intra-
1120 specifically as a function of a number of interacting ecological pressures (e.g., resource
1121 distribution, predation risk, behavioral activity; Jarman 1974; Connor et al. 2000; Gowans et al.
1122 2008), baseline data on naturally occurring group size and cohesion and the influence of site-
1123 specific ecological factors (e.g., species body size, food distribution) need to be established for a
1124 particular region, set of species and seasonal distribution of resources before using these
1125 parameters as behavioral indicators. For example, Henderson (2010) found that behavioral state
1126 of common dolphins in the SCB was correlated with group cohesion: dolphin were less cohesive
1127 while traveling rapidly than while resting or milling; vocalizations were also higher while spread-
1128 out during fast travel.

1129

1130 The objective of this study was to determine whether there is a predictable relationship between
1131 cetacean body length (using species as a proxy), group size, and group cohesion. Frameworks
1132 proposed for terrestrial and marine species lead to development of the study prediction that as
1133 cetacean body size increases, group size and group cohesion should decrease as trade-offs to
1134 reduce predation risk and adapt to patchily distributed food resources characteristic of open-
1135 ocean environments. Group size and cohesion data contribute to further understanding what
1136 constitutes a socially synchronized group and the variations thereof (Krause and Ruxton 2002).

1137 Both group size and cohesion are known to change in response to natural and human-related
1138 factors (e.g., predation risk, behavioral state such as resting or foraging, noise exposure, close
1139 vessel approaches; Richardson et al. 1995; Smultea and Würsig 1995; Visser et al. 2011). Data
1140 on group size and cohesion of poorly known offshore cetacean species may also provide a
1141 reference scale for potential behavioral indicators of anthropogenic disturbance. The proposed
1142 predictive framework builds on the predictive framework of Gowans et al. (2008) for delphinids
1143 by considering group cohesion, incorporating an additional dimension to understanding the
1144 evolution of cetacean social strategies.

1145 **3.3 Methods**

1146 *3.3.1 Study Area and Species*

1147 The study area in the SCB encompassed waters extending from approximately 10 km off the
1148 mainland coast up to approximately 200 km offshore, and from San Diego to approximately 100
1149 km north near Los Angeles (approximately 17,555 km²; Fig. 3-1). The study area includes San
1150 Clemente and Santa Catalina islands, the southernmost California Channel Islands. Water depth
1151 in the study area ranged from 0 to approximately 2000 m. Bathymetric topography is highly
1152 variable, characterized by underwater canyons, seamounts, a relatively narrow continental shelf,
1153 deep flat basins, and steep slopes (Fig. 3-1). Aerial surveys were flown out of Montgomery
1154 Airport, San Diego using primarily (79 of 90 flight days) a small high-wing, twin-engine
1155 Partenavia P68-C or P68-OBS (glass-nosed) airplane equipped with bubble observer windows
1156 on the left and ride sides of the middle seats. A high-winged twin-engine Aero Commander
1157 airplane was used on nine days and a Bell 206 helicopter on two days. Aerial survey periods
1158 were typically one-week long and occurred at least once during every month of the year except
1159 December from 2008 - 2013. Observations usually occurred between 9:00-15:00 Pacific
1160 Standard Time (depending on survey conditions) to maximize overhead light and sighting
1161 conditions.

1162
1163 Analyses were limited to the six most commonly sighted cetacean species with sample sizes
1164 considered adequate to conduct meaningful statistical analyses ($n > 20$). In descending order of
1165 body length these six species included the blue whale, fin whale, gray whale, Risso's dolphin,
1166 bottlenose dolphin, and unidentified common dolphin spp. From the aircraft, short- and long-
1167 beaked common dolphins were difficult to differentiate given the subtle physical differences
1168 between the two species (Heyning and Perrin 1994; Perrin 2009; Smultea and Jefferson 2014)
1169 from the high survey altitude (213-305 m), and the image quality and resolution (10.1-18
1170 megapixels) limitations of cameras at the time. Only 23% of the 564 common dolphin sightings

1171 photographed and examined by a species expert (T.A. Jefferson, Clymene Enterprises, Inc.)
1172 were confirmed to species: 17% as short-beaked common dolphin and 6% as long-beaked
1173 common dolphins. Species confirmation was typically only based on one or at most a few
1174 individuals in large groups of hundreds of individuals. Thus, for the purposes of this study all
1175 three species were pooled to increase sample size.

1176 *3.3.2 Data Collection and Equipment*

1177 The survey team consisted of one (2008-2010) or two pilots (2011-2013), two trained marine
1178 mammal biologists and a data recorder. Two biologists observed from center seats; the data
1179 recorder operated from the front right co-pilot seat (2008-2010) or rear left bench seat (2011-
1180 2013). Survey design followed line-transect protocol (Buckland et al. 2015) to obtain sighting
1181 data for estimating density and abundance (Jefferson et al. 2014a). Systematic survey lines
1182 were oriented generally southeast-northwest perpendicular to bathymetric contours (Fig. 1-2).
1183 Surveys were flown at speeds of approximately 100 knots ground speed and altitudes of 227-
1184 357 meters (m).

1185

1186 Sightings used for analysis were collected during observation effort along systematic line
1187 transect and connector survey legs (shorter lines connecting and perpendicular to systematic
1188 lines) to ensure systematic data collection. Data collected included date, time, species, Global
1189 Positioning System (GPS) location, best estimated group size including estimated number of
1190 calves, group cohesion (maximum distance between nearest neighbors within a group,
1191 estimated in adult BL), observation effort on or off, survey leg type, and environmental data
1192 (Beaufort sea state, visibility, glare, cloud cover). Typical photos for each of the study species
1193 from the aerial perspective of the aircraft showing examples of group cohesion are provided in
1194 Fig. 3.1 and 3-1. For the purposes of this study, a “group” was defined as >50% of polarized
1195 individuals engaged in the same behavioral state (e.g., travel, mill, rest) within visual range of the
1196 observers to a maximum of 100 BL apart (after Norris and Schilt 1988; Baird and Dill 1996;
1197 Lusseau et al. 2005; Table 1). Within observed groups, individuals were typically within 10-20 BL
1198 of each other but occasionally up to 50-100 adult BL apart. For common dolphins that formed
1199 much larger groups than other cetaceans (on the order of hundreds to thousands), cohesion was
1200 based on distinct subgroups that met the above group definition. A “calf” was defined as an
1201 animal less than or equal to one-half the body length of the adult individual with which it was
1202 closely associated (within 0.5 adult BL). Point-sampling (Mann 2000; Martin and Bateson 2011)
1203 was used to record the first-observed group size and cohesion. Sightings were circled as needed
1204 to confirm these parameters including with photographs or High Definition (HD) video. This

1205 sometimes included conducting a focal behavioral group session for up to 60 min as part of a
1206 separate study (Smultea et al. 2014; Lomac MacNair and Smultea 2016).

1207

1208 Data were collected using a variety of software and hardware that changed with technological
1209 advances. In 2008-2009, BioSpectator software was used on a Palm Pilot TX or an Apple
1210 iPhone or iTouch. In 2010-2011, a customized Excel spreadsheet was used on a Windows-
1211 based laptop. In 2011-2013, customized Mysticetus™ System (Mysticetus™) software was
1212 used on a laptop. GPS data were recorded using a Wide-Area Augmentation System (WAAS)
1213 handheld and aircraft Garmin, and a Bluetooth or USB GPS. Each new entry was automatically
1214 assigned a time stamp, a sequential sighting number, and a GPS position. Photographs and
1215 video recordings were made through a small opening porthole through either the co-pilot seat
1216 window (2008-2010) or the rear left bench-seat window (2011-2013). Species and group size
1217 were documented as needed with a DSLR camera (Canon EOS 40D or D60 or Nikon D300 or
1218 D7000 with 100-400 mm Image Stabilized zoom lenses), a Sony Handycam HDR-XR550 or
1219 HDR-XR520 video camera, and Steiner 7 X 25 or Swarovski 10 X 32 binoculars.

1220

3.3.3 Data Analysis

1221 The three variables of interest consisted of one response variable (group size) and two
1222 explanatory variables; (group cohesion and species [as a proxy for species body length]). Table
1223 3-2 identifies the mean reported body lengths of the six study species, prioritizing data collected
1224 nearest to the SCB. Statistical analyses were conducted using R software. Due to the non-
1225 parametric nature of the data, Mann-Whitney U tests and Kruskal-Wallis tests were applied to
1226 determine if group size and group cohesion varied significantly between suborder (Mysticete
1227 relative to Odontocete) and also between species or pooled species within each suborder. For
1228 investigations into group cohesion only those groups with two or more animals were included,
1229 while all investigations into group size included single animals. Where there were significant
1230 differences within the suborder, post-hoc tests were applied to determine which species differed
1231 significantly from another. These non-parametric post-hoc tests were achieved using functions
1232 available in the R-package 'PMCMR' (The Pairwise Multiple Comparison of Mean Ranks
1233 Package, Pohlert 2016).

1234

3.4 Results

1235 During 18 aerial surveys conducted in 2008–2013, there were a total of 670 sightings of an
1236 estimated 88,487 individuals of the six study species during approximately 82,502 km of
1237 observation effort (Fig. 3-3). Overall, 97 percent of the total flight time was associated with a
1238 Beaufort sea state less than 4. Numbers of groups seen for each species in descending order of

1239 frequency were 362 common dolphin spp., 320 Risso's dolphin, 130 fin whale, 107 bottlenose
1240 dolphin, 68 gray whale, and 66 blue whale. Associated summary statistics, total number of
1241 individuals by species, and total number of sightings by species are shown in Table 3-1 and 3-2
1242 and Fig. 3-3 through 3-6 and include frequency plots and box plots.

1243

1244 Frequency distributions of group size and group cohesion by species are shown in Fig. 3-3 and
1245 3-4. Blue whale group size ranged from 1-6 and fin whales occurred in groups of 1-4 animals
1246 (Table 3-1). Gray whale group size ranged from 1 to 9 animals, however the most common
1247 group size for these baleen species was 1. In contrast, the three dolphin species were rarely
1248 seen as a single individual (Fig. 3-4). Common dolphins (pooled) occurred in the largest group
1249 sizes (estimated maximum 2,500 individuals) while bottlenose and Risso's dolphins occurred in
1250 groups of no more than 150 animals (estimated maximum 120 Risso's dolphins and 150
1251 bottlenose dolphins, respectively) (Table 3-2 and Fig. 3-4).

1252

1253 The non-parametric analysis found significant differences in both group size (Mann-Whitney U
1254 test, $W=198359.5$, $p<0.001$) and group cohesion (Mann-Whitney U test, $W=63433.5$, $p<0.001$)
1255 between mysticete and odontocete suborders. Group size and group cohesion also differed
1256 significantly for both the odontocete species (Kruskal Wallis, group size $\chi^2=356.84$,
1257 $df=2$, $p<0.001$, Kruskal Wallis, group cohesion $\chi^2=10.54$, $df=2$, $p=0.005$) and the
1258 mysticete species (Kruskal Wallis, group size $\chi^2=8.65$, $df=2$, $p=0.013$, Kruskal Wallis,
1259 group cohesion $\chi^2=27.97$, $df=2$, $p<0.001$). For the odontocete species, common
1260 dolphin species were found to occur in significantly larger groups than both Risso's ($p<0.001$)
1261 and bottlenose dolphins ($p<0.001$), but there was no significant difference in the group sizes of
1262 Risso's and bottlenose dolphins. There was also no significant difference in the group cohesion
1263 of Risso's and bottlenose dolphins; however, bottlenose dolphin group cohesion was found to
1264 differ significantly to that of common dolphin species ($p=0.008$). There was no significant
1265 difference between the group cohesions of Risso's dolphins and common dolphin species. Of
1266 the mysticete species gray whales had a significantly tighter group cohesion than both blue
1267 whales ($p<0.001$) and fin whales ($p<0.001$), though there was no significant difference in the
1268 group cohesion of blue and fin whales. In terms of group size only blue whale group size differed
1269 significantly to gray whales ($p=0.015$) but not to fin whales, and gray whale group size also did
1270 not vary significantly to fin whale group size.

1271

1272 Mean group sizes for the three mysticetes (gray whale 2.1, Standard Deviation [SD] 1.40; fin
1273 whale 1.7, SD 0.90; and blue whale 1.6, SD 1.10) were much smaller than for the three

1274 odontocetes (Tables 3-1 and 3-2). Mean group size was largest for the pooled common dolphins
1275 (254.9, SD 408.50), followed by the bottlenose dolphin (18.3, SD 21.70) and Risso's dolphin
1276 (16.6, SD 16.30). Group cohesion among baleen whales was closest for gray whales (1.7 BL,
1277 SD 3.30), followed by blue and fin whales (12.0 BL, SD 2.62 and 4.9 BL, SD 6.40, respectively).
1278 Group cohesion for the three odontocetes were similar: Risso's dolphin (7.7 BL, SD 12.80),
1279 bottlenose dolphin (5.2 BL, SD 9.90), and common dolphin spp. (5.3 BL, SD 5.30).

1280

1281 The blue whale sample size for at least two individuals in a group was too small to be tested, as
1282 most blue whales were single individuals. However, when proportional comparisons were made
1283 assessing the probability of each species occurring in group size of 1, the results supported the
1284 overall gist of the hypothesis: blue whales were the most likely to occur in a group size of one,
1285 which is actually the "largest" group spacing among all the species examined. Furthermore, the
1286 probability of a species occurring in group size of 1 generally decreased with increasing group
1287 size.

1288

3.5 Discussion

1289 Examination of species-specific relationships for body size, group size and group cohesion
1290 suggested predictable patterns as a function of presumed semi-pelagic and pelagic predation
1291 pressure and clumped, unpredictable prey patches. Group-size patterns of odontocetes in deep
1292 waters of the SCB match predictions for social structure (in terms of group size and cohesion) in
1293 open terrestrial habitat reported for distant-related open-savannah ungulates (e.g., Jarman 1974;
1294 Davies et al. 2012, Ch 2), and semi-pelagic and pelagic deep delphinids (Gygax 2002a,b; Gowans
1295 et al. 2008).

1296 Separate correlative but parallel relationships were found within odontocetes and mysticetes,
1297 respectively. Species body size was inversely related to group size and group cohesion within
1298 each of these taxonomic groups on a different scale. The separate scaling patterns found between
1299 mysticetes and odontocetes may be related to phylogenetic differences that led to different
1300 foraging strategies, body size, energy requirements, and anti-predator responses (Ford and
1301 Reeves 2008). Shared ancestry between closely related species may result in similar behaviors
1302 (Beauchamp 2014, Ch 9).

1303

1304 Among mysticetes, blue whales were most likely to be observed alone, in the smallest groups,
1305 and with the largest separation distance between individuals within groups. This pattern changed
1306 on a continuum for the smaller-sized fin whale and the even smaller-sized gray whale. Gray whales
1307 had the largest mean group size and the tightest group cohesion among the three mysticete
1308 species. Killer whale predation on whales is common in California waters, while shark predation is

1309 likely most common on small dolphins and pinnipeds (Weller 2009). Smaller-body-sized species
1310 are presumably more vulnerable to predatory attacks. Forming larger group sizes is predicted to
1311 reduce predation pressure on individuals by diluting the odds of being preyed upon, among other
1312 benefits (Gowans et al. 2008; Acevedo-Gutierrez 2009; Pearson and Würsig 2013). In contrast,
1313 the largest body-sized cetaceans in the SCB, the blue and fin whales, are presumably less likely
1314 to be attacked than smaller-sized species. Though both species and in fact all cetacean species
1315 are known to be consumed at least occasionally by killer whales (Jefferson et al. 1991), large
1316 baleen whales and sperm whales are presumably a higher risk prey target than smaller more
1317 defenseless delphinids, and have been documented to inflict serious injuries to attacking killer
1318 whales (Ford and Reeves 2008). Larger, tighter common dolphin and gray whale groups match
1319 presumed higher predation pressure associated with smaller relative body size among
1320 odontocetes and mysticetes, respectively. Similarly, common dolphins had much larger group
1321 sizes and tighter group cohesion than the larger-bodied Risso's and bottlenose dolphins. The lack
1322 of significant difference between Risso's and bottlenose dolphins may be related to similar body
1323 sizes.

1324

1325 While results suggested general trends, cetacean group size and group cohesion are known to
1326 vary spatiotemporally and by behavioral state, particularly among delphinids (e.g., Henderson
1327 2010), and presumably also influence general group size and cohesion patterns. These influences
1328 are examined in Chapter IV, as this chapter focused on examining a simple potential predictive
1329 framework within which to compare inter-specific differences and relationships between body size,
1330 group size and cohesion. Based on a literature review, this correlation does not appear to have
1331 been previously examined among cetaceans and merits further investigation and testing.

1332

3.6 Conclusion

1333 In conclusion, the initially proposed hypothesis was supported when mysticetes were considered
1334 separately from odontocetes. Within each of these two groupings, as species body length
1335 decreased, group size increased and group cohesion decreased with decreasing likelihood of
1336 occurring alone. Different cetacean species have exhibited ecological diversion in the same
1337 habitat in response to differing predation pressure and food resource availability as predicted by
1338 terrestrial mammal group-living patterns. As hypothesized, blue whales as the largest cetacean,
1339 occurred in small, dispersed groups and were most likely to occur alone compared to all other
1340 smaller cetaceans. The latter pattern progressively continues with other species as body size
1341 decreases. While these correlative patterns were apparent in the SCB, further research is
1342 needed to corroborate or reject this trend in other open marine habitats. Group cohesion data
1343 are difficult to collect from the low vantage point of vessels, but the "bird's eye" perspective of an

1344 overflying aircraft operating outside the zone of sound disturbance to cetaceans offers a unique
1345 3-dimensional and wide-angle view of group structure and spacing.

1346

1347 In summary, similar to their terrestrial counterparts, cetacean group size and social complexity
1348 appear to vary with body size and environmental conditions related primarily to resource
1349 distribution and availability, balanced with presumed predation risk. As summarized by others
1350 (e.g., Gowans et al. 2008; Acevedo-Gutierrez 2009; Pearson and Würsig 2013), open-ocean
1351 habitats presumably represent the most formidable ecological pressures to form large groups to
1352 minimize predation pressures as well as challenges to finding dispersed patches of food
1353 sufficient to sustain large group of cetaceans.

1354

1355 Data lend insight into baseline behavior and ecological triggers influencing behavior, and provide
1356 site-specific life history information on group size and group cohesion patterns of cetaceans
1357 inhabiting offshore SCB waters. These parameters define species-specific behavioral indicators.
1358 Such information is needed to differentiate naturally occurring behavior relative to potential
1359 impacts of anthropogenic sources. Correlative patterns reported here between species body
1360 size, group size and group cohesion present a preliminary predictive framework for semi-pelagic
1361 and pelagic-dwelling small odontocete and mysticete species that remains to be examined in
1362 other environments and among other populations and species.
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CHAPTER 4

1365

INFLUENCES ON CETACEAN BEHAVIOR, GROUP SIZE AND

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COHESION, SOUTHERN CALIFORNIA

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4.1 Synopsis

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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.

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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

1394

1395 Phylogeny and the environment are predicted to shape behavioral ecology through adaptation
1396 relative to the distribution of resources (e.g., food, mates) balanced with predation risk (Jarman
1397 1974; Sumpter 2010). Animal behavior, group size, and group cohesion may thus vary intra- and
1398 interspecifically in response to local variability in ecological factors. It is important to identify
1399 environmental and social factors that influence animal behavior and habitat use to assess the
1400 opportunity for potential spatiotemporal management and conservation measures, and to
1401 understand and differentiate how these patterns may change in response to anthropogenic
1402 activities (Blumstein and Fernández -Juricic 2010; Berger-Tal et al. 2011). Conservation
1403 behavior focuses on linking ecological principles with practical applied conservation and
1404 management (Blumstein and Fernández -Juricic 2010). The practical conceptual framework
1405 suggested for effective implementation of conservation behavior by Berger-Tal et al. (2011) is to
1406 develop standardized approaches for quantifying behavior and habitat use, subsequently
1407 measure potential changes related to anthropogenic effects, and then evaluate effectiveness of
1408 management and conservation strategies. Two recommended primary behavioral ecology
1409 domains (i.e. pathways) to accomplish this step-wise approach are studies of: (1) social and
1410 reproductive behavior patterns, and (2) foraging and predator-prey related behaviors and
1411 patterns (Berger-Tal et al. 2011)

1412

1413 Among terrestrial and aquatic animals, spatiotemporal distribution and availability of needed
1414 resources influence behavior and habitat use (e.g., Gittleman 1989; Kappeler et al. 2013; Rooker
1415 et al. 2013). Different species in the same region may adjust group size, spacing between
1416 individuals, distribution and behavioral tactics (e.g., foraging patterns) in response to changes in
1417 resource availability and related tradeoffs between group size and predation risk (Burkpile et al.
1418 2013; Hopcraft et al. 2014). Spatiotemporal variations and patterns in cetacean behavior, group
1419 dynamics, and habitat use are better described for easily accessible coastal cetaceans than for
1420 more offshore open and semi-pelagic ocean environments (Gowans et al. 2008; Würsig 2009;
1421 Würsig and Pearson 2014). These studies show that behaviors are strongly influenced by
1422 calving and mating seasons, distribution and behavior of prey, and presumed predation pressure
1423 that vary accordingly across regions and populations.

1424

1425 Most inter- and intra-specific comparisons showing variable behavioral patterns across
1426 cetaceans have involved coastal gray whales, humpback whales, and coastal bottlenose dolphin
1427 and dusky dolphin populations (Darling et al. 1998; Defran et al. 1999; Würsig and Würsig 2010).
1428 Some pelagic sperm whale populations have also been well-studied from relatively large, live-

1429 aboard vessels that follow behind the whales for extended weeks and months (Biggs et al. 2000,
1430 2005; Whitehead 2003; Jochens et al. 2008). Coastal feeding bowhead and gray whales display
1431 different feeding strategies depending on regional and seasonal prey availability (Würsig et al.
1432 1985; Dunham and Duffus 2002). Dusky dolphin populations off Argentina feed during daylight,
1433 cooperatively herding bait fish (Würsig and Würsig 1980; Vaughn et al. 2007, 2010). In contrast,
1434 dusky dolphin populations off Kaikoura, New Zealand rest nearshore during the day and forage
1435 in offshore deep waters at night when vertically migrating fish are closer to the surface (Benoit-
1436 Bird et al. 2004; Würsig and Würsig 2010). In comparison, relatively little has been described for
1437 social or group characteristics or foraging patterns of less accessible, oceanic species including
1438 blue and fin whales, and Risso's, offshore bottlenose and common dolphins, as well as offshore
1439 migrating gray whales (Jefferson et al. 2014b, 2015; Perrin 2009; Henderson 2010; Visser
1440 2014). However, similar to more well-described coastal cetacean species, semi-pelagic and
1441 pelagic cetacean species are expected to display behavioral tactics adapted to diurnal and
1442 seasonal changes in food resources as well as availability of mates and presence of calves.

1443
1444 Because it is expensive and difficult to track offshore cetaceans, and they are at the surface for
1445 only brief periods, data on group behavior are limited or lacking. Most such studies have been
1446 based from vessels, though these platforms are challenged by relatively low vantage points, and
1447 the vessel itself can be a potential source of disturbance (Constantine 2001; Dawson et al. 2008;
1448 Henderson et al. 2014b). An aerial platform (e.g., fixed wing aircraft, helicopter, dirigible, blimp,
1449 unmanned aerial system), as used in this study, provides the advantage of an overhead three-
1450 dimensional view of animals at and somewhat below the water, such that near-surface numbers,
1451 behaviors, and intraspecific orientations and spacing can be seen and video recorded (Würsig et
1452 al. 1985; Smultea and Würsig 1995; Durban et al. 2015). This latter technique has the further
1453 advantage of not disturbing the animals when proper protocols are followed, including sufficient
1454 altitude, flying outside the air-to-water cone of sound, and other precautions such as not letting
1455 the airplane's shadow fall on members of a group (Richardson et al. 1995; Patenaude et al.
1456 2002; Lomac-MacNair and Smultea 2016).

1457 **4.3 Objectives and Hypotheses**

1458 The purpose of this study was to look beyond simplified inter-specific correlations and predictive
1459 framework between cetacean species with respect to body size, group size and group cohesion
1460 explored in Chapter III by adding in temporal, spatial environmental, and calf presence
1461 explanatory factors to examine their influence on behavioral state, group size and group
1462 cohesion. To maximize sample size, analyses focused on the same six most commonly
1463 observed cetacean species as used in Chapter III. Hypotheses focused on whether (1) calf

1464 presence relative to reported peak calving and mating seasons influenced group characteristics,
1465 and (2) diurnal and seasonal behavioral state patterns followed presumed prey distribution
1466 based on reported predominant nocturnal foraging tactics of Risso's and common dolphins.

1467

1468 Response variables were selected based on results of other studies identifying quantifiable
1469 parameters shown to be responsive to natural threats (e.g., predators) and human-related
1470 disturbance: group size and group cohesion (i.e., inter-individual distance). Similar to Chapter III,
1471 the study goal included gathering species- and SCB-specific baseline data on group size and
1472 cohesion to provide a source of comparison at the scale of the SCB to evaluate whether these
1473 parameters change as a result of anthropogenic disturbance. Baseline data were further meant
1474 to provide potential behavioral indicators of future anthropogenic disturbance.

1475

1476 The general null hypothesis inversely matching the study objectives above was as follows:

- 1477 • **Null Hypothesis:** Behavioral state, group size, and group cohesion of cetaceans in the SCB
1478 are not influenced by calf presence and environmental factors.

1479

1480 The three specific alternative hypotheses were as follows.

- 1481 1. **Alternative Hypothesis 1:** Groups with calf presence are larger with tighter group cohesion
1482 than groups without a calf across cetacean species.
- 1483 2. **Alternative Hypothesis 2:** For nighttime foraging Risso's and common dolphins, rest/slow
1484 travel peak during midday while faster travel peaks in the early morning and late afternoon.
- 1485 3. **Alternative Hypothesis 3:** Individual spacing within groups is closer during the calving and
1486 mating seasons across cetacean species.

1487

4.4 Methods

1488

4.4.1 Study Area and Survey Design

1489 The study area consisted of the SCB extending from offshore the mainland coast to ~70 km west
1490 of San Clemente Island, and from the Mexican border north to near Los Angeles (Fig. 1-1).

1491 Surveys were flown out of San Diego using three types of aircraft: (1) most (88%; $n=79$) of the
1492 90 survey days were conducted from a small high-wing, twin-engine Partenavia P68-C or P68-
1493 OBS (glass-nosed) airplane equipped with bubble observer windows on the left and right sides of
1494 the middle seats; (2) the remaining 11 survey days (12%) occurred from an Aero Commander
1495 airplane (9 days) or a helicopter (2 days). The 15 surveys occurred at least once during 11 of the
1496 12 calendar months: October and November 2008; June, July and November 2009; May,
1497 July/August and September 2010; February, March, April, and May 2011; and January,

1498 February, and March/April 2012. Daily field observations typically occurred between 9:00-15:00
1499 Pacific time to maximize overhead light and sighting conditions. The survey team consisted of
1500 one (2008-2010) or two pilots (2011-2012), three professionally trained marine mammal
1501 biologists (two with over 10 years of related experience) or two such biologists and a computer
1502 scientist. Two biologists observed from center seats; the third biologist (or computer scientist)
1503 recorded data from the front right co-pilot seat (2008-2010) or rear left bench seat (2011-2012).
1504 Surveys were flown at speeds of approximately 100 kt and altitudes of approximately 227-357 m
1505 (averaging 261 ± 49 m per the Wide-Area Augmentation System-enabled GPS).

1506

1507 Surveys followed line-transect protocol (Buckland et al. 2015) along generally east-west-oriented
1508 lines perpendicular to bathymetric contours (Jefferson et al. 2014a). Observations included in
1509 this analysis occurred during both systematic and connector effort (i.e., shorter perpendicular
1510 lines connecting longer systematic survey lines). Point-sampling (Martin and Bateson 2011) was
1511 used to record the first-observed group behavioral state (mill, rest/slow travel, medium/fast
1512 travel; Table 2-1) (Shane 1990; Smultea 1994; Henderson 2010), and (2) group cohesion
1513 (maximum nearest neighbor distance within a group, estimated in adult species Body Lengths
1514 (BL)) (Table 2-2 and Fig. 4-1). A group was defined as all individuals within 10-20 adult BL but
1515 occasionally as many as 50 BL apart, interacting or engaged in similar activities (after Shane
1516 1990; Smultea 1994; Lusseau et al. 2005). For common dolphins that formed much larger
1517 groups (on the order of hundreds to thousands) than other cetaceans, cohesion was based on
1518 individual spacing within distinct subgroups that met the above stated definition of "group". A calf
1519 was defined as a smaller individual \leq one-half the BL of the closely accompanying larger animal.
1520 For common dolphins, the minimum number of calves observed was estimated because it was
1521 not possible to count all calves in the characteristically larger groups; for other species, the
1522 estimated number of calves was indicated as a minimum or the actual observed number. From
1523 the aircraft, short - and long-beaked common dolphins were difficult to differentiate given the
1524 subtle physical differences between the species (Jefferson et al. 2015), and the lower resolution
1525 (12 megapixels (MP)) of camera lenses used during 2008-2011. However, starting in 2012, a
1526 higher-resolution (24 MP) camera lens allowed the identification of a higher subset of photos in
1527 situ and post-field by a species identification expert. Of the total 564 common dolphin sightings,
1528 12% were identified to contain short-beaked common dolphin(s), and 6% to include long-beaked
1529 common dolphin(s).

1530

1531 Environmental data were collected at the beginning of each effort type and whenever conditions
1532 changed. Sightings were circled to photo-document and confirm species, group size, and calves.

1533 Blue, fin, and gray whales, bottlenose and Risso's dolphins, and occasionally other cetacean
1534 species were sometimes circled for longer (>5 min) periods to conduct a detailed focal group or
1535 individual behavioral session by increasing altitude to ~365 - 455 m and radial distance ~0.5-1.0
1536 km and video recording animal behavior. Field data (sighting, effort, and environmental data
1537 including Beaufort sea state, visibility, glare, and cloud cover) were collected with various
1538 hardware and software that changed across the study period with development of new systems.
1539 In 2008-2009, BioSpectator software was used on a Palm Pilot TX or an Apple iPhone or iTouch
1540 in. In 2010-2011, a customized Excel spreadsheet on a Windows-based notebook computer was
1541 used. In 2011-12, customized Mysticetus Observation (Mysticetus™) Software was used on a
1542 notebook computer. Locations were determined using a WAAS handheld and aircraft Garmin,
1543 and a Bluetooth or USB Global Positioning System (GPS). Each new entry was automatically
1544 assigned a time stamp, a sequential sighting number, and a GPS position. A Suunto handheld
1545 clinometer was used to measure declination and horizontal angles to sightings. In 2008-2010,
1546 declinations were converted post-survey to perpendicular sighting distance; in 2011-2012,
1547 declinations were instantly converted to perpendicular and radial sighting distances by
1548 Mysticetus.

1549
1550 Photographs and video recordings were made through a small opening porthole on either the co-
1551 pilot seat window (2008-2010) or the rear left bench-seat window (2011-2012). Photographs
1552 were collected using a Canon EOS 40D or D60 or D300 or D7000 Nikon digital camera with 100
1553 -400 mm Image Stabilized zoom lenses. A Sony Handycam HDR-XR550 or HDR-XR520 video
1554 camera was used to document behaviors while circling focal groups. Observers used Steiner 7 X
1555 25 or Swarovski 10 X 32 binoculars as needed to identify species, group size, behaviors, etc.

1556 *4.4.2 Data Analysis*

1557 Analyses focused on three response variables and explored potential relationships with 11
1558 explanatory variables (Table 2-2). For analyses, time of day was represented as the number of
1559 minutes from sunrise each day, calculated using sunrise tables for San Diego, California. Julian
1560 day was used to represent the integer day number beginning with 1 on January 1 of each year of
1561 the study (Table 2-2). Water depth, closest distance to shore (including islands), slope, and
1562 slope aspect were determined using geo-spatial analysis capabilities of Mysticetus (Table 2-2).
1563 Aspect was transformed into a variable pair via the cosine and sine transformations, and was
1564 subsequently treated as a single variable in the model selection process.

1565
1566 Statistical analyses were conducted using the software program R and included Pearson
1567 Correlation, Fisher's two-sided exact test, t-test, and regression modeling. Pearson correlations

1568 between all pairs of continuous variables were calculated; correlations >0.6 in absolute value
1569 were not permitted to enter regression models together (described below). Each pair of
1570 categorical variables was cross-tabulated and results were examined for evidence of
1571 association. If Fisher's two-sided exact test was significant ($p < 0.05$), the two variables were not
1572 permitted to enter any model together. The association between each mixed pair of categorical
1573 and continuous variables was examined via an independent sample t-test; if the test was
1574 significant ($p < 0.05$), the two variables were not permitted to enter any model together. The
1575 cosine and sine transformations of aspect were treated as a single variable: either both
1576 transformations entered a model together or both were excluded. If either member of the pair
1577 was associated with any other variable using the criteria above, neither member of the pair was
1578 permitted to enter a model with the associated variable.

1579

1580 Separate regression modeling was conducted for the three response variables. A different type
1581 of model was used based on the results of each type of response. Only models with five or fewer
1582 variables were examined. An automated routine was used to generate all main effects models
1583 with 1, 2, 3, 4, or 5 variables that met the criteria above for absence of strong pairwise
1584 associations. Because observations with missing values do not contribute to regression models,
1585 observations with missing values were excluded from further analyses. Each resulting reduced
1586 dataset was then re-examined for associations among variables. As dictated by the criteria for
1587 associations among variables, different candidate sets of models were constructed as
1588 necessary.

1589

1590 Akaike's Information Criterion (AIC) (Burnham and Anderson 2002) was calculated for each
1591 candidate model. The top 10 models with the lowest (best-fitting) AIC value were evaluated, and,
1592 the difference between this AIC value (AIC_i) and that of the top-ranked model (AIC_1) was
1593 calculated as

1594

$$1595 \Delta_i = [AIC]_i - [AIC]_1$$

1596

1597 Akaike weights were then calculated for all 10 models from these differences as

1598

$$1599 w_i = \exp(-1/2 \Delta_i) / (\sum_{m=1}^{10} \exp(-1/2 \Delta_m))$$

1600

1601 The importance value for each variable was then calculated based on the sum of the Akaike
1602 weights for each model within which that variable appeared. The importance value represented

1603 the number of times a variable appeared in the top 10 models. For example, if a variable
1604 appeared in all 10 models, its importance value equaled 1; otherwise, the importance value was
1605 bounded between 0 and 1.

1606

1607 Each of the three response variables (behavior, group size, and group cohesion) were evaluated
1608 with separate regression models based on variable characteristics. The response variable
1609 behavioral state (with three categories) (Table 2-2) was analyzed using multinomial logistic
1610 regression. This involved pooling medium/fast travel as the reference category, with the odds of
1611 being in either of the other two categories (rest/slow travel or mill) calculated relative to the
1612 reference. Log-linear models were used for the response variable group size, since it was an
1613 integer count variable. Poisson and negative binomial regression models were both examined
1614 for group size. Because variance was generally greater than expected under the Poisson
1615 distribution, Vuong's (1989) test was applied to compare the fit of Poisson and negative binomial
1616 regression models. The negative binomial model described variance better than the Poisson
1617 model. When negative binomial regression models exhibited convergence problems, a Poisson
1618 regression was used. The variable "group cohesion" was log transformed to approximate a
1619 normal distribution. Standard multiple linear regression was applied to model the relationship
1620 between individual spacing and the variables.

1621

4.5 Results

1622 A total of 588 sightings of an estimated 160,494 individuals were made during the approximately
1623 82,502 km of observation effort conducted during the 15 aerial surveys in 2008–2012 (Fig. 4-1).
1624 Overall, 99 percent of the total flight time was associated with a Beaufort sea state less than 4.
1625 Numbers of groups seen by species in descending order of frequency were 564 common dolphin
1626 spp., 286 Risso's dolphin, 115 fin whale, 96 bottlenose dolphin, 78 gray whale, and 65 blue
1627 whale.

1628

4.5.1 Blue Whale

1629 For blue whale group size, Julian day was the only significant and most important response
1630 variable among the Poisson regression models (importance value 0.95) (Tables 4-1 and 4-2).
1631 Group size increased with increasing Julian day from 1.0 whale in spring to 3.5 whales in fall.
1632 Depth had a much lower importance value of 0.42 and was non-significant. For group cohesion,
1633 none of the candidate variables accounted for significant variation in cohesion, and the best
1634 model contained only slope with importance value of 0.62.

1635

1636

4.5.2 *Fin Whale*

1637 The best predictors of fin whale behavioral state were (1) distance to shore and (2) Julian day
1638 (importance value 1.0 for Julian day and 0.96 for distance to shore) (Tables 4-1 and 4-3). All
1639 remaining explanatory variables were nonsignificant for behavioral state. Milling was most likely
1640 to occur close to shore: for each 10 km increase in distance, the odds of milling decreased by a
1641 factor of 0.2. Fin whales were also 0.8 times more likely to slow travel earlier relative to later in
1642 the year, with odds decreasing by a factor of 0.22 for each 100 days. The best model for fin
1643 whale group size included (1) calf presence and (2) time of day. Mean observed group size with
1644 a calf was 3.2 fin whales relative to 1.6 whales with no calf. Although insignificant, there was
1645 some indication ($p < 0.10$) that group size decreased with increasing time since sunrise. All
1646 remaining variables were nonsignificant for group size. The best predictors of group cohesion
1647 were (1) calf presence followed by (2) subregion (importance values 0.93 and 0.41,
1648 respectively). The top model showed that cohesion was closer with calf presence (1.0 BL apart)
1649 than absence (2.5 BL). In contrast, cohesion tended to be farther apart (4.7 BL apart) when
1650 compared to the subregion East of San Clemente Island (2.5 BL) (Tables 4-1 and 4-3).

1651

4.5.3 *Gray Whale*

1652 The best predictor of behavioral state for gray whales was aspect and was the only explanatory
1653 variable in the best model (importance value 0.72) (Table 4-1). Odds ratios showed that
1654 rest/slow travel was five times more likely than medium/fast travel to occur over south-facing vs.
1655 north-facing slope aspects. Inversely, medium/fast travel was primarily associated with north-
1656 facing slopes. All other variables were nonsignificant for behavioral state. The best predictors of
1657 gray whale group size were (1) subregion and (2) to a lesser extent aspect (importance values
1658 0.92 and 0.72, respectively). Group size tended to be larger west vs. east of San Clemente
1659 Island (2.7 vs. 1.7 whales, respectively; $p < 0.10$). Predicted group size as a function of aspect
1660 suggested a trend for highest group size over east-northeast-facing slope aspects.
1661 Correspondingly, lowest predicted group size was associated with west-southwest-facing slope
1662 aspects. Remaining variables in the top-ranked group size models were insignificant ($p > 0.10$).
1663 For group cohesion, the best predictors were: (1) subregion, (2) aspect, and (3) Julian day
1664 (importance values > 0.72). Gray whale groups tended to be less cohesive when west vs. east of
1665 San Clemente Island (1.4 BL vs. 0.7 BL, respectively; $p < 0.10$). Group cohesion also tended to
1666 decrease across the winter-spring from 0.8 BL in February to 0.5 BL in April, though this trend
1667 was not significant ($p < 0.10$).

1668

4.5.4 *Risso's Dolphin*

1669 The best predictors of behavioral state for Risso's dolphins were: (1) distance to shore, (2) Julian
1670 day, and (3) to a lesser extent time of day (Table 4-4 and 4-5). Distance to shore and Julian day
1671 appeared in all top models (importance value 1.0). Milling increased across the year but slow
1672 travel decreased (both relative to medium/fast travel). Odds ratios indicated that for each 100
1673 days of the year, Risso's dolphins were 1.67 times more likely to mill than medium/fast travel. As
1674 time progressed within a day, dolphins were less likely to either mill or rest/slow travel than
1675 medium/fast travel. The time of day odds ratios showed that for each hour (60 min) after sunrise,
1676 dolphins were 0.93 times as likely to mill and 0.89 times as likely to rest/slow travel (both relative
1677 to medium/fast travel). Risso's dolphins milled more (by a factor of 1.39) and rest/slow traveled
1678 less (by a factor of 0.84) with each 10 km increase in distance from shore. The best group size
1679 predictors were: (1) calf presence, (2) other cetacean presence, and (3) Julian day, all appearing
1680 in all top models. Predicted group size was higher with calf presence vs. absence (25 vs 15
1681 dolphins), and also when another cetacean species was present vs. absent (26 vs 15 dolphins).
1682 As Julian day increased from February to late-November, predicted group size increased linearly
1683 (on a log scale) from approximately 12 to 23 dolphins (including calves). The best predictors of
1684 group cohesion were: (1) time of day, (2) Julian day, and (3) to a lesser extent depth. All 10
1685 models contained time of day and Julian day as important predictors of cohesion. A relatively
1686 high importance value for depth (0.88) explained variability in cohesion among models. Like
1687 common and bottlenose dolphins, Risso's dolphin group cohesion increased (dolphins were
1688 closer together) with time of day (6.5 BL in early morning to 2.1 BL in late afternoon) and
1689 decreased across the year (2.4 BL in February to 6.0 BL in November). Cohesion also
1690 decreased with deeper bottom depth: from 2.3 BL over 100-m bottom depth compared to 5.7 BL
1691 over 2000 m depth.

1692

4.5.5 *Bottlenose Dolphin*

1693 The best predictors for bottlenose behavioral state were (1) depth, (2) slope aspect, (3) Julian
1694 day, and (4) time of day (Table 4-4 and 4-6). All top 10 models had 3–5 explanatory variables;
1695 simpler models did not perform as well. Rest/slow travel increased with deeper water depths (by
1696 a factor of 1.3 for every 100 m increase in depth). Mill behavior increased across the year (by a
1697 factor of nearly 3 for every 100 Julian days). Mill progressively increased ($p < 0.05$) as slope
1698 aspect changed from southeast to west-northwest. Dolphins were 100 times more likely to mill
1699 over west-northwest-facing vs. southeast-facing slope aspects. In addition, the odds of slow
1700 travel increased progressively as slope aspect changed from approximately south-southeast to
1701 northwest by a maximum factor of 12. Bottlenose dolphin group size was significantly ($p < 0.05$)

1702 higher with calf presence vs. absence by a factor of 2.3 (mean=38.9 vs 17.1, respectively;
1703 importance value 1.0). No explanatory variables appeared in any of the 10 regression models for
1704 group cohesion. However, in the best model, the three most frequently occurring variables were
1705 distance to shore, time of day, and Julian day, and all three had relatively high importance
1706 values. Cohesion was closer in afternoon compared to morning (mean=2.9 vs. 4.9 BL,
1707 respectively). Dolphin groups were significantly ($p<0.05$) less cohesive as Julian day progressed,
1708 from a mean of 2.2 BL in February to 5.8 BL in October. Dolphins were also significantly
1709 ($p<0.05$) more likely to swim close together near shore vs. offshore, though this effect was small
1710 (3.3 BL within 300 m of shore vs 3.0 BL near 8 km from shore).

1711 *4.5.6 Common Dolphin spp.*

1712 The best predictors for common dolphin behavioral state were (1) subregion and (2) water
1713 season (importance values 0.91 and 1.0, respectively) (Table 4-4 and 4-7). Rest/slow travel was
1714 4.1 times more likely to occur in waters west of San Clemente Island ($p<0.05$). The odds of
1715 milling was 1.9 times greater in the warm versus cold season ($p<0.05$). The best group size
1716 predictors were (1) calf presence, (2) slope aspect, and (3) to lesser extent Julian day
1717 (importance values 1.0, 1.0 and 0.92, respectively). Mean size of groups with calf presence had
1718 over twice as many individuals ($n=485$) as groups without a calf ($p<0.05$) (Table 4-4 and 4-7).
1719 Group size was also highest for north-facing slopes and lowest for south-facing slope aspects
1720 ($p<0.05$). Group size decreased significantly ($p<0.05$) across the calendar year from a mean of
1721 245 to 170 individuals. The best group cohesion predictors were (1) calf presence and (2) time of
1722 day (importance values 1.0). Cohesion decreased significantly ($p<0.05$) with calf presence from
1723 a mean of 3.4 to 5.1 BL. Cohesion also significantly ($p<0.05$) increased across the day from a
1724 mean of 4.8 BL in early morning to 2.8 BL near dusk.

1725 **4.6 Discussion**

1726 The biological meaning of significant behavioral patterns may be linked to species-specific
1727 foraging strategies, and reproductive, calving and migratory periods. Some observed behavioral
1728 patterns were also hypothesized to be influenced by relative predation risk, though the latter
1729 factor cannot be easily ascertained and lacks consistent enumeration in available literature (e.g.,
1730 Weller 2009).

1731 *4.6.1 Group Size: Calf Presence and Reproductive Timing*

1732 Mean group size of fin whales, Risso's dolphins, bottlenose dolphins, and common dolphins was
1733 larger with calf presence, consistent with the hypothesis that groups with a calf are larger than
1734 groups without a calf. Samples sizes of groups with a calf were too small ($n<5$) to conduct

1735 meaningful analyses for blue and gray whales. Among the four analyzed cetacean species,
1736 calving and mating periods experience some degree of overlap based on available data.
1737 Observed larger group size with calf presence likely resulted from a combination of proximate
1738 overlapping mating and calving periods, and behavioral responses and ultimate adaptations to
1739 reduce calf predation risk. Behavioral ecology theory predicts that in habitats characterized by
1740 high predation pressure and clumped food resources, females should form groups which reduce
1741 predation risk on young and attract males to females during the mating season (Krause and
1742 Ruxton 2002; Beauchamp 2014). These factors are believed to favor larger group sizes. Larger
1743 group size presumably decreases predation risk to calves through dilution in numbers, group
1744 defense, predator confusion, etc., as summarized in various reviews for multiple species and
1745 taxa (e.g., Crook and Gartlan 1966; Fertl 1994a,b; Würsig et al. 1997; Acevedo-Gutierrez 2009).
1746
1747 Larger mean group size found for groups with a calf is also likely due to the close physical
1748 association and reliance of young calves on their mothers for nursing, protection, and assisted
1749 locomotion (Aguilar 2009). Among mysticetes, females with a calf do not form groups, unlike
1750 among most odontocetes (Jefferson et al. 2015). Thus, the mean group size of 3.2 for fin whale
1751 groups with a calf indicates that mother-calf pairs tended to be accompanied by at least one
1752 other non-calf whale. An accompanying fin whale may be a courting male waiting for a mating
1753 opportunity, as a small percentage of female fin whales with a calf experience estrus (Aguilar
1754 2009; Mizroch et al. 2009). This behavior appears to be an alternative mating strategy among
1755 male humpback whales (Smultea 1991, 1994; Craig et al. 2002).
1756
1757 Among Risso's dolphins, calf presence was the only variable explaining differences in group
1758 size, resulting in nearly doubling of group size with calf presence. Again, this pattern appears to
1759 be related to at least two factors: decreased predation risk and possibly male attraction to estrus
1760 females. The latter premise is based on reported partial overlap of peak parturition and mating
1761 periods of Risso's dolphins (Baird 2009). Bottlenose dolphin group size also doubled when
1762 calves were present. The same pattern is commonly reported for bottlenose dolphins elsewhere
1763 (Weller 1991; Bearzi et al. 1997; Vermeulen et al. 2015), including in Santa Monica Bay in the
1764 SCB (Bearzi 2005). Associated benefits of larger group sizes likely provide increased protection
1765 for young bottlenose dolphins through increased vigilance (e.g., Shane et al. 1986; Fertl
1766 1994a,b; Mann et al. 2000). Bottlenose dolphins and Risso's dolphins may also form segregated
1767 nursery groups as reported elsewhere (e.g., Lusseau and Newman 2004; Gowans et al. 2008;
1768 Gibson and Mann 2008). Group size of segregated female bottlenose dolphins with calves
1769 appears to vary with predation risk, availability of food resources, and social/mating pressure

1770 from males (Connor et al. 2000; Gibson and Mann 2008). Risso's dolphins in the Azores, an
1771 isolated oceanic island ecosystem, have also been found to form separate nursery groups,
1772 possibly due to shared ecological and social constraints associated with calf care (Hartman et al.
1773 2008). Dusky dolphin females with calves off New Zealand likewise form variably sized nursery
1774 groups typically though not consistently separate from other age and sex classes (Weir et al.
1775 2010).

1776

1777 Similar to Risso's and bottlenose dolphins, common dolphin groups with a calf were over 2.5
1778 times larger than groups without calves. Common dolphin group size also decreased across the
1779 year from about 245 individuals in winter to about 170 dolphins during fall. This pattern fits the
1780 biological trend that peak calving and mating occur in winter and early spring in the SCB, when
1781 males would be expected to join females in estrus. However, in apparent contrast to typical
1782 segregation of mothers with calves as reported for some Risso's and bottlenose populations,
1783 common dolphin mother-calf pairs form subgroups within a larger encompassing group during
1784 the peak calving and mating seasons (Chivers et al. 2015), likely to derive group benefits
1785 discussed previously.

1786

4.6.2 *Group Cohesion: Calf Presence and Reproductive Timing*

1787 Consistent with my second hypothesis, group cohesion was closer during the calving and mating
1788 seasons for the four species with sample sizes adequate for regression analyses: fin whales,
1789 Risso's dolphins, bottlenose dolphins and common dolphins. This hypothesis was based on the
1790 premise that newborn calves remain close to their mothers during early development when they
1791 are highly dependent on their mother for survival (Norris and Dohl 1980). Cohesion was closest
1792 during Julian days coinciding with the reported peak calving and mating seasons for Risso's
1793 dolphin and bottlenose dolphin. As described above for group size, increased group cohesion
1794 during these overlapping reproductive periods may be related to males joining and closely
1795 following females in estrus during the mating season. In addition, calves swim closer to their
1796 mothers during the early development months as evidenced among other cetaceans including
1797 dusky dolphin populations off Kaikoura (Weir et al. 2010) and common bottlenose dolphins in
1798 Monkey Mia, Australia (e.g., Connor et al. 2000).

1799

1800 Cohesion among Risso's dolphin groups was most strongly influenced by time of day and Julian
1801 day, increasing across the day (i.e., animals closer together) but decreasing with Julian day
1802 across the calendar year. Group cohesion among Risso's dolphins also decreased with water
1803 depth. Decreased cohesion between individuals across the day and with deeper water is
1804 consistent with patterns summarized for nocturnal foraging Hawaiian spinner and Kaikoura

1805 dusky dolphin populations (Cipriano 1992; Norris et al. 1994; Würsig and Pearson 2014). During
1806 late morning through early afternoon rest periods, these spinner and dusky dolphin populations
1807 form small tight groups. However, near dawn and several hours after nocturnal offshore foraging,
1808 and again several hours before dusk, individuals of both species spread out in larger groups;
1809 near dusk, the small tight groups actively coalesce to form larger looser groups, an apparent
1810 coordinated staging before moving offshore to feed in a large aggregation (Norris et al. 1994;
1811 Würsig et al. 1997). Similarly, Risso's dolphins formed tighter groups from late morning through
1812 mid-afternoon, with looser group formations occurring later in the day when they would be
1813 expected to move offshore to forage on solitary spread-out cephalopod prey. As no observations
1814 occurred in the few hours after dawn, cohesion at that time and near dusk were unknown.
1815 However, no significant changes in group size occurred across the day, unlike reported among
1816 the aforementioned Kaikoura dusky and Hawaiian spinner dolphin populations. Differences may
1817 be related to the Risso's dolphin's approximately 200% larger body size (Jefferson et al. 2015),
1818 potentially associated with lower risk of predation. SCB Risso's dolphins also appear to be
1819 behaviorally more aggressive interspecifically and possibly intraspecifically, the latter based on
1820 opportunistic and incidental reports of their agonistic behaviors towards both smaller and larger
1821 cetaceans, including larger killer whales (Dahlheim et al. 2008), sperm whales (Smultea et al.
1822 2014), and pilot whales (Shane 1995) within the SCB.

1823
1824 Similar to Risso's dolphin, Julian day significantly influenced cohesion within bottlenose dolphin
1825 groups: groups were less cohesive as the year progressed, i.e., after the reported peak calving
1826 and mating periods. Again, this pattern is hypothesized to result from tighter group spacing
1827 during the reported peak calving and mating season occurring earlier in the year during spring-
1828 summer (Urian et al. 1996; Thayer et al. 2003; Danil et al. 2010). At these times, close proximity
1829 may be needed by males to determine whether a female is in estrus and to determine sexual
1830 readiness, perhaps via taste imparted to waters (Caldwell and Caldwell 1967; Norris and Dohl
1831 1980; Muraco 2015). Another factor likely contributing to tighter group spacing earlier vs. later in
1832 the year is that younger cetacean calves are more tightly bonded to their mothers as measured
1833 by physical spacing; this average spacing gradually increases with increasing calf age (e.g.,
1834 Taber and Thomas 1982; Gibson and Mann 2008; Cartwright and Sullivan 2009). Calves
1835 consistently swim closer to their mother than other group members do to each other (Norris and
1836 Dohl 1980).

1837
1838 The potential biological meaning of the observed increase in group cohesion with time of day
1839 among common dolphin groups with calf presence is unclear. Groups of common dolphins with

1840 calf presence typically included multiple calves in what appeared to be segregated mother-calf
1841 subgroups, consistent with Chivers et al. (2015). Increased cohesion across the day among
1842 common dolphins may indicate increased socializing near dusk or possibly coalescing to move
1843 to other areas to feed on the Deep Scattering Layer (DSL), as documented for Hawaiian spinner
1844 dolphins and Kaikoura dusky dolphin populations (see Risso's dolphin above; e.g., Norris et al.
1845 1994; Würsig et al. 1997; Würsig and Pearson 2014). Huddling behavior and close cohesion is
1846 commonly associated with socializing delphinids (e.g., Norris and Dohl 1980; Norris et al. 1994;
1847 Würsig and Würsig 2010).

1848 *4.6.3 Diurnal Activity Patterns of Nocturnal Foragers*

1849 Diurnal behavioral patterns of Risso's dolphins and common dolphins were generally consistent
1850 with my third hypothesis that rest/slow travel by these two reported nighttime-foraging species
1851 peaks during midday, while faster travel peaks in the morning and late afternoon. For both
1852 species, rest/slow travel was more common during morning through midday, while faster travel
1853 was more common in early morning or late afternoon. This is consistent with studies indicating
1854 that increasing hunger is linked to increased locomotion (e.g., speed and turning angles) and
1855 increased inter-individual distances (Wieser et al. 1988). Similarly, Henderson (2010) found that
1856 common dolphins in the SCB increased their speed of travel across the day, with a morning
1857 peak in slow travel with occasional foraging. From combined visual and acoustic behavioral data,
1858 Henderson (2010) concluded that common dolphins fed predominantly at night, presumably on
1859 the DSL. The combined studies indicate that common dolphin and Risso's dolphin behavioral
1860 patterns reflect those of other delphinids that feed at night on the DSL, most notably the
1861 Hawaiian spinner dolphin (Norris et al. 1994; Benoit-Bird and Au 2003) and Kaikoura dusky
1862 dolphin populations (Benoit-Bird et al. 2004; Vaughn et al. 2007; Würsig et al. 2007, 2010).
1863 During early morning, the latter two species return from offshore nocturnal foraging on DSL prey
1864 in deeper waters to shallow, more protected coastal waters. Here, they transition over several
1865 hours from initially elevated activity state levels to rest mode. As the afternoon progresses, the
1866 dolphins transition back over several hours into higher-level activity. This includes increasing
1867 group sizes and coalescing into a large group before heading offshore again to feed in deep
1868 waters. However, I did not find that group size changed by time of day for Risso's and common
1869 dolphins.

1870
1871 I made no observations of Risso's and common dolphin behavior near dawn and dusk to confirm
1872 a parallel pattern to Hawaiian spinner and Kaikoura dusky dolphins (effort typically did not occur
1873 within 2-3 h of sunrise or sunset to avoid low-light conditions limiting observer visibility). I
1874 hypothesize that had I collected data during early morning, I would have similarly seen

1875 increasing levels of rest/slow travel since I found this behavior peaked at midday. During early
1876 morning (6:00-9:00), Henderson (2010) found that common dolphin behavior in the SCB was
1877 similar to mid-morning, with slow travel at its peak. These observations are consistent with the
1878 aforementioned Hawaiian spinner and Kaikoura dusky dolphin populations. Furthermore,
1879 combined studies indicate that fastest movement occurs near dusk, culminating in offshore
1880 foraging expeditions, given shared similarities in habitats and nighttime DSL foraging strategies
1881 with other delphinids. Increasing speed of movement across the day for Risso's dolphins is
1882 consistent with their apparent crepuscular and nocturnal foraging habits in the SCB (Henderson
1883 2010; Soldevilla et al. 2011; G. Schorr, unpubl. data). The increased activity levels in late
1884 afternoon that I found for common and Risso's dolphins is consistent with the social facilitation
1885 hypothesis described by Markowitz et al. (2004) for Kaikoura dusky dolphins. In the latter
1886 situation, and among Hawaiian spinner dolphins, leaping and faster moving behavior are
1887 believed to cue individuals and small groups to coalesce into a large loose aggregation and
1888 move offshore again to feed at night, in a safer formation of higher diluted numbers (Norris and
1889 Dohl 1980; Norris et al. 1994; Heithaus and Dill 2009; Würsig 2009).

1890

1891 The observed peak in resting during morning and midday for common and Risso's dolphins is
1892 presumably important energetically. Rest allows individuals to restore high energy expended
1893 during apparent crepuscular and nocturnal feeding on DSL prey. Notably, changes in group size
1894 or heading were rarely observed during rest/slow travel among 51 focal group sessions on SCB
1895 Risso's dolphin lasting up to 1 h (mean duration 21.6 min, Standard Deviation [SD]=12.9 min;
1896 Smultea and Bacon 2012).

1897

1898 Henderson (2010) found that common dolphins off north San Clemente Island moved inshore
1899 (east) in the mornings and offshore (west) in late afternoon. Smultea and Bacon (2012) using
1900 data from my study found that common dolphin heading was related to bottom depth: as depth
1901 increased, dolphins were more likely to be headed northeast than northwest, southeast, or
1902 southwest (SW). Further analyses of my data may indicate diurnal trends in heading, but I did
1903 not examine this relationship herein.

1904

4.7 Conclusions

1905 Calf presence, time of day, and Julian day were important factors influencing group size, group
1906 cohesion, and behavioral state among fin whales, Risso's dolphins, bottlenose dolphins and
1907 common dolphins in the SCB study area. Calf presence was the most consistent variable
1908 explaining increased group size. Decreased group cohesion was correlated with temporal factors
1909 coinciding with the peak calving and/or mating seasons for all three delphinid species and the fin

1910 whale. Risso's and common dolphin behavioral activity levels and states fluctuated predictably
1911 across the day, with rest peaking near midday and higher activity behaviors peaking during early
1912 morning and late afternoon, closer to nocturnal foraging periods. These diurnal behavioral
1913 patterns were similar to patterns described in studies of both species in the SCB and other
1914 nocturnally foraging delphinids. Mid-afternoon thus appears to be an important rest period for
1915 both Risso's and common dolphins in the SCB. An unexpected result was that slope aspect
1916 consistently influenced only the gray whale and is hypothesized to serve as a migration cue.

1917

1918 Findings demonstrate that behavior and group characteristics were influenced by factors that
1919 may be useful for potential spatiotemporal management relative to anthropogenic activities and
1920 sensitive biological periods documented among the four SCB cetacean species. Mating, calving
1921 and/or foraging/feeding activities of fin whales and Risso's, bottlenose and common dolphins in
1922 the SCB overlap areas used for military training exercises across the year in the SCB (2008a,b).
1923 The few behavioral response studies that have been conducted on Risso's dolphins suggest
1924 sensitivity to anthropogenic disturbance by tourism vessels. For example, midday resting
1925 behavior by Risso's dolphins was disrupted with increased whalewatching activity as observed
1926 from shore in the Azores (Visser et al. 2011). Common dolphins may also respond to mid-
1927 frequency active sonar in the SCB, though the naturally high variability in their behavior requires
1928 a large sample size to differentiate natural and anthropogenic effects (Henderson et al. 2014b).
1929 Although long-term population and health impacts of anthropogenic disturbance are uncertain,
1930 chronic and cumulative long-term disturbance can lead to impacts of concern. These include
1931 displacement and disruption of behaviors important for survival, potentially resulting in
1932 decreased animal energy reserves and increased stress levels (NRC 2005; Southall et al. 2007;
1933 Ellison et al. 2012).

1934

1935 Important biological periods for cetaceans with respect to results of this study in the SCB include
1936 (1) summer-fall peak feeding and early winter socializing periods for fin whales, (2) reported
1937 winter/spring calving and mating periods for Risso's, bottlenose, and common dolphins, and (3)
1938 morning/midday resting periods exhibited by Risso's and common dolphins. Spatio-temporal
1939 management measures have not been previously implemented in the SCB for cetaceans.

1940 Results of this systematic study conducted over a five-year period from 2008-2012 and focused
1941 on the relatively fine management scale of the SCB identify temporal windows that may be more
1942 important than others in terms of biological function and sensitivity. Information on such temporal
1943 windows may assist in species-specific adaptive management and monitoring of cetaceans in
1944 the SCB and elsewhere. Future work could consider integration of this information across

1945 species to identify overlapping periods of temporal biological sensitivity relative to overlapping
1946 temporal and spatial windows of anthropogenic activity. Further research on potential
1947 geographical and species variation in biologically sensitive periods merits further investigation in
1948 other areas where anthropogenic activities are of concern to cetaceans.

1949

CHAPTER 5

1950

SUMMARY

1951

5.1 Summary of Findings

1952

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.

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1955

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1957

5.1.1 Chapter II: Spatial Factors

1958

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.

1979

1980

Although it was beyond the scope of this study, a systematic approach to analyzing the spatial

1981 overlap of species would contribute to adaptive management of the SCB region. Software such
1982 as “Marxan” were useful for implementation of a multi-species and multi-use ecosystem
1983 approach in the Azores (Schmiing et al. 2015). Separation of “fisheries related” scenarios and
1984 “biodiversity” scenarios was key to the success of this approach. Lessons have been learned
1985 from the use of collaborative decision support software in implementation of the California
1986 Marine Life Protection Act (Cravens 2016). The SCB region and cetaceans were not included in
1987 previous initiatives under this policy (Fox et al. 2013). Although Naval training exercises may be
1988 under public scrutiny, many other natural and anthropogenic changes in the region should be
1989 considered in the scientific interpretation of the meaning of data generated by ongoing
1990 monitoring efforts.

1991 *5.1.2 Chapter III: Focal Species*

1992 The two largest whale species in the SCB (blue, fin) are also listed as endangered. This raises the
1993 question of whether they might serve as “umbrella species”, whose protection might also benefit
1994 the smaller species in the region. However, it is important to know to what extent their social
1995 behavior differs from the smaller species. This study focused on group size and cohesion.

1996
1997 I developed and tested a model (the Smultea model) expanding and combining socioecological
1998 models developed for ungulates and cetaceans inhabiting open environments. This Smultea
1999 model predicted that in open semi-pelagic and pelagic waters, as cetacean species body size
2000 increases, overall mean group size decreases, groups become less cohesive (i.e. individuals are
2001 spaced farther apart), and individuals are more likely to occur alone. The Smultea model drew
2002 from socioecological models predicting relationships between body size, group size, home range,
2003 and/or resource predictability and availability for ungulates inhabiting open African savannah
2004 (Jarman 1974), and delphinids (Gowans et al. 2008) and mysticetes (Ford and Reeves 2008)
2005 inhabiting semi-pelagic and pelagic waters. These models are based on the premise that in open
2006 habitats, food resources are clumped and relatively unpredictable in space and time, and predation
2007 risk is high. In response to these ecological pressures, smaller species should form larger groups
2008 to reduce predation risk through the benefits of dilution, enhanced predator detection, and
2009 increased predator confusion, etc. (Beauchamp 2014).

2010
2011 My Smultea model built on the aforementioned ungulate, mysticete and delphinid socioecological
2012 models by additionally considering the roles of group cohesion and cetacean body size in semi-
2013 pelagic and pelagic environments. Study results from data collected during 18 aerial surveys in
2014 2008-2013 supported Smultea model predictions, when mysticetes were considered separately
2015 from odontocetes. Species body size was inversely related to group size and group cohesion, and

2016 positively related to frequency of lone animals among the three examined mysticetes and three
2017 delphinid odontocete groups, respectively. Blue whales (largest body size) were most frequently
2018 found alone ($p < 0.05$), while gray whales had significantly ($p < 0.05$) larger mean group size, were
2019 less likely to occur alone, and were more cohesive than blue and fin whale groups. The same
2020 pattern was found among delphinids; the largest-sized Risso's dolphin and the slightly smaller-
2021 sized bottlenose dolphin occurred in significantly ($p < 0.05$) smaller and less cohesive groups than
2022 the smaller-sized common dolphin spp. (Table 1.2).

2023

2024 Smultea model and results were consistent with hypotheses proposed originally by Jarman (1974)
2025 for ungulates and by Ford and Reeves (2008) for mysticetes that species with larger body sizes
2026 have smaller group sizes and are more likely to occur alone. The open environment leads to
2027 species-specific ecological trade-offs through various combinations of group size, cohesions, body
2028 size, and prey specialization/foraging strategy. For example, larger-sized prey (e.g., blue and fin
2029 whales) are more costly to predators because they require higher predator energy expenditure
2030 and risk of injury to successfully pursue and kill, and they sink quickly (i.e. less time to consume
2031 the body near the surface) compared to the smaller and more rotund gray and right whales (Ford
2032 and Reeves 2008). The latter factors are hypothesized to reduce the likelihood that large-bodied
2033 cetaceans will be attacked by predatory killer whales and perhaps sharks (Ford and Reeves 2008;
2034 Weller 2009; Beauchamp 2014). Thus, cetaceans with larger body sizes should be able to survive
2035 in smaller group sizes than smaller-sized cetaceans in oceanic waters. My results also agreed
2036 with Ford and Reeves' (2008) hypothesis that the robust but shorter-bodied gray whale should
2037 occur in larger mean group sizes than blue and fin whales in open waters, and should seek refuge
2038 (from predation) close to more structurally complex shorelines. Similarly, Gygax (2002b) tested a
2039 model examining the evolution of group size in dolphins and porpoises and found that species was
2040 the most influential variable affecting differences in group size. Findings also supported my
2041 prediction that smaller-sized cetacean species would swim closer together. This prediction was
2042 based on the hypothesis that increased cohesion improves sensory integration, including
2043 coordinated defense and food finding and capturing abilities among schooling fish and dolphins
2044 (Norris and Schilt 1988). In contrast, larger cetaceans should form smaller groups based on an
2045 increased ability to successfully fight off or flee from predators (Ford and Reeves 2008) combined
2046 with increased food needs required to sustain a larger body.

2047

2048 Observations of semi-pelagic Risso's dolphins, coastal and semi-pelagic island-associated
2049 bottlenose dolphins, and semi-pelagic/pelagic common dolphin spp. fit the Gowans et al. (2008)
2050 model as well as the Smultea model. The Risso's dolphin and bottlenose dolphin were found in

2051 medium-sized groups (>10-100) while common dolphin spp. occurred in large-sized groups
2052 (>100). This is consistent with the larger body size of the Risso's dolphin and bottlenose dolphin
2053 compared to the common dolphin spp. (Table 1.2). Group cohesion was also significantly ($p<0.05$)
2054 higher for the smaller-sized common dolphins than the Risso's dolphin and bottlenose dolphin.

2055

2056 Based on study results and other integrated studies (e.g., Falcone and Schorr 2012, 2013, 2014;
2057 Calambokidis et al. 2015), waters near San Clemente and Santa Catalina islands and the mainland
2058 coast provide important habitat for fin whales. The latter areas overlap areas used for summer-fall
2059 feeding/socializing blue whales, as well as migrating gray whales, Risso's dolphins, bottlenose
2060 dolphins and common dolphins. By focusing attention on the fin and blue whales as flagship
2061 species popular with the general public, other species may benefit from fin and blue whale directed
2062 spatiotemporal management efforts and research.

2063

5.1.3 Chapter IV: Temporal Factors

2064 To the extent that reproductive cycles, prey distribution and predation risk vary over time, I
2065 predicted species-specific behavior would change over diel and seasonal cycles. To address these
2066 questions, I conducted multiple regression analyses using three response variables (group size,
2067 group cohesion, and behavioral state) considering eight environmental and group composition
2068 explanatory variables (Table 2-2). Results based on 2008-2012 aerial survey data were consistent
2069 with the first prediction that group size was significantly ($p<0.05$) larger with calf presence for the
2070 fin whale, Risso's dolphin, bottlenose dolphin and common dolphin. In all four taxa calving and
2071 mating periods show some degree of overlap based on available data, consistent with correlations
2072 between mammalian body size and reproductive events (e.g., Gittleman and Thompson 1988).
2073 Larger group size with calf presence is hypothesized to reduce calf predation risk. This is
2074 consistent with behavioral ecology theory that in open habitats, some females form groups to
2075 reduce predation risk on newborn young, and males are attracted to females during the mating
2076 season (Davies et al. 2012, Ch. 2, 7 and 9). These factors favor overall larger group sizes.

2077

2078 I also tested the prediction that groups are more cohesive (i.e., individuals are closer together on
2079 average) during the calving and mating seasons. My results supported this prediction: among fin
2080 whales, Risso's dolphins, and common dolphins, group cohesion was tighter during the expected
2081 peak calving and mating seasons. These results were consistent with studies indicating that
2082 newborn cetacean calves remain close to their mothers during early development when they are
2083 dependent on milk, protection, and assisted locomotion from their mother (Norris and Dohl 1980;
2084 Weir et al. 2010). Cohesion was closest during Julian days coinciding with the expected peak
2085 calving and mating seasons for the bottlenose dolphin and Risso's dolphin. The biological meaning

2086 of this pattern may be related to males joining and closely following females in estrus during the
2087 mating season, and young calves swimming closer to their mothers as described for numerous
2088 cetacean ontogeny studies (e.g., Taber and Thomas 1982; Weir et al. 2010; Orbach et al. 2014).

2089

2090 My final temporal prediction was that rest/slow travel should peak during midday while faster travel
2091 should peak in the early morning and late afternoon for nighttime foraging odontocetes. Behavioral
2092 state regression modeling for the Risso's and common dolphins were generally consistent with
2093 this prediction. For both species, rest/slow travel was more common than faster travel during late
2094 morning through midday, while faster travel was more common than rest/slow travel in early
2095 morning or late afternoon. This contrasting pattern in activity levels is supported by studies
2096 indicating that increasing hunger is linked to greater locomotion (e.g., speed and turning angles)
2097 and larger inter-individual distances (Wieser et al. 1988). I also found that group size and cohesion
2098 increased across the day for Risso's dolphins, but only group cohesion increased diurnally for
2099 common dolphins. Spatiotemporal behavioral patterns for Risso's and common dolphins reflected
2100 those of other delphinids that feed at night on the DSL, most notably the Hawaiian spinner dolphin
2101 and the Kaikoura dusky dolphin populations. During early morning, the latter two species return
2102 from offshore nocturnal foraging forays on DSL prey in deeper waters to shallow, more protected
2103 coastal waters where they transition over several hours from initially elevated activity state levels
2104 to rest mode (Norris et al. 1994; Dahood and Benoit-Bird 2010; Vaughn et al. 2010). As the
2105 afternoon progresses, the dolphins transition over several hours into higher-level activity again.

2106

5.2 Conclusions and Implications

2107 From a basic science perspective, this study contributed to testing models based on a conceptual
2108 framework of behavioral ecology. Knowledge of cetacean habitat use relative to biologically
2109 important behaviors and time periods is a prerequisite to effectively manage and monitor impacts
2110 of anthropogenic activities. Study results provide localized information for the period from 2008-
2111 2013 that may be useful for spatio-temporal management of cetaceans and human-related
2112 activities in the SCB. Study data contribute to meeting adaptive management goals of the Navy's
2113 MSMP and Integrated Comprehensive Monitoring Program (ICMP) by providing spatio-temporal
2114 occurrence and behavioral information on cetaceans within the Navy's SOCAL Range Complex
2115 (DoN 2009, 2010, 2011). New software systems (Mysticetus™) made it possible to systematically
2116 collect data over a 5-year period tailored to the relatively fine scale of the SCB and the Navy's
2117 SOCAL Range Complex. Sophisticated statistical analyses (Resource Selection Functions)
2118 facilitated mapping of species-specific behaviors relative to habitat selection. High-probability
2119 locations associated with important biological activities and periods were predicted for fin whales,
2120 gray whales, Risso's dolphins, bottlenose dolphins, and common dolphin spp. The SCB region is

2121 of public concern because shipping has injured and killed cetaceans, cetaceans have died and
2122 become entangled in fishing gear, and MFA sonar has been shown to behaviorally disturb some
2123 cetaceans in the SCB (Melcon et al. 2012; DeRuiter et al. 2013; Goldbogen et al. 2013; Henderson
2124 et al. 2014b). MFA sonar has been implicated with cetacean injury and death in regions outside
2125 the SCB (Jepson et al. 2003; Cox et al. 2006). Due to plans for continued and increased use as a
2126 military training range, the SCB is designated for long-term monitoring of marine mammals, as
2127 required under the ESA and Marine Mammal Protection Act (MMPA) (DoN 2008a, 2011, 2015;
2128 NMFS 2015).

2129

2130 One of the most effective strategies to minimize and mitigate repetitive anthropogenic effects in
2131 marine and terrestrial ecosystems involves spatiotemporal-based management measures (Daly
2132 and Harrison 2012; Fernández et al. 2013; Dolman and Jasny 2015). Synthesis of species-specific
2133 habitat and temporal behavioral patterns could be useful for adjustments of human-related
2134 activities in the SCB, particularly for endangered fin and blue whales. There are certain periods of
2135 the year and day when some cetacean species are in higher numbers or engaged in behaviors
2136 considered to be more sensitive to anthropogenic disturbance (e.g., resting, feeding) than others.
2137 Important locations and periods relative to study results are summarized in Table 5-2 and
2138 illustrated in Fig. 2-1 through 2-4. The future challenge in assessing impacts of anthropogenic
2139 activities will be to implement study protocols involving sample sizes and statistical analyses
2140 sufficiently sensitive to differentiate anthropogenic versus naturally induced changes in cetacean
2141 distribution and behavior, given that results herein clearly indicate that multiple socioecological
2142 and environmental variables interact to influence species-specific cetacean habitat use and
2143 behavior in the SCB.

2144

2145 Results demonstrate that behavioral data shown to be indices of stress and anthropogenic
2146 disturbance, including displacement and interruption of behavioral activity (e.g., nursing,
2147 socializing, group cohesion, mother-calf behavior) can be collected systematically and
2148 quantitatively from a small circling aircraft covering relatively inaccessible deep water areas of
2149 the SCB. This aerial perspective provides a unique “bird’s eye” three-dimensional view in a non-
2150 intrusive manner when operating outside documented potential aircraft sound-transmission
2151 disturbance zones (Richardson et al. 1995). The aerial platform enables behavioral data
2152 collection at and below the water surface (in the SCB to approximately 20-30 m depth),
2153 facilitating extended observation and video recording periods of intricate details on inter-animal
2154 spacing, orientations and physical interactions that are difficult to obtain from the typically lower-

2155 vantage points or further distances available from vessel- and shore-based platforms (e.g.,
2156 Würsig et al. 1984; Lomac MacNair and Smultea 2016; Durban et al. 2015).

2157 **5.3 Future Research Recommendations**

2158 Baseline results from this five-year study revealed further questions and provided insight into
2159 future research useful for science-based adaptive management relative to growing public
2160 concern over impacts of anthropogenic activities on cetaceans within the SCB. Results identified
2161 spatiotemporally important areas (selected at higher rates of probability than expected) for four
2162 of the most commonly seen cetacean species in the SCB, two of which are listed as endangered
2163 (blue, fin). Obtaining a larger sample size for the endangered blue whale sufficient to conduct
2164 RSF modeling of preferred habitat characteristics, and conducting similar RSF modeling for
2165 common dolphins (ideally separating out short- and long-beaked common dolphins) within the
2166 study area would fill species research gaps. Collection of genetic photo-identification data from
2167 the apparent island ecotype of bottlenose dolphins that may be resident to Santa Catalina and
2168 San Clemente Islands would help determine if this population is genetically distinct from other
2169 “offshore” ecotypes. For example, recent studies found that the California coastal ecotype is
2170 genetically distinct from offshore bottlenose dolphins, but sample sizes were too small to assess
2171 differences among offshore ecotypes (Lowther-Thieleking et al. 2015). This information is
2172 relevant to evaluating levels of anthropogenic impact (i.e., number of “takes”) for separate
2173 species stocks as required by NMFS.

2174

2175 Another area of research that may contribute to a better understanding of cetacean occurrence
2176 and habitat use in the SCB and meets Navy MSMP and ICMP strategic goals is determining
2177 lengths of times cetaceans remain within the SCB, particularly endangered species and those
2178 that occur there year-round. There is currently very little information on whether these animals
2179 are the same individuals across hours and days. This information is needed to address strategic
2180 management goals identified in the Navy’s MSMP and ICMP (DoN 2010, 2011, 2012) to
2181 understand how often and how long individuals may be exposed to Navy sonar and underwater
2182 detonations in the SCB. Because this study and others show that most cetacean species are
2183 social in the SCB, especially delphinids, a subsample of tagged animals should be followed
2184 using non-intrusive platforms capable of collecting detailed social and behavioral data (e.g.,
2185 social interactions and cohesion, group composition, calf presence), since they have been
2186 shown to affect behavior and habitat selection. Examples include using autonomous unmanned
2187 vehicles such as remotely operated hexacopters equipped with high-resolution video (Durban et
2188 al. 2015), or conducting focal group follows from shore or from small aircraft at distances that do
2189 not disturb animals under observation.

2190

2191 There is also a need to determine how prey and dynamic oceanographic factors (e.g., SST,
2192 currents) influence relative small-scale use of the SCB by cetacean species. Such information is
2193 needed to differentiate naturally occurring changes from potential anthropogenic activities. I am
2194 currently working with NMFS-affiliated scientists with Navy funding to re-examine data collected
2195 during this study to assess if densities of species with adequate sample sizes (e.g., likely fin
2196 whale, common dolphin spp., Risso's dolphin) are influenced by these bottom-up factors.
2197 Further, given inter-seasonal, inter-annual and inter-decadal changes in oceanographic
2198 conditions off California (e.g., Becker et al. 2010; Campbell et al. 2015), it is important to
2199 continue long-term multi-platform monitoring in the SCB to detect potential changes in habitat-
2200 use and behavior patterns while also monitoring multiple sources of potential anthropogenic
2201 disturbance (e.g., commercial shipping, tourism, fishing, offshore oil and gas development, and
2202 military activities).

2203

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Appendix A

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TABLES AND FIGURES

2930

A.1. Chapter I Introduction

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Table 0-1. 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	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
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	summer? spawn shallow water summer? 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?, 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 relative group size	Mostly single, small	Small	Small-Medium	Medium	Medium	Large

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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; 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

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Table 0-2. Comparison of life history traits of cetacean study species while in the Southern California Bight.

Trait (N hemis.)	Blue whale¹	Fin whale²	Gray whale³	Risso's dolphin⁴	Bottlenose dolphin⁵	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 possibly	Seen year round near islands	Seen year round, abundance higher summer
Migratory?	yes	yes, some possibly resident	yes		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	NA	Late fall-winter, year-round?	Winter-early spring
Calving peak	Winter	Dec-Jan	Mid-Dec	Fall	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

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SCB=Southern California Bight; DSL=Deep Scattering Layer

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

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

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³ Rice and Wolman 1971; Wolman 1985

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⁴ Kruse 1989; Kruse et al. 1999; Chen et al. 2011; Henderson 2010

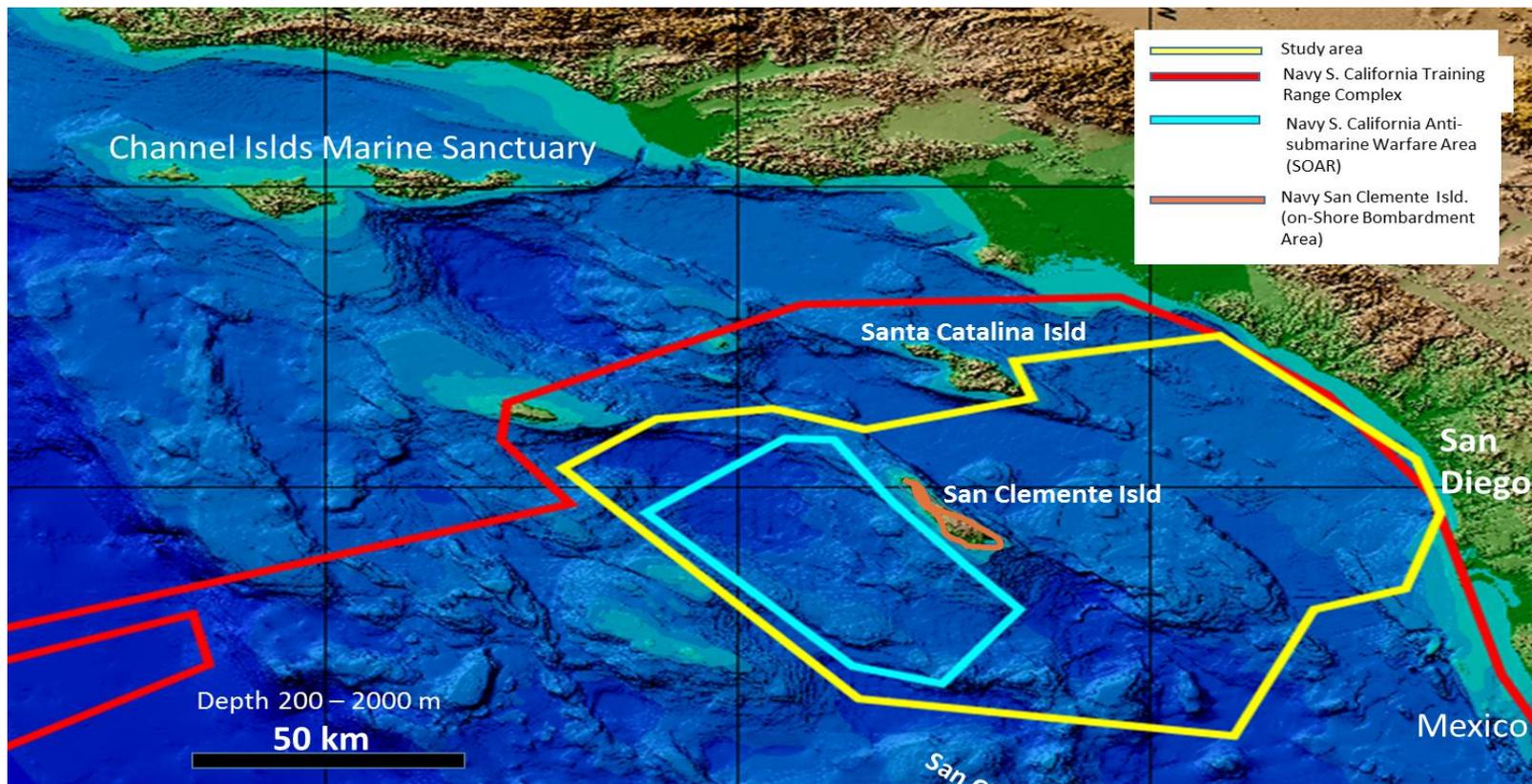
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⁵ Norris and Prescott 1961; Carretta et al. 2015 (newborn calves seen year-round in coastal ecotype with possible peak in spring-summer based on stranding data)

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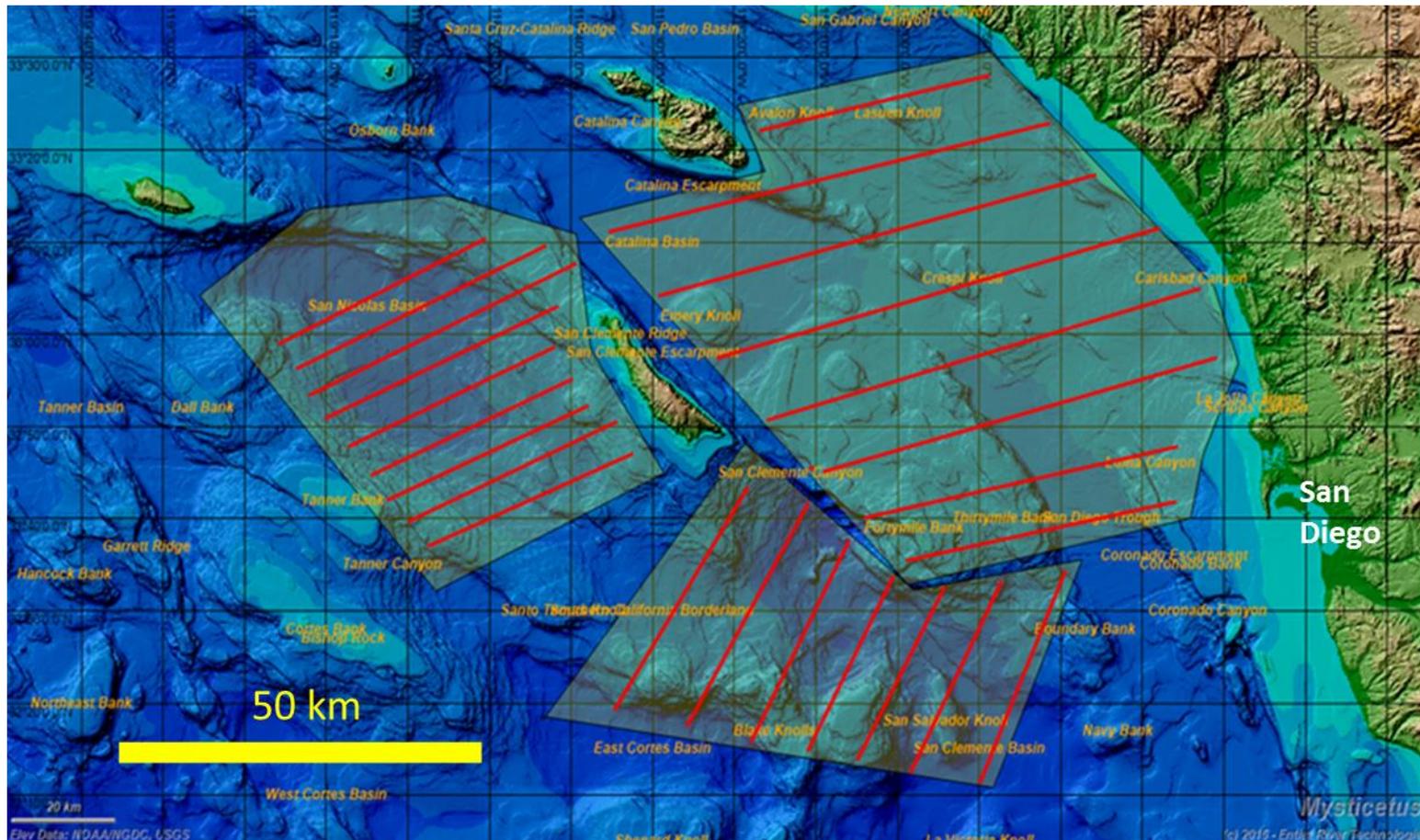
⁶ Heyning and Perrin 1994; Henderson 2010; Henderson et al. 2012, 2014a,b; Chivers et al. 2015

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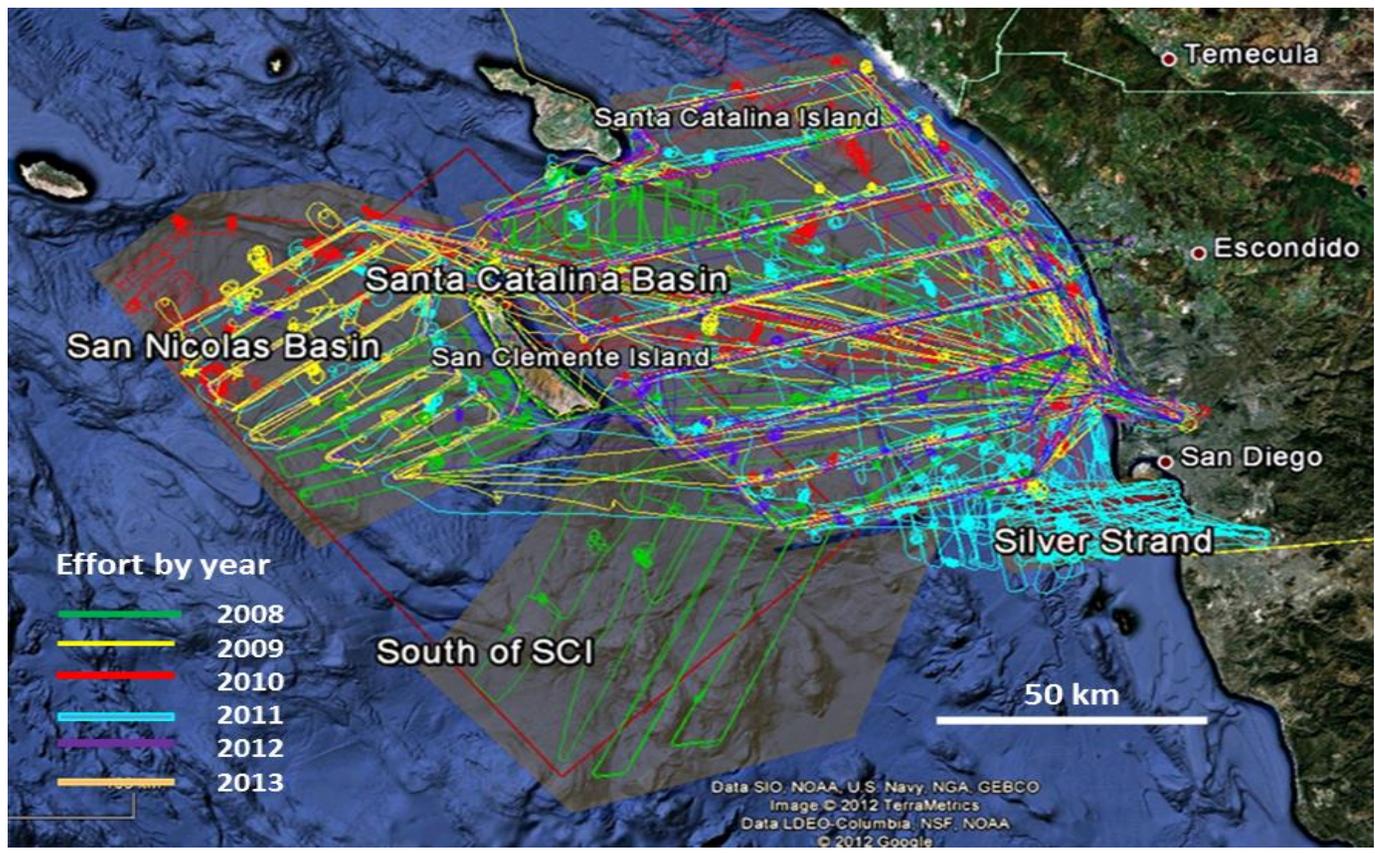
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Fig. 0-1. The Southern California Bight (SCB) study area and U.S. Navy training areas (DoN 2008b).



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Fig. 0-2. 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.



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2959 Fig. 0-3. All 2008-2013 aerial survey effort conducted in the Southern California Bight study area.

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A.2. Chapter II Modeling Cetacean Habitat Using Behavior

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Table 0-3 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).

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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

^aHeithaus and Dill (2009)

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Table 0-4 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 $\leq 1/2$ 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™*

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>

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Table 0-5 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 <i>(italics= ≤0.05)</i>		
Fin whale	All	59	Latitude	-	<i>0.0413</i>		
			Longitude	+	<i>0.0517</i>		
			Depth	+	<i>0.0053</i>		
			Shore Distance	+	<i>0.0359</i>		
			Shore Distance	-	<i>0.3970</i>		
Gray whale	Rest/slow travel	22	Longitude	+	<i>0.0276</i>		
	Medium/fast travel	36	Depth	+	<i>0.0017</i>		
			Longitude	+	<i>0.0074</i>		
	All	40	Longitude	+	<i>0.0639</i>		
	Rest/slow travel (pooled with 1 mill behavior)	19	Aspect North	-	<i>0.0958</i>		
Risso's dolphin	Medium/fast* travel	21	Longitude	+	<i>0.1630</i>		
			Shore distance	-	<i>0.1480</i>		
	All	134	Latitude	-	<i>0.0190</i>		
			Longitude	+	<i>0.001</i>		
			Shore distance	-	<i>0.0006</i>		
Bottlenose dolphin	Mill	14	Longitude	+	<i>0.2370</i>		
	Rest/slow travel	63	Longitude	+	<i>0.0149</i>		
			Shore distance	-	<i>0.0084</i>		
			Depth	+	<i>0.0803</i>		
	Med/fast travel	56	Latitude	-	<i>0.0192</i>		
			Longitude	+	<i>0.0259</i>		
			Shore distance	-	<i>0.0378</i>		
Depth			-	<i>0.1298</i>			
Bottlenose dolphin	All	31	Latitude	+	<i>0.0579</i>		
			Depth	-	<i>0.0003</i>		
			Shore distance	-	<i>0.0201</i>		
			Latitude	-	<i>0.0378</i>		
	Rest/slow travel (pooled with 1 mill behavior)	12	Longitude	-	<i>0.0302</i>		
			Med/fast travel	19	Depth	-	<i>0.0003</i>
					Shore distance	-	<i>0.0419</i>

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Table 0-6. 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

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

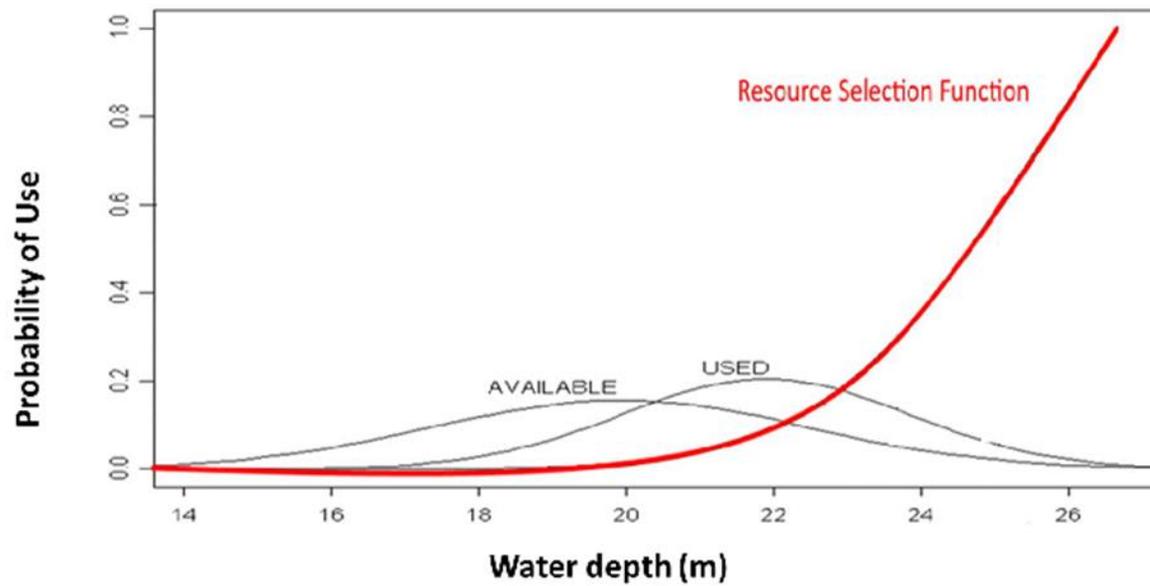
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¹Long=longitude, Lat=latitude, Dist=closest distance from shore including islands, Aspect N=Aspect north, Aspect E=aspect east. See Table 2-2 for definitions of variables.

²AIC=Akaike's Information Criteria

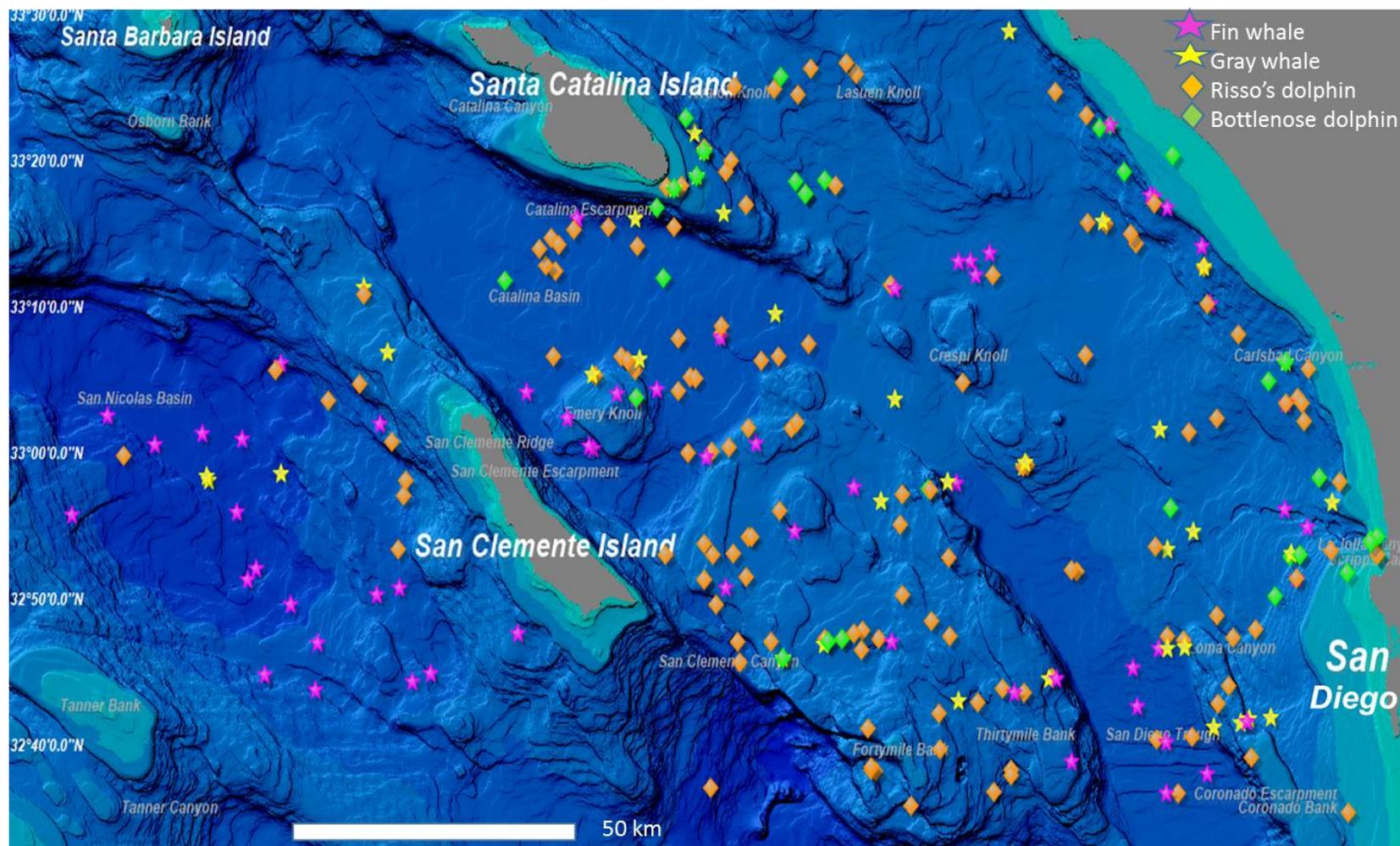
³ΔAIC=difference in consecutive AIC scores

$$RSF(x) = \frac{f_{used}(x)}{f_{available}(x)}$$



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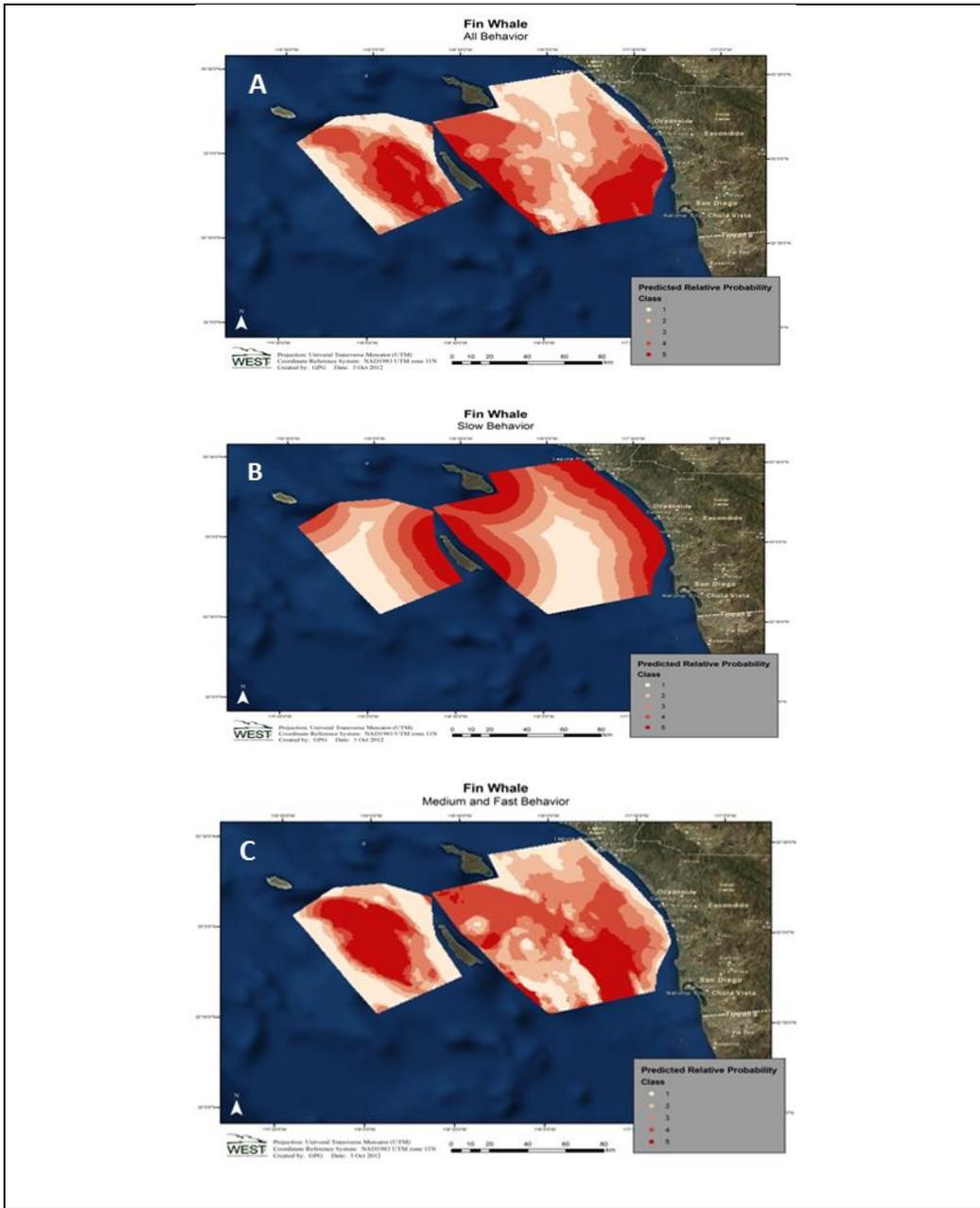
2978 Fig. 0-4 Example graphic of a Resource Selection Function and associated equation (Manly et al. 2010).



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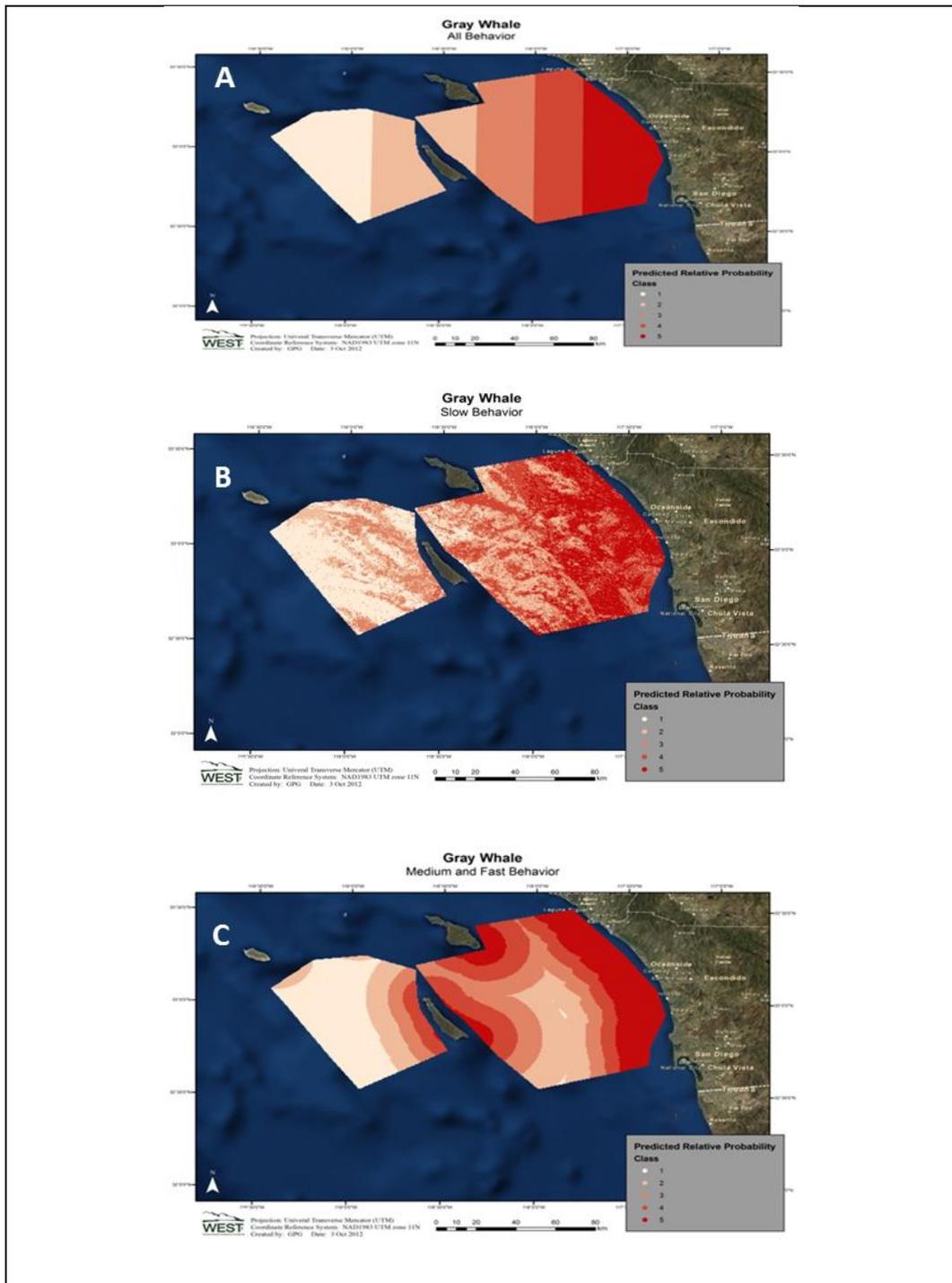
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Fig. 0-5 Cetacean sightings made during systematic and connector aerial survey effort used for Resource Selection Function analyses in the Southern California Bight study area 2008-2012.

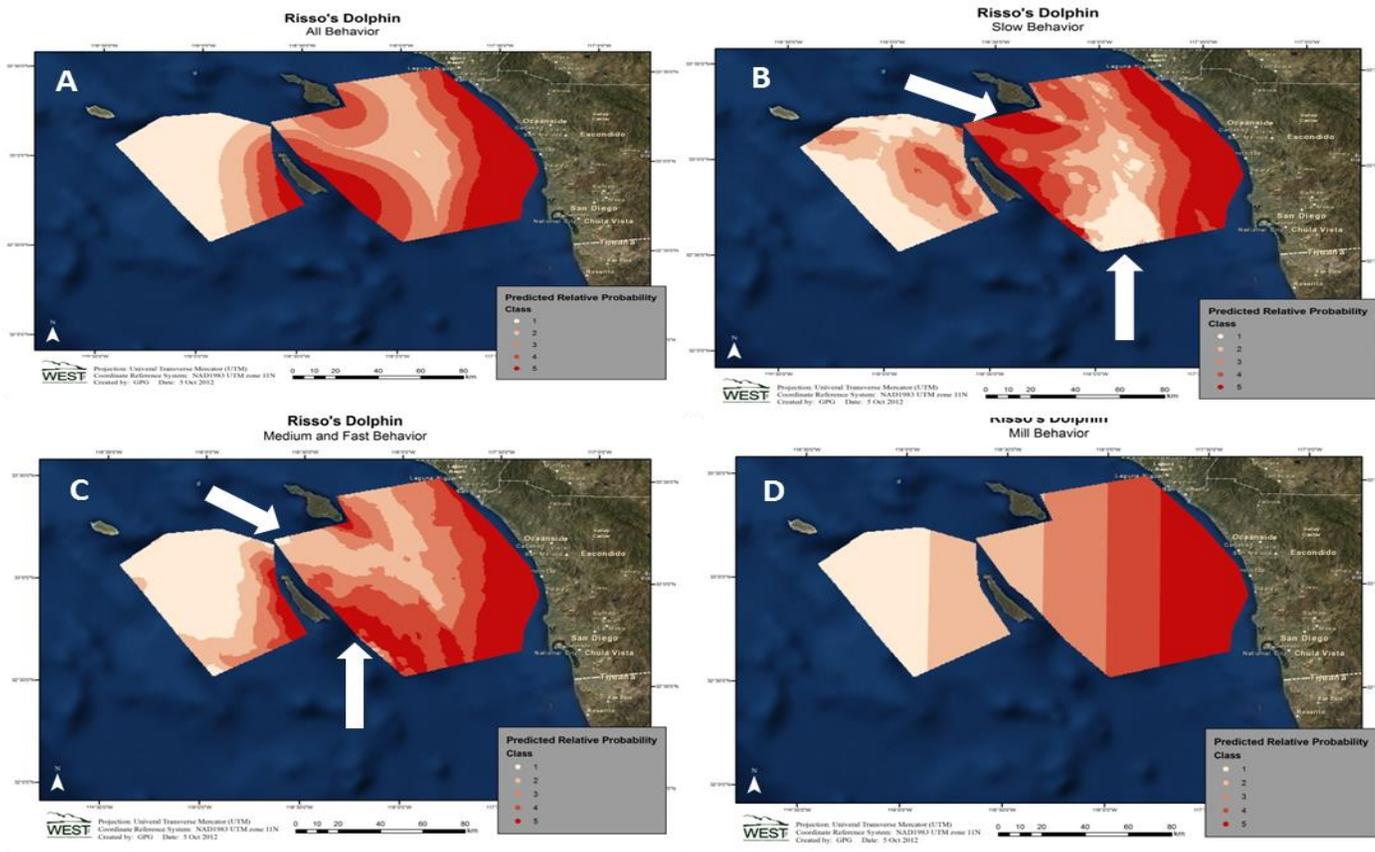


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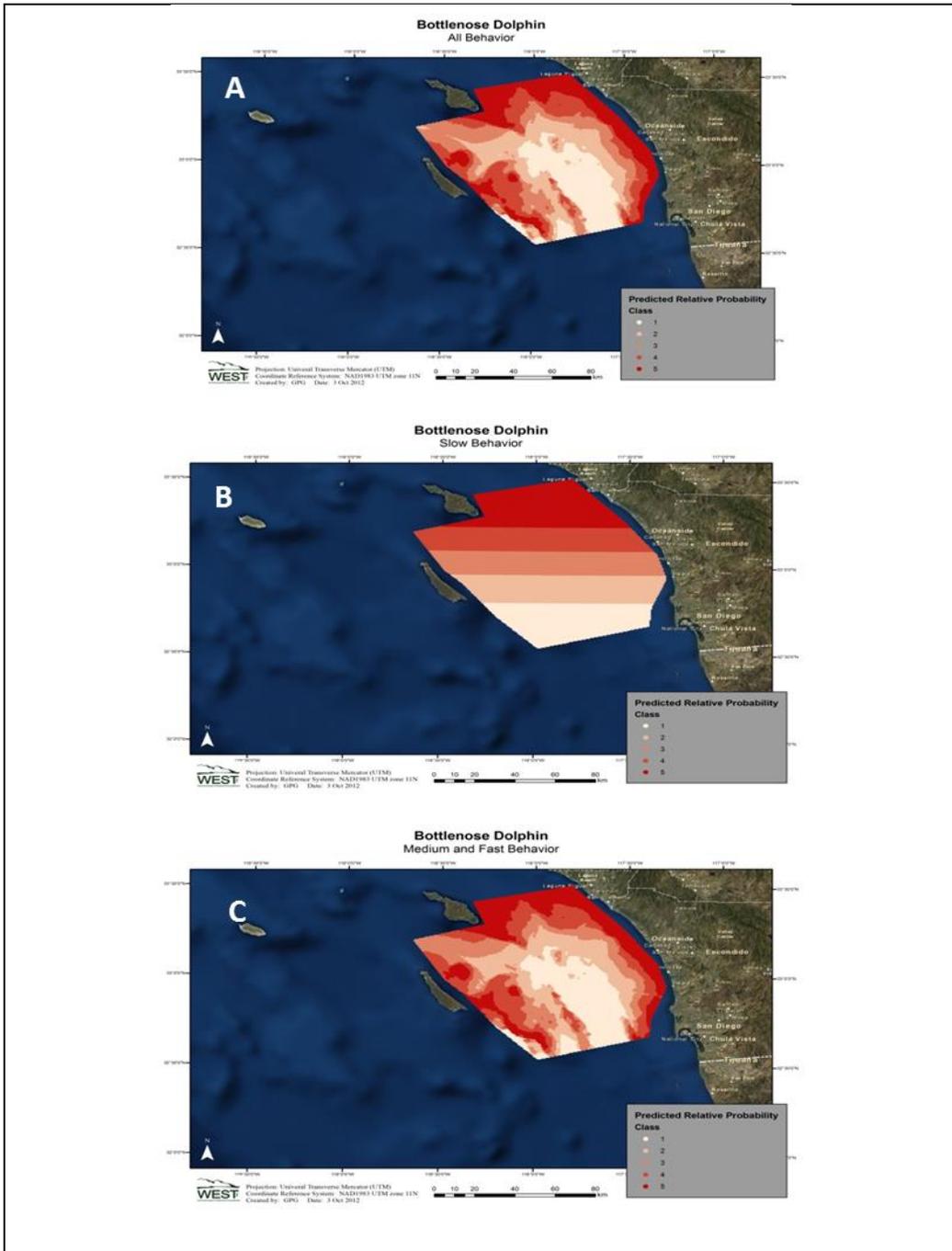
Fig. 0-6 Predicted relative probability of habitat selection for fin whale by behavioral states: A) all behavior, B) rest/slow travel, and C) medium/fast travel. Areas with highest probability of selection are represented by red; areas with lowest probability of selection are represented by white.



2986 **Fig. 0-7 Predicted relative probability of habitat selection for gray whale by behavioral**
 2987 **states: A) all behavior, B) rest/slow travel, and C) medium/fast travel. Areas**
 2988 **with highest probability of selection are represented by red; areas with lowest**
 2989 **probability of selection are represented by white**



2990 **Fig. 0-8 Predicted relative probability of selection for Risso's dolphin by behavioral states: A) all behavior, B) rest/slow travel, C)**
 2991 **medium/fast travel, and D) mill. Areas with highest probability of selection are represented by red; areas with lowest**
 2992 **probability of selection are represented by white. Arrows highlight spatial differences between rest/slow travel and**
 2993 **medium/fast travel.**



2994 **Fig. 0-9 Predicted relative probability of habitat selection for the bottlenose dolphin by**
 2995 **behavioral states: A) all behavior, B) rest/slow travel, and C) medium/fast**
 2996 **travel. Areas with highest probability of selection are represented by red; areas**
 2997 **with lowest probability of selection are represented by white.**
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2999 **A.3. Chapter II Cetacean Body Size, Group Size, and Group Cohesion**

3000 **Table 0-7. Summary statistics for observed group sizes of mysticete and odontocete**
 3001 **species in the Southern California Bight 2008-2012. These data include those**
 3002 **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

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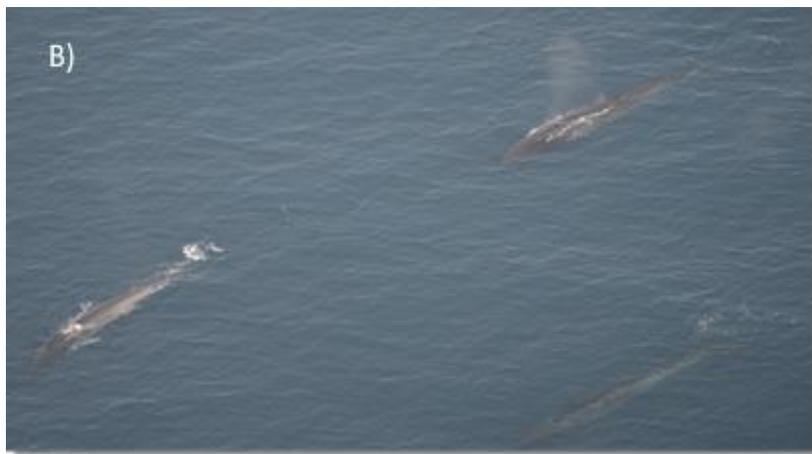
3005 **Table 0-8. Summary statistics for observed group cohesion, measured in maximum body**
 3006 **lengths, for mysticete and odontocete species in the Southern California Bight**
 3007 **2008-2012. These data only include those sightings where group sizes were ≥ 2**
 3008 **animals.**

	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

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3013 **Fig. 0-10 Photographs of A) a mother and calf blue whale, B) three fin whales, and C) two**
3014 **gray whales showing variation in group cohesion based on maximum distance between**
3015 **nearest neighbors estimated in adult species body length. Photographs taken by D.**
3016 **Steckler, B. Würsig, and B. Würsig, respectively, under NMFS permit 14451.**

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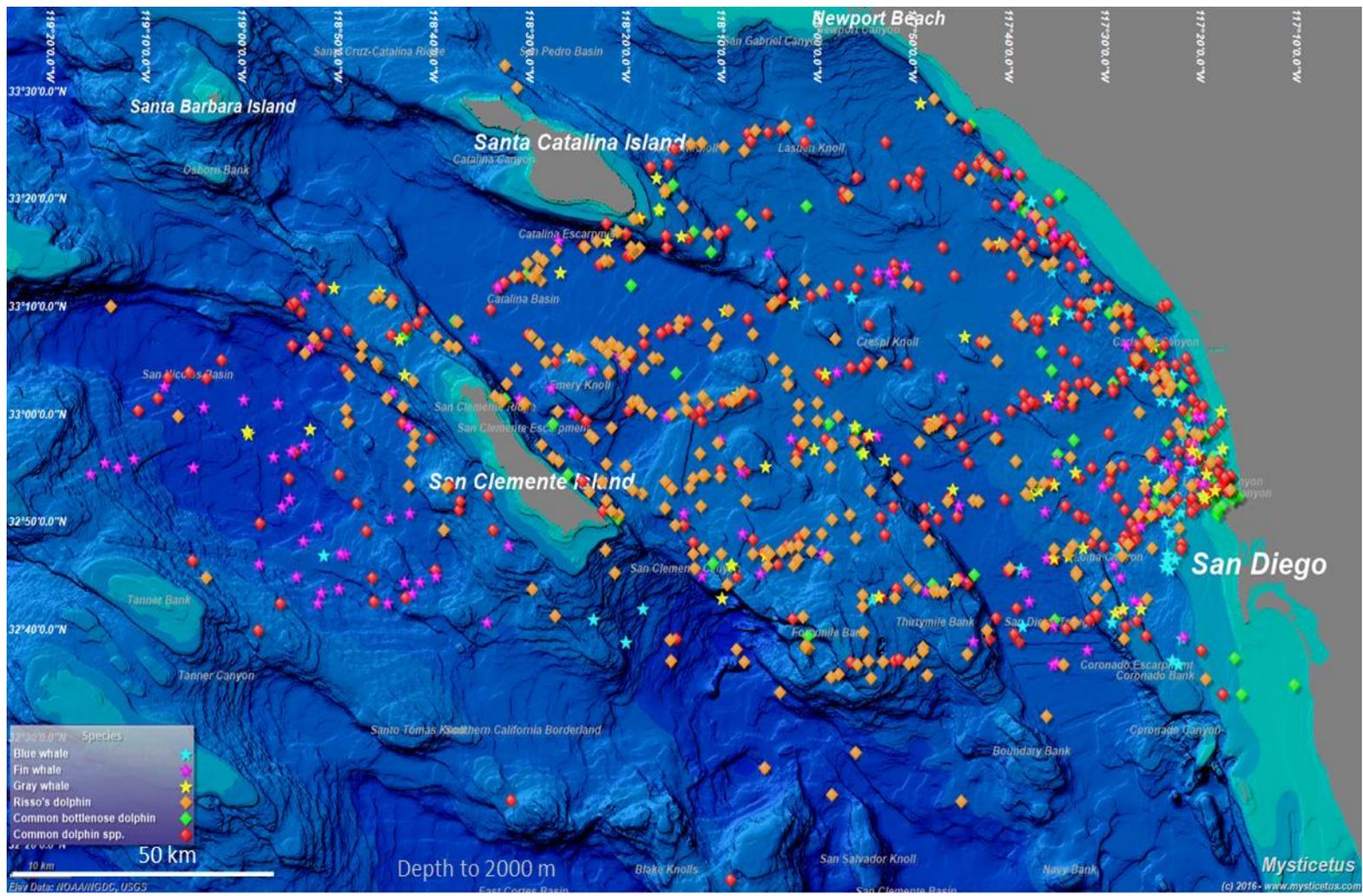
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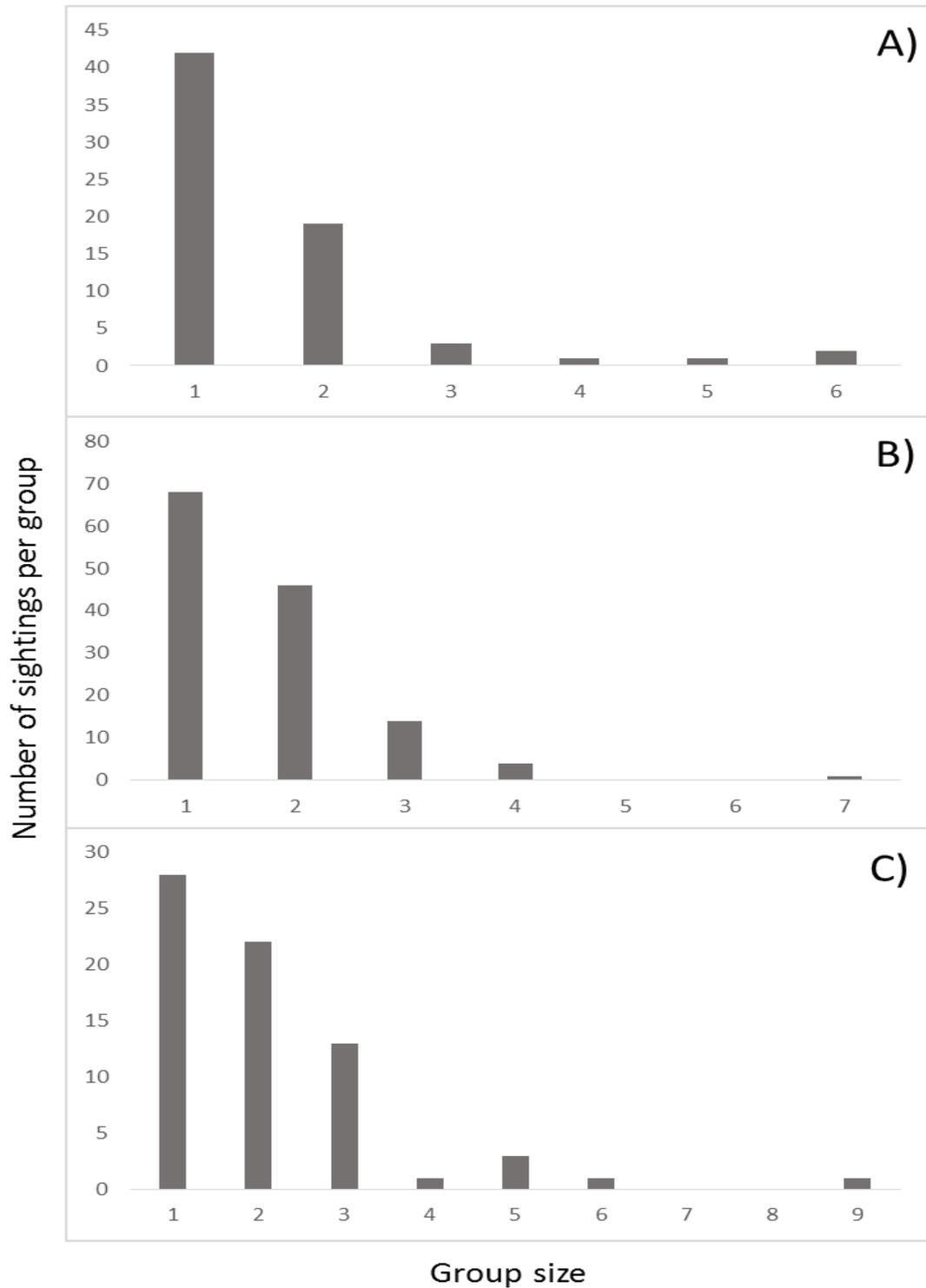
Fig. 0-11 Photographs of A) Risso's dolphins, B) bottlenose dolphins, and C) common dolphins showing variation in group cohesion based on maximum distance between nearest neighbors estimated in adult species body length. Photographs taken by L. Mazzuca, A. Henry (NMFS/NOAA website), and B. Würsig, respectively, under NMFS permit 14451.



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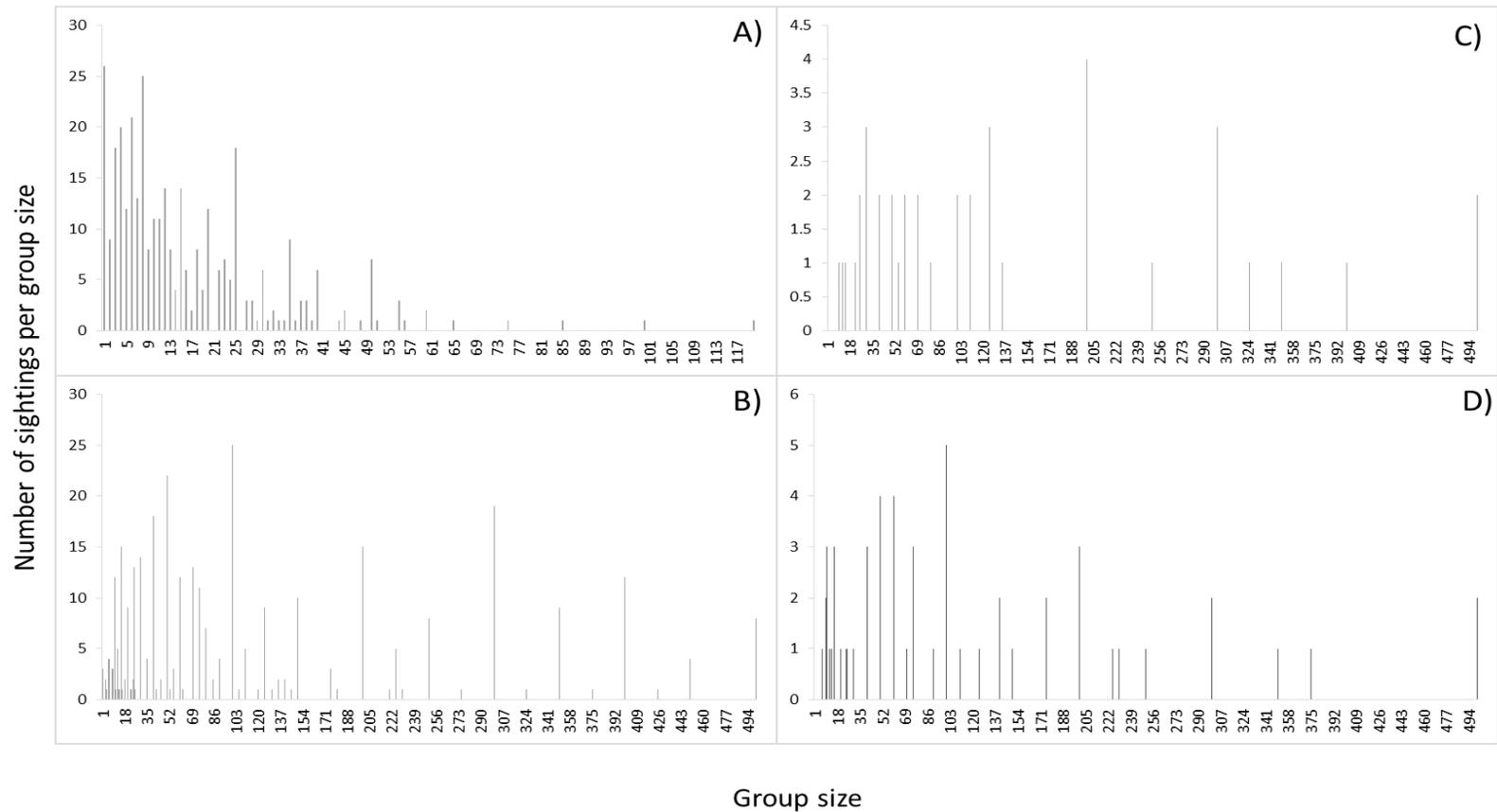
Fig. 0-12 All cetacean sightings made during the 2008-2013 aerial surveys in the Southern California Bight study area.



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Fig. 0-13 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.



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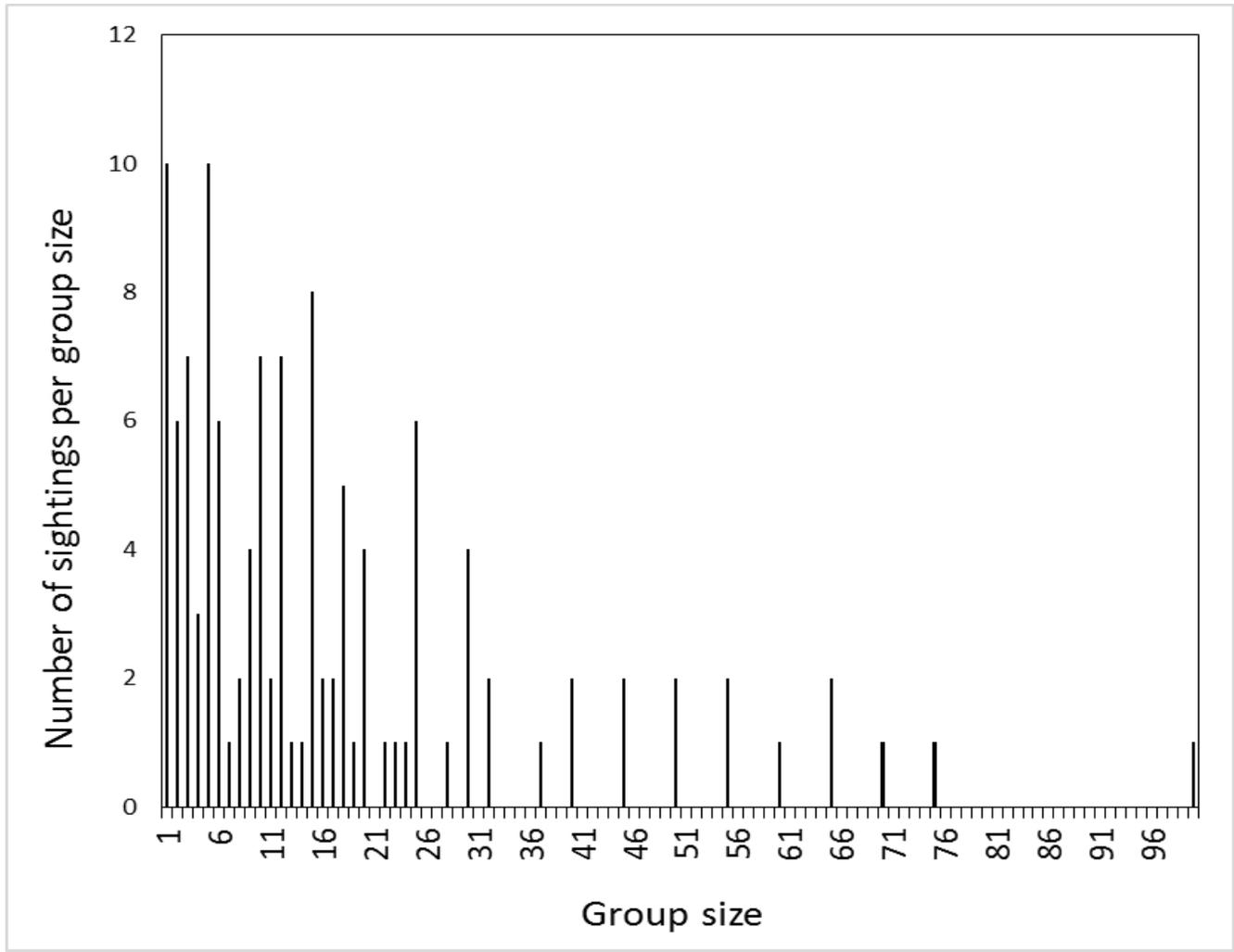
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Fig. 0-14 Distribution frequency by group size of A) Risso's dolphin, B) common dolphin spp., C) long-beaked common dolphin, and D) short-beaked common dolphin based on aerial survey data in the Southern California Bight 2008-2013. For all common dolphin 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 occasionally seen; the x-axes for these dolphin species have been shortened for display scale purposes

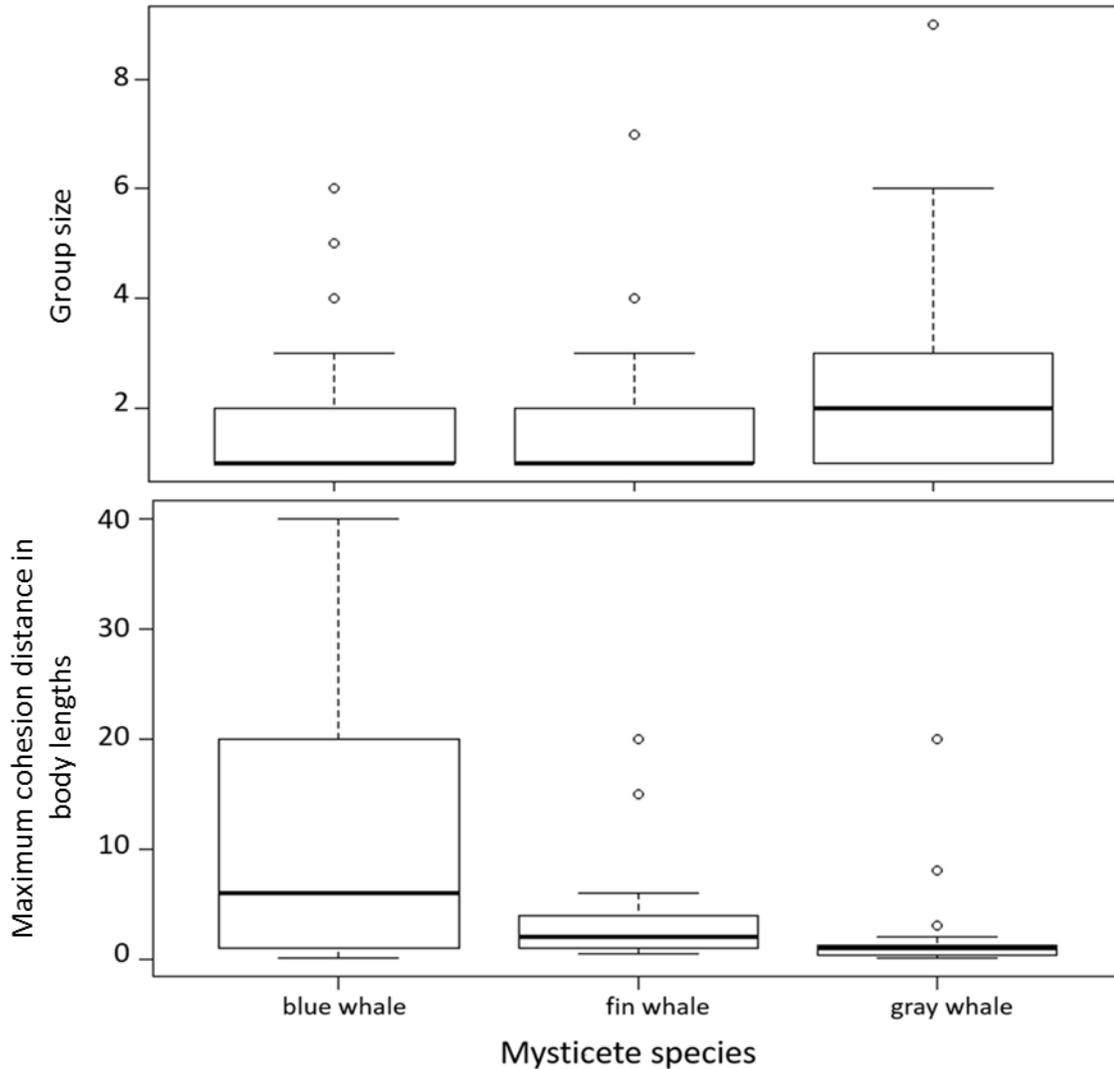


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Fig. 0-15 Distribution frequency by group size of common bottlenose dolphins.

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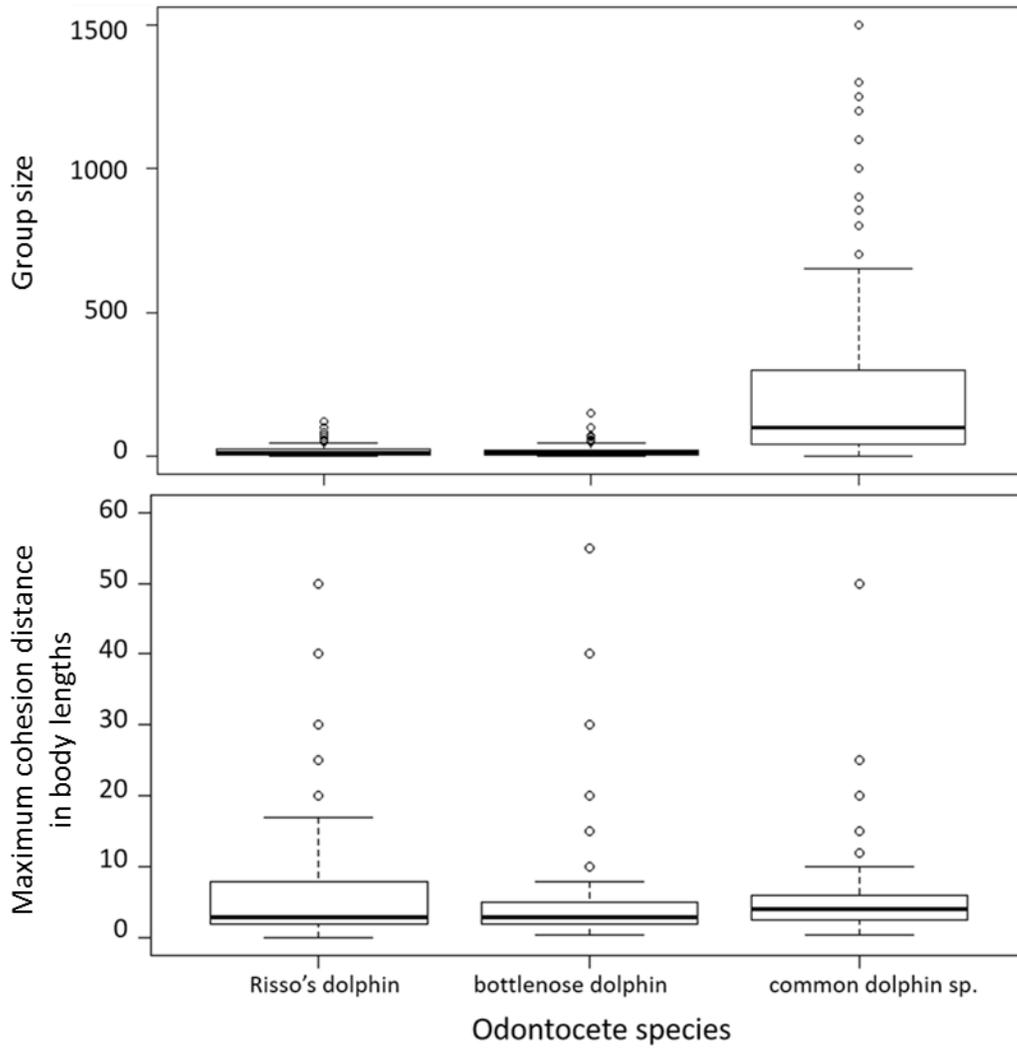


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3041 **Fig. 0-16** Box plot of median group size and median maximum group cohesion distance
3042 of three mysticete whale species. The bottom and top of the box represent the
3043 first (Q1) and third quartiles (Q3), and the band inside the box is the median
3044 The upper whisker outside the box is $Q3+1.5*Interquartile\ Range\ (IQR)$, and the
3045 lower whisker is $Q1-1.5*IQR$. Data points outside the hash marks are outliers.

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Fig. 0-17 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.

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

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Table 0-9. Top three multinomial logistic regression models and AIC values for blue whale, fin whale, and gray whale response variables for data collection.

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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

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3058 **Table 0-10. 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	

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3061¹ CI=Confidence Interval
² Odds ratio for 100 days

3062 **Table 0-11. 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	
NW	Intercept	-0.2292	0.3692	-0.9528	0.4944	
	Slope	0.0742	0.0583	-0.0401	0.1885	2.101
SE	Intercept	-0.0171	0.4158	-0.8320	0.7978	
	Slope	-0.1126	0.1132	-0.3345	0.1092	0.321
SW	Intercept	0.5629	0.3524	-0.1279	1.2537	
	Slope	-0.0880	0.0848	-0.2543	0.0782	0.411

3063 ¹ CI=Confidence Interval
 3064 ² Odds ratio for 100 days
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Table 0-12. 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	Δ 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	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
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	
Common bottlenose dolphin	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	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

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Table 0-13. 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	-	0.00042	-	-	
		0.00169		0.00252	0.00087	

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¹Odds ratio for 100 days
²Odds ratio for 60 minutes
³Odds ratio for 10 kilometers

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Table 0-14. 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	

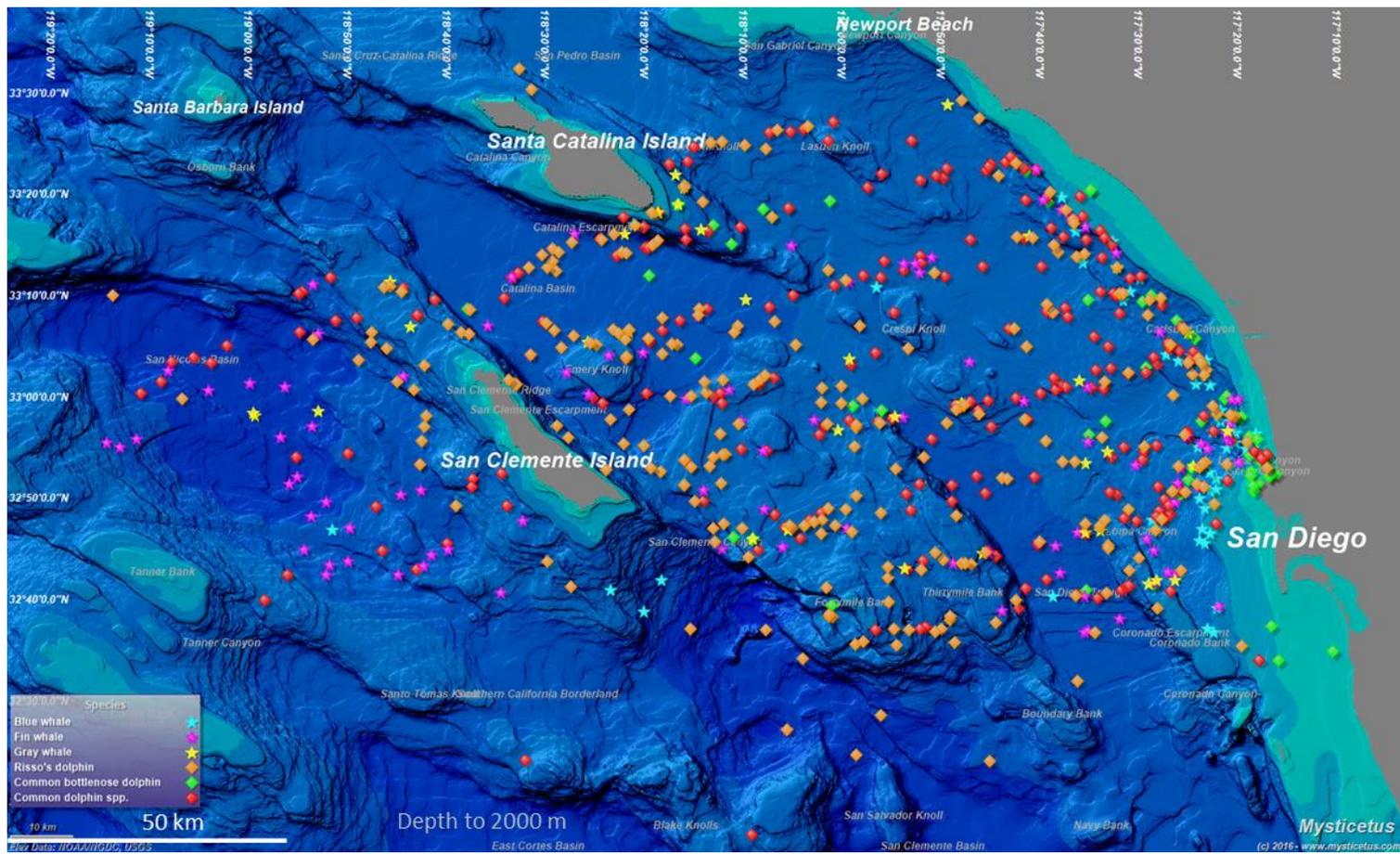
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Table 0-15. Summary statistics and odds ratios for the top-ranked common dolphin spp. model by response variable.

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

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Fig. 0-18 All cetacean sightings made during aerial surveys in the Southern California Bight study area 2008-2012.

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A.5. Chapter V Summary

3085 **Table 0-16. 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
Ch IV/Q3.1: Does calf presence influence group size and cohesion of	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

cetacean species in the SCB?

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

3087 **Table 0-17. High probability habitat locations and peak periods of biological use based on study results and literature review for**
 3088 **six cetacean species in the Southern California Bight.^{1,2}**

Species	ESA Status³	High-Probability Habitat⁴	Peak Biological Use Period⁴
All six species	Includes ESA-listed fin & blue whale	Overlap across species in coastal mainland, SCI & SCal 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, SCal & mainland waters	Summer-fall peak feeding
Gray whale	n/a	coastal mainland, SCI, & SCal 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 SCal, SCI & mainland waters	Spring peak calving/mating
Common dolphin spp. ⁵	n/a	Slope waters	Winter-spring peak calving/mating

3089 ¹ Evans 1974, 1975, 1994; Poole 1984; Forney et al. 1995; Urian et al. 1996; Carretta et al. 2000; Thayer et al. 2003; Rugh et al. 2005; Oleson et al. 2007; Baird 2009; Sears
 3090 and Perrin 2009; Becker et al. 2007, 2010, 2012, 2014; Danil et al. 2010; Campbell et al. 2011; Falcone and Schorr 2011, 2012, 2013, 2014; Sumich and Show 2011;
 3091 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;
 3092 Chivers et al. 2015; Lomac-MacNair and Smultea 2016

3093 ² See summary of species life history in Appendix A

3094 ³ ESA=U.S. Endangered Species Act

3095 ⁴ SCI=San Clemente Island, SCal=Santa Catalina Island, SNB=San Nicolas Basin. E/SE=east-southeast

3096 ⁵ Common dolphin spp.= short- and long-beaked common dolphins

3097

Appendix B

3098

LIFE HISTORY SUMMARY OF CETACEAN STUDY SPECIES

3099

B.1. Blue Whale

3100 Blue whales in the SCB belong to the Eastern Pacific Stock that feeds during summer-fall from
3101 the Gulf of Alaska to California, and subsequently migrates south to overwinter in tropical waters
3102 off Mexico, in the Gulf of California (Calambokidis et al. 1990; Reilly and Thayer 1990; Sears et.
3103 al 2014) and off Central America (Costa Rica and Nicaragua, Mate et al. 1999). Blue whales
3104 inhabit the SCB biannually during spring and fall migrations, with some animals remaining to
3105 feed primarily during summer-fall, peaking from July through September (Larkman and Veit
3106 1998; Oleson et al. 2007; Calambokidis et al. 2015; Lomac-MacNair and Smultea 2016). Blue
3107 whale peak presence in feeding areas has been shown to occur several months after peak
3108 chlorophyll-a concentrations (Burtenshaw et al. 2004). Predictive modeling of blue whale density
3109 relative to environmental factors in the California Current ecosystem (CCE) indicates their
3110 seasonal presence is linked with seasonal changes in SST based on decades of survey data
3111 (e.g., Becker et al. 2010). Foraging occurs in waters characterized by steep bathymetric relief
3112 (e.g., the continental shelf edge, island edges, seamounts) that tend to concentrate invertebrate
3113 prey downstream from core upwelling areas (Fiedler et al. 1998; Schoenherr 1991). Blue whales
3114 are considered selective consumers, typically feeding at depths of 100 to 200 m nearly
3115 exclusively on dense subsurface layers of *Euphausia pacifica* and *Thysanoessa spinifera*
3116 associated with the Deep Scattering Layer (DSL, consisting of a stratified, dense organism-rich
3117 layer such as zooplankton and fishes that undergoes a daily vertical migration closer to the
3118 surface at night; Allaby 2004) (Croll et al. 1998; Fiedler et al. 1998; Sears and Perrin 2009; NOAA
3119 2014). Shallower dives typically occur during darkness when prey move closer to the surface
3120 (Sears and Perrin 2009). Feeding blue whales typically swim at 3-6 km/hr while traveling
3121 individuals swim faster at 5-35 km/hr (Sears and Perrin 2009).

3122

3123 Given their oceanic tendencies and low population numbers, blue whale social and group
3124 dynamics (e.g., courting, breeding, nursing, calving) are poorly understood. However, they are
3125 known to produce geographically specific calls at very low frequencies. Available data indicate
3126 that blue whales tend to occur alone or in pairs, and social associations are believed to be short
3127 term (Sears and Perrin 2009). Stable pairings were documented for periods of up to 1 h during
3128 focal studies conducted during a separate aspect of this study (Lomac-MacNair and Smultea

3129 2016, Smultea unpublished data). While some females exhibit site fidelity to nursing grounds in
3130 the Gulf of California, birthing has never been documented. Sears et al. (2014) hypothesized that
3131 female blue whales calve in open pelagic water, subsequently moving to coastal waters as
3132 calves mature. This is contrary to other baleen whales including gray, humpback and South and
3133 North Atlantic right whales that aggregate each winter on coastal calving grounds (e.g., Herman
3134 and Tavolga 1980; Sears et al. 2014).

3135

3136 Mating occurs from late fall through winter, coinciding with peak calling rates including in the
3137 SCB (Wiggins et al. 2005; Sears and Perrin 2009). Birthing to a single calf occurs from fall
3138 through winter and calves are weaned near the age of 6–7 months (Sears and Perrin 2009). In
3139 the Gulf of Saint Lawrence during summer-fall, female-male pairings have been documented,
3140 sometimes for as long as five weeks (Sears and Perrin 2009). When such a pair is approached
3141 by a third blue or even a fin whale, vigorous surface-active behaviors that involve high-speed
3142 chasing, splashing, breaching and porpoising out of the water for typically 7–25 min (Sears and
3143 Perrin 2009). Blue whales in the eastern North Pacific produce relatively simple but long-
3144 duration, low-frequency (16 Hertz [Hz] songs throughout the year, known as Type A and B calls
3145 (Stafford et al. 2001; McDonald et al. 2006). These songs are produced by males (primarily lone
3146 males) and are believed to be associated with reproduction (Oleson et al. 2007a,b). In the SCB,
3147 blue whale B songs were found to peak crepuscularly (Oleson et al. 2007b). Killer whales
3148 regularly attack blues whales as 25% of individuals in the Gulf of Mexico had killer whale teeth
3149 rake marks on their tails (Sears and Perrin 2009).

3150

B.2. Fin Whale

3151 Fin whales belonging to the Northeast Pacific Stock occur year-round in the SCB (Douglas et al.
3152 2014; Jefferson et al. 2014a; Smultea and Jefferson 2014). Although some individuals inhabit
3153 the SCB for multiple days, months and years, it is unknown if any remain year-round (Falcone
3154 and Schorr 2014). Other fin whales have been sighted as they migrate southward through the
3155 SCB during fall and again as they pass northward in late spring (Forney et al. 2012;
3156 Calambokidis et al. 2015). Highest densities are in late summer/early fall during high
3157 zooplankton and fish densities associated with seasonal upwellings (Forney et al. 2012; Douglas
3158 et al. 2014; Calambokidis et al. 2015). Water depth and SST have been the most useful broad-
3159 scale environmental predictors for the CCE using predictive habitat-density modeling and
3160 summer-fall data (Forney 2000; Barlow et al. 2009; Becker et al. 2010). Data prior to 2008
3161 suggest that during summer-fall, SCB fin whales may move shoreward west of San Clemente
3162 Island to coastal waters further out in winter-spring (Douglas et al. 2014; Falcone and Schorr

3163 2014; Calambokidis et al. 2015). However, this trend was not apparent during SCB aerial
3164 surveys in 2008-2012 (Jefferson et al. 2014a). Fin whales in the SCB prey primarily upon krill
3165 and small schooling fish such as herring and sardines (Calambokidis et al. 2015; Jefferson et al.
3166 2015).

3167
3168 Virtually nothing is known about fin whale social behavior including courting, breeding, nursing
3169 and intra- and inter-specific competition for food (Aguilar 2009). However, fin whales are
3170 hypothesized to likely exhibit physical competition between multiple males vying to monopolize a
3171 female rather than sperm competition based on testes size (Lockyer 1984). Courting and mating
3172 behaviors have similarly been documented to sometimes occur during migration periods among
3173 humpback, gray, and bowhead (*Balaena mysticetus*) whales (Nerini et al. 1984; Würsig et al.
3174 1985; Jones and Swartz 2009).

3175

B.3. Gray Whale

3176 Gray whales of the Northeastern Pacific Stock migrate through the SCB twice a year between
3177 more northern feeding grounds ranging from northern California to Alaska and southern winter
3178 calving/breeding grounds off Mexico (Rice and Wolman 1971; Jones et al. 1984; Jones and
3179 Swartz 2009; Jefferson et al. 2015). Southbound animals pass through the SCB from October–
3180 March, peaking in December–March; they return northward with newborn calves, moving
3181 through the SCB from late January–July, peaking in April July (Rice and Wolman 1971; Swartz
3182 1986; Rugh et al. 2001, 2005). Courting and mating among California gray whales appears to
3183 occur throughout the year (Norris and Dohl 1980). The vast majority of migrating animals remain
3184 within 10 km of the mainland coast, and were presumably outside the study area; however,
3185 some individuals in the SCB travel offshore and migrate through the Channel Islands including
3186 near San Clemente Island and Santa Catalina Island, within the study area (Daily et al. 1993;
3187 Sumich and Show 2011; see Chapter II).

3188

B.4. Risso's Dolphin

3189 Risso's dolphins in the SCB belong to the California/Oregon/Washington Stock inhabiting shelf,
3190 slope and offshore waters from the SCB to Washington (Carretta et al. 2014), preferring waters
3191 400–1000 m deep (Baird 2009). In the SCB, the abundance of Risso's dolphins has increased
3192 over the last 50 years (Jefferson et al. 2015). Risso's dolphins were considered relatively rare
3193 (e.g., Shane 1995; Forney et al. 1995; Carretta et al. 2000; Smultea and Jefferson 2014), but
3194 they now are the second-most common cetacean species in the SCB, occurring year-round in
3195 relatively high numbers (Smultea and Jefferson 2014; Jefferson et al. 2014a). Historically, the
3196 species' abundance and distribution was assumed to vary seasonally. Lowest numbers were

3197 reported during the SCB's November–April cold-water season, with highest numbers during the
3198 May–October warm-water season (Green et al. 1992; Forney and Barlow 1998; Barlow and
3199 Forney 2007; Forney et al. 2012; Becker et al. 2012). However, from 2008-2012, Jefferson et al.
3200 (2014a) reported seasonal trends opposite to these earlier reports. Soldevilla et al. (2010) found
3201 that Risso's dolphin echolocation activity peaked in the SCB during fall. Seasonal and yearly
3202 variability is likely influenced by ENSOs and decadal oscillations (Shane 1994; Barlow and
3203 Forney 2007; Forney et al. 2012; Becker et al. 2012; Douglas et al. 2014; Campbell et al. 2015).
3204 Water depth has been the only useful predictive environmental parameter for this species using
3205 complex in-situ and predictive habitat-density modeling for broad-scale data collected in the CCE
3206 over multiple years (Becker et al. 2010).

3207

3208 The social, reproductive, feeding, and diving behavior of Risso's dolphins are little known, given
3209 their preference for abrupt underwater slopes typically found in offshore waters. Most information
3210 on reproduction and feeding comes from dead Risso's dolphins hunted during drive fisheries (i.e.
3211 where dolphins are herded into small bays against shorelines) (Amano and Miyazaki 2004), and
3212 research studies in areas where steep slopes and/or currents meet land producing upwelling and
3213 accompanying high biological productivity. The latter includes Monterey Bay (Kruse et al. 1999),
3214 the Azores (Hartman et al. 2008; Visser et al. 2011), and the SCB (Shane 1994, 1995a,b;
3215 Campbell et al. 2011; Falcone and Schorr 2014). The species' lack of functional teeth similar to
3216 known cetacean squid-eaters (Jefferson et al. 2015), combined with limited stomach content,
3217 and diurnally observed feeding behavioral data suggest that this species feeds predominantly at
3218 night on squid (e.g., Baird 2009; Jefferson et al. 2015; Soldevilla et al. 2011). Recent tagging
3219 data revealed that their deep foraging dives peak crepuscularly (G. Schorr unpubl. data). Risso's
3220 dolphins in the SCB may also exhibit alternative foraging strategies including kleptoparasitism
3221 (Smultea et al. 2014). Cockroft et al. (1993) reported that Risso's dolphins off South Africa feed
3222 predominantly on solitary cephalopod species that tend to be distributed widely, evenly and
3223 solitarily. Shane (1995) observed Risso's dolphins feeding on spawning squid near San
3224 Clemente Island. Typical group sizes for Risso's dolphins in the CCE and SCB range from 10-50
3225 individuals (Forney and Barlow 1998; Baird 2009; Jefferson et al. 2014a,b).

3226

3227 Peak calving in the eastern Pacific appears to occur during winter (Baird 2009). Based on an
3228 estimated gestation period of 13–14 months (Baird 2009), mating correspondingly peaks in late
3229 fall. Both sexes display extensive apparent intra-specific teeth raking scars that are not found on
3230 newborn calves (Baird 2009). Hartman et al. (2008) suggest that the most heavily scarred
3231 animals are mature males based on photo-identification and limited sexing studies in the Azores.

3232 The latter studies reported strong site fidelity for some individuals, limited evidence of
3233 segregation by small groups of females with calves or lone female-calf pairs, and some relatively
3234 stable associations between mature males and between mature females (Hartman et al. 2008).
3235 Hartman et al. (2008) suggested that relatively stable male social associations or “clusters” may
3236 be alliances that benefit from improved mating access to females through physical coercion and
3237 cooperative breeding opportunities for males that take turns mating, as documented among male
3238 bottlenose dolphins (Connor et al. 2000). Hartman et al. (2008) based their hypothesis on
3239 observations of a known Risso’s dolphin male mating with a known female in front of four social-
3240 cluster members and a number of consistently high association indices among several groups of
3241 males. Perrin and Reilly (1984) inferred that Risso’s dolphins may be characterized by a multi-
3242 male breeding system based on relative testes size. Hartman et al. (2008) further hypothesized
3243 that such a system would be consistent with high competition among males to breed with
3244 females. A similar stratified social organization occurs among spinner dolphins associated with
3245 isolated tropical atolls (Karczmarski et al. 2005). However, stable associations may not be a
3246 unilateral species characteristic. The latter social system may be a result of the relatively isolated
3247 habitat and relatively insulated breeding population in the Azores, since it has not been previously
3248 reported among Risso’s dolphins. The latter social system appears intermediate to the fission-
3249 fusion and matrilineal society models applied to many odontocetes (Würsig and Würsig 1980;
3250 Norris and Dohl 1980; Connor et al. 2000).

3251 **B.5. Common Bottlenose Dolphin**

3252 Common bottlenose dolphins are generally split worldwide into coastal and offshore populations
3253 (Hansen 1990; Carretta et al. 1998; Defran and Weller 1999; Bearzi et al. 2009; Wells and Scott
3254 2009). In the SCB, morphology (Walker 1981), photo-identification (Campbell et al. 2011) and
3255 genetics (Lowther 2006) provide evidence that bottlenose dolphins occur in two distinct stocks: a
3256 coastal stock of approximately 450 individuals inhabiting waters within 1 km of the mainland
3257 coast (Defran and Weller 1999; Dudzik et al. 2006) and an offshore stock of 3,000 individuals
3258 inhabiting offshore waters from a few km off the mainland coast to deep pelagic waters (Caretta
3259 et al. 2009). It is hypothesized that the offshore stock of bottlenose dolphins may be further
3260 divided into inshore/island-associated animals occurring near the Channel Islands and pelagic
3261 animals occurring in deep offshore waters (Shane 1994; Carretta et al. 2000; Campbell et al.
3262 2011; Smultea and Jefferson 2014; Jefferson et al. 2014a). However, the combined evidence
3263 remains inconclusive as to whether bottlenose dolphins on the offshore continental shelf and/or
3264 near islands in the SCB are distinct from those inhabiting pelagic waters. Recent photo-
3265 identification data indicate that the island ecotype displays some degree of site fidelity as well as

3266 interchange between Catalina and San Clemente islands: the same individuals were frequently
3267 resighted during survey periods ranging from 5-14 days (Campbell et al. 2011).

3268

3269 Bottlenose dolphins are considered opportunistic feeders, though most prey consist of a variety
3270 of fish and squid species; some individuals in the same population express specific prey
3271 preferences (Barros and Odell 1990; Wells and Scott 2009). Calving has been reported year-
3272 round in this species, though peaks occur in spring-summer (Urian et al. 1996; Thayer et al.
3273 2003). In captivity, females are spontaneous sporadic ovulators, though male testosterone levels
3274 remain high year-round (Wells and Scott 2009). Data on calving and breeding periods specific to
3275 the SCB are not available (DoN 2008). However, newborn calves have been observed year-
3276 round in mainland coastal waters off southern California (D. Weller, NMFS-SWFSC, personal
3277 communication in DoN 2008a). SCB stranding data suggest that calving peaks May to
3278 September (Danil et al. 2010). During the SCB aerial surveys, 84% of all groups with calf
3279 presence were seen during January-May (uncorrected for effort), with only two groups containing
3280 a calf during June-November. Differences in peak calf sightings may reflect differences between
3281 offshore and coastal populations. Gestation lasts about 12 months, and calves may remain with
3282 their mothers for 3-6 years (Wells and Scott 1999). Sharks (Wells and Scott 1999) and killer
3283 whales attack and prey upon bottlenose dolphins based on body scarring patterns (Jefferson et
3284 al. 1991).

3285

B.6. Common Dolphins

3286 Two species of sympatric common dolphins, the short- and long-beaked species, inhabit
3287 primarily deep offshore waters of the SCB (Carretta et al. 2015). Due to the inherent difficulty in
3288 distinguishing them at sea, they historically have been considered the same species until the
3289 mid-1990s (Jefferson et al. 2014a). Some authors have reported that they occur in distinct
3290 species-specific groups (e.g., Evans 1975; Bearzi 2005), while others have reported seeing them
3291 in mixed groups (Hill and Barlow 1992; G. Campbell, Texas A&M University, personal
3292 communication). Via photograph examination by a species expert (T. Jefferson), only 23% (17%
3293 short-beaked and 6% long-beaked common dolphin) of the 191 examined sightings were
3294 confirmed to species. Species confirmation was based on one or at most a few individuals in
3295 large groups of hundreds to thousands of individuals, given the limited camera and lens
3296 technology at the time relative to the 310-m flight altitude. The two species were pooled for
3297 analyses. Historically, short-beaked dolphins have outnumbered long-beaked common dolphins
3298 in the SCB. Results of a 2009 survey indicated a 1:1 ratio in the SCB (Carretta et al. 2015). Both
3299 species have been consistently reported as the most common cetacean species in the SCB

3300 since the 1950s (Smultea and Jefferson 2014). The most recent abundance estimate for the
3301 study area is 8,520 short-beaked and 3,314 long-beaked common dolphins during the May-
3302 October warm-water season; the November-April cold-water season estimates were nearly twice
3303 as high at about 15,955 short-beaked and 6,440 long-beaked common dolphins (based on pro-
3304 rating of 80% of the unidentified common dolphins; Jefferson et al. 2014a).

3305

3306 In the SCB, common dolphins are strongly associated with areas of steep bathymetric relief
3307 where their preferred prey tend to concentrate (Evans 1974, 1975; Reilly and Fiedler 1994;
3308 Becker et al. 2010). Forney and Barlow (1998) report historical changes in abundance in the
3309 SCB potentially related to inshore-offshore and/or north/south movements associated with
3310 changes in oceanographic conditions, most evidently sea surface temperature. Predictive
3311 density habitat-modeling conducted for hundreds of sightings throughout the CCE indicate that
3312 common dolphin density is most closely linked with large seasonal changes in sea surface
3313 temperatures (Forney and Barlow 1998; Becker et al. 2010). Short-beaked common dolphins in
3314 the SCB are considered opportunistic feeders, with prey choice related to the availability and
3315 catchability of the most abundant prey (Evans 1975, 1994). Based on stomach content analyses,
3316 short-beaked common dolphins in the SCB consume a variety of prey, all of which are
3317 associated primarily with pelagic mesopelagic waters and the DSL (e.g., fishes and squid) or
3318 epipelagic waters (e.g., opalescent inshore squid (*Doryteuthis opalescen*), and small schooling
3319 fishes such as small scombroids and clupeoids ; Evans 1994; Pusineri et al. 2007). Anchovies
3320 (*Engraulis mordax*) comprised 62% of all identified prey reported by Evans (1975). In
3321 comparison, others have reported that squid (family *Gonatidae* and *Loliga opalescens*) and
3322 Pacific whiting (*Merluccius productus*) were the most commonly consumed prey species (Fitch
3323 and Brownell 1968; Schwartz et al. 1992). Anchovies in particular are strongly associated with
3324 escarpments and submarine canyons characterized by biologically productive upwelling in the
3325 SCB (Mais 1974; Hui 1979). Common dolphin foraging dives are reported to reach 200 m, and
3326 prey diet varies seasonally and regionally with prey distribution and abundance (Evans 1994;
3327 Perrin 2009).

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3329 Little is known about the social or reproductive systems of common dolphins. Murphy et al.
3330 (2005) proposed that they practice a promiscuous breeding system characterized by sperm
3331 competition based on relatively large testes and sexual dimorphism. Gestation is estimated to
3332 last about 10-12 months, with weaning occurring when the calf is about 5-6 months old (Murphy
3333 and Rogan 2006; Danil and Chivers 2007; Perrin 2009). Based on 2009 data from the eastern
3334 North Pacific, Chivers et al. (2015) concluded peak calving occurs in winter among short-beaked

3335 common dolphins, and in early spring for long-beaked common dolphins. Perryman and Lynn
3336 (1993) found that most short-beaked common dolphin births off southern California and Baja
3337 California occurred from January-June, although some calves were born throughout the year.
3338 Evans (1975, 1994) hypothesized that these large groups include subgroups of ~20-30
3339 individuals that may be closely related. Chivers et al. (2015) reported that calves were observed
3340 in 100 of 109 groups, though visual observations from the aircraft indicated calves tended to be
3341 randomly clustered together within larger encompassing schools in the eastern North Pacific
3342 Ocean. Chivers et al. (2015) notes the resemblance of this group structure to other studies of
3343 schools of small delphinids (e.g., Norris and Dohl 1980; Weir et al. 2010), further suggesting that
3344 differences occur in behavioral sensitivity among the two species (e.g., differences in swim
3345 depth, school shape, sensitivity to the overflying aircraft).
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