

Abstract—Documenting year-round diversity and distribution of marine mammals off Southern California is important for assessment of effects of potentially harmful anthropogenic activities. Although the waters off Southern California have been surveyed extensively for marine mammals over the past 18 years, such surveys have been periodic and were conducted primarily from summer to fall, thereby missing potential seasonal shifts. We examined seasonal abundance and population density of cetaceans off Southern California from 16 shipboard line-transect surveys conducted quarterly during 2004–08. The study area consisted of 238,494 km² of coastal, shelf, and pelagic oceanic habitat from near-shore waters to 700 km offshore. Based on 693 encounters of 20 cetacean species, abundance estimates by seasonal period (summer–fall or winter–spring) and depth (shallow: <2000.5 m; deep: ≥2000.5 m) were determined for the 11 most commonly encountered species. The following are values of uncorrected density (individuals/1000 km², coefficients of variation in parentheses) for the seasonal period and depth with greatest density for a selection of the species in this study: blue whale (*Balaenoptera musculus*), summer–fall, shallow, 3.2 (0.26); fin whale (*B. physalus*), summer–fall, shallow, 3.7 (0.30); humpback whale (*Megaptera novaeangliae*), summer–fall, shallow, 3.1 (0.36); short-beaked common dolphin (*Delphinus delphis*), summer–fall, shallow, 1319.7 (0.24); long-beaked common dolphin (*D. capensis*), summer–fall, shallow, 687.9 (0.52); and Dall’s porpoise (*Phocoenoides dalli*), winter–spring, deep, 48.65 (0.28). Seasonally, density varied significantly by depth for humpback whales, fin whales, and Pacific white-sided dolphins.

Manuscript submitted 24 January 2013.
Manuscript accepted 23 May 2014.
Fish. Bull. 112:197–220 (2014).
doi:10.7755/FB.112.2-3.7

The views and opinions expressed or implied in this article are those of the author (or authors) and do not necessarily reflect the position of the National Marine Fisheries Service, NOAA.

Seasonal distribution and abundance of cetaceans off Southern California estimated from CalCOFI cruise data from 2004 to 2008

Annie B. Douglas¹ (contact author)

John Calambokidis¹

Lisa M. Munger²

Melissa S. Soldevilla^{3,2}

Megan C. Ferguson⁴

Andrea M. Havron^{1,5}

Dominique L. Camacho^{1,5}

Greg S. Campbell²

John A. Hildebrand²

Email address for contact author: abdouglas@cascadiaresearch.org

¹ Cascadia Research Collective
218½ West Fourth Avenue
Olympia, Washington 98501

² Scripps Institution of Oceanography
University of California, San Diego
8635 Discovery Way
La Jolla, California 92093-0210

³ Southeast Fisheries Science Center
National Marine Fisheries Service, NOAA
75 Virginia Beach Drive
Miami, Florida 33149

⁴ National Marine Mammal Laboratory
Alaska Fisheries Science Center
National Marine Fisheries Service, NOAA
7600 Sand Point Way NE
Seattle, Washington 98115-6349

⁵ Spatial Ecosystems
P.O. Box 2774
Olympia, Washington 98507

At least 30 species of cetaceans are found in the California Current (Leatherwood et al., 1982), including 5 species of large whales listed as endangered under the U.S. Endangered Species Act. The abundance and diversity of species along the West Coast of the United States and the continental slope are closely linked to the high level of biological production that is caused by upwelling and mixing of 4 different water masses along the California coast on a seasonal and interannual basis (Reid et al., 1958; Smith et al., 1986; Munger et al., 2009). Although these waters are important to marine fauna, they are also increasingly important to humans who use them for commercial shipping and fishing; oil and gas exploration, development, and production; naval exercises; and recreation. The combined use of these highly productive waters by cetaceans and humans can lead to ships striking large whales (Jensen and Silber, 2003; Berman-Kowalewski et al., 2010), entanglements

of cetaceans in fishing gear (Julian and Beeson, 1998; Laist et al., 2001; Carretta et al., 2011b), and disruption of normal behaviors by underwater sound (McDonald et al., 2006; Weilgart, 2007). To assess long-term impacts of fisheries, industry, and ecosystem variability on marine mammals, it is necessary to estimate abundance, understand stock structure, and determine seasonal habitat use by the species that inhabit these waters.

Abundance for the summer and fall seasons has been estimated for many cetacean species in waters off California, Oregon, and Washington through the use of ship-based line-transect surveys or mark-recapture techniques of photographically identified whales (Calambokidis and Barlow, 2004; Barlow and Forney, 2007; Carretta et al., 2011b). However, weather conditions make ship-based line-transect surveys difficult to conduct year-round, and few studies have quantified habitat and distribution shifts of marine mammals during the

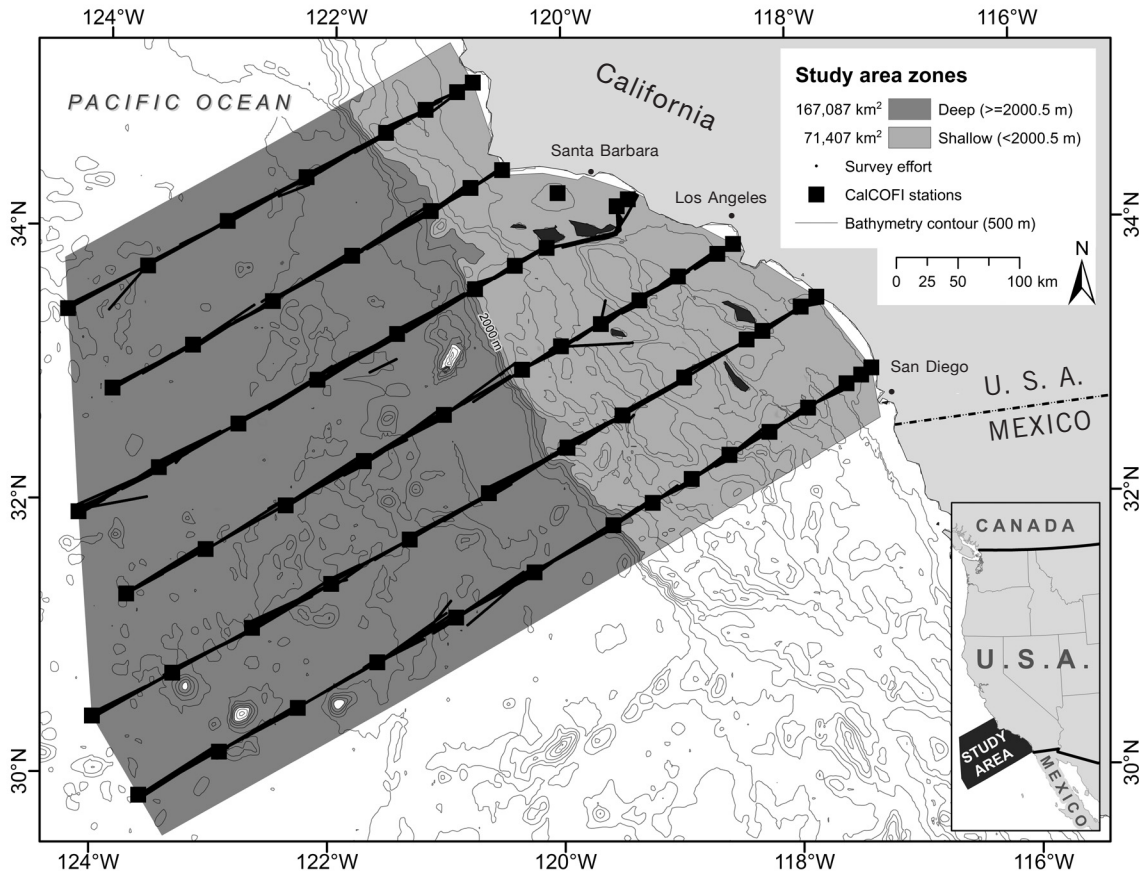


Figure 1

Map of the study area and 6 southern transect lines of 16 quarterly California Cooperative Oceanic Fisheries Investigation (CalCOFI) surveys conducted from July 2004 to April 2008 off Southern California. Shallow survey area (< 2000.5 m) is lighter gray and deep survey area (≥ 2000.5 m) is dark gray. Dark squares on CalCOFI transect lines indicate oceanographic sampling stations. The CalCOFI study area (238,494 km²) occurs completely inside the larger southern stratum (318,500 km²) of the Southwest Fisheries Science Center shipboard surveys that extends farther to the northwest.

winter and spring months (Dohl et al.¹; Forney and Barlow, 1998; Becker, 2007). In this study, new estimates of cetacean abundance were calculated off Southern California with marine mammal sighting data collected during 16 cruises undertaken as part of the California Cooperative Oceanic Fisheries Investigation (CalCOFI) (Bograd et al., 2003; Ohman and Venrick, 2003; Soldevilla et al., 2006). Marine mammal surveys on CalCOFI cruises are conducted quarterly, along predetermined transect lines between oceanographic water sampling stations (Fig. 1). The depth of the study area is extremely variable, with shallow waters inshore of the Channel Islands, a steep slope west of these islands, and an expansive deepwater plain offshore. Almost

30% of CalCOFI transect lines occur in water depths of 20–2000 m, and 69% of them occur in water depths of 3001–4600 m, and there is minimal (1%) coverage with transect lines in water depths of 2001–3000 m owing to the steep slope and orientation of the transect lines. Therefore, this study provides information on seasonal and interannual presence of cetaceans in both coastal and deep offshore waters. Such information is important to understanding and potentially mitigating effects of human activities on cetacean populations off Southern California.

Materials and methods

Data collection

Dedicated visual observers conducted line-transect surveys for marine mammals (Buckland et al., 1993; Kinzey and Gerrodette, 2003) during 16 quarterly Cal-

¹ Dohl, T. P., K. S. Norris, R. C. Guess, J. D. Bryant, and M. W. Honig. 1980. Summary of marine mammal and seabird surveys of the Southern California Bight area, 1975–1978. Part II. Cetacea of the Southern California Bight. Final report to the Bureau of Land Management, NTIS Rep. No. PB81248189, 414 p.

Table 1

Individual cruise identification, vessel, schedule (beginning, ending, season), line-transect-survey effort in kilometers, and marine mammal visual observers of 16 California Cooperative Oceanic Fisheries Investigation (CalCOFI) surveys conducted from July 2004 to April 2008. Height of observer platform on the 3 research vessels from which these surveys were completed: 13.2 m on RV *Roger Revelle* [RR], 8.1 m on RV *New Horizon* [NH], and 11.0 m on NOAA Ship *David Starr Jordan* [DSJ].

CalCOFI cruise ID	Vessel	Begin	End	Season	Survey effort (km)	Visual observers ¹
0407JD	DSJ	13-Jul-2004	28-Jul-2004	Summer	1543	RWB, ABD
0411RR	RR	2-Nov-2004	19-Nov-2004	Fall	1295	ABD, AM, MS, SEY
0501NH	NH	4-Jan-2005	20-Jan-2005	Winter	1006	DLC, EV
0504NH	NH	15-Apr-2005	30-Apr-2005	Spring	1485	DLC, SMC
0507NH	NH	1-Jul-2005	16-Jul-2005	Summer	1571	DLC, ABD, VI
0511NH	NH	4-Nov-2005	20-Nov-2005	Fall	1104	DLC, SMC
0602JD	DSJ	4-Feb-2006	25-Feb-2006	Winter	1144	GSC, SMC
0604NH	NH	1-Apr-2006	17-Apr-2006	Spring	1624	DLC, ABD
0607NH	NH	8-Jul-2006	24-Jul-2006	Summer	1595	DLC, AMH
0610RR	RR	21-Oct-2006	5-Nov-2006	Fall	1208	ABD, AMH
0701JD	DSJ	12-Jan-2007	2-Feb-2007	Winter	1080	GSC, ABD
0704JD	DSJ	28-Mar-2007	18-Apr-2007	Spring	911	GSC, SMC
0707NH	NH	28-Jun-2007	13-Jul-2007	Summer	1502	AMH, SEY
0711NH	NH	02-Nov-2007	18-Nov-2007	Fall	1109	DLC, LJM
0801JD	DSJ	07-Jan-2008	23-Jan-2008	Winter	935	DLC, GSC
0803JD	DSJ	24-Mar-2008	09-Apr-2008	Spring	884	DLC, GSC

¹Observers: R. W. Baird, D. L. Camacho, G. S. Campbell, S. M. Claussen, A. B. Douglas, A. M. Havron, V. Iriarte, A. Miller, L. J. Morse, M. Smith, E. Vazquez, and S. E. Yin.

COFI cruises from July 2004 to April 2008 (Table 1). Covering an area of 238,494 km², the study area consisted of coastal, shelf, and pelagic oceanic habitat from nearshore waters to waters 700 km offshore and up to 4600 m deep. Observers used unaided eye or handheld 7×50 reticle Fujinon² binoculars (Fujifilm Corp., Tokyo) to sight, identify, and estimate group sizes of cetaceans and pinnipeds encountered along the transect lines between CalCOFI hydrographic sampling stations (Fig. 1). The Southern California hydrographic sampling station sites are set along 6 parallel lines running southwest to northeast, with lines increasing in length from north to south (470–700 km). Stations occur every 37 km in coastal and continental shelf waters and every 74 km in offshore locations (Fig. 1). Occasionally, transect lines were interrupted by naval activity or adverse weather conditions; in these cases, the observers discontinued effort until their vessel adjusted to a course that intersected with the interrupted transect line. Transit lines that ran along the CalCOFI transect lines, as well as to and from the study area, were surveyed opportunistically in addition to the primary transect lines; however, these data were excluded from the analyses and results described here. Five northern

lines were surveyed partially during 2 winter cruises; however, only a few sections of these lines were surveyed with acceptable sea conditions, and therefore these data also have been excluded from the analyses and results in this study.

Three vessels were used for the line-transect surveys: the RV *Roger Revelle* (2 surveys) and RV *New Horizon* (8 surveys) of the Scripps Institution of Oceanography, University of California, San Diego, and the NOAA Ship *David Starr Jordan* (6 surveys) (Table 1). Survey speeds ranged from 18.5 to 22.2 km/h. Height of the observer platform varied by vessel from 8.1 to 13.2 m, raising the possibility that there would be a vessel or a vessel-season bias. To test these biases, we ran single-factor analyses of variance (ANOVAs) to determine whether visual observers made initial sightings at significantly different distances for each vessel or vessel-season combination. Additionally, we ran tests to determine whether the number of transect line kilometers surveyed in good weather varied by season.

Scanning from directly abeam to 10° past the bow on either side of the vessel, 2 observers recorded marine mammal sightings. During 2 survey cruises, an additional person was available to record data and provide relief for observers at meal times (Table 1). Recorded sighting data included date, time, vessel latitude and longitude, vessel true heading, distance of animal from the vessel, sighting angle, θ , from the transect line, de-

² Mention of trade names or commercial companies is for identification purposes only and does not imply endorsement by the National Marine Fisheries Service, NOAA.

terminated with an angle board (zero at bow, negative to port, positive to starboard), sighting number, species, group-size estimate (best, high, low), presence of calves, general behavior of animals, photographs (if taken), and comments pertaining to the sighting. Because of the surfacing behavior of cetaceans and lack of visibility while submerged, animal counts were only estimates, with the recorded “low” estimate being the minimum number of individuals observed during the sighting, the “high” estimate being the maximum, and the “best” estimate was always recognized as the value closest to the actual number of individuals. Group-size estimates and species confirmation were generally made by the lead observer but were agreed upon by all observers present.

Transect lines were surveyed in “passing mode,” which does not allow for any alteration of course for closer examination of groups encountered. Barlow³ stated that surveys conducted in passing mode yield less biased estimates of encounter rates but result in a higher number of unidentified groups and more biased estimates of group size and species percentages compared with surveys conducted in closing mode. Closing mode allows for all observers to go “off effort” and to adjust the course and speed of the vessel in order to approach animals sighted at a distance from the transect line. To assist with species identification and group-size estimation, 25× binoculars were available for all surveys on the *Roger Revelle*, for most surveys on the *David Starr Jordan*, and occasionally on the *New Horizon*. The 25× binoculars were used only as an aid once a group had been located with the naked eye or 7×50 binoculars to maintain a consistent search method between surveys.

Observers recorded effort (on or off), weather (sea state, swell height, visibility [or estimated distance that observers can detect a small cetacean], and precipitation), changes in course and speed, and sighting information onto data sheets. Observations were considered on effort if observers were actively searching with the unaided eye and 7×50 binoculars in a sea state 0–5, the vessel was traveling no less than 6 km/h, and there was a minimum visibility of 0.9 km (0.5 nmi) in front of the vessel. All sightings of all species of marine mammals were recorded with the exception of California sea lions (*Zalophus californianus*), which were sighted most often near the coast because estimation of group size and documentation of sighting details of high numbers of California sea lions in coastal waters would have compromised the ability of observers to sight and record other species that occur in the same area.

Because these surveys were conducted in passing mode and with limited use of 25× binoculars,

some common dolphins (*Delphinus* sp.) that were encountered could be confirmed only to the genus level. Short-beaked common dolphins (*D. delphis*) and long-beaked common dolphins (*D. capensis*) have very similar morphological features and pigmentation, and they are difficult to distinguish at a distance (Rosel et al., 1994); therefore, observers were encouraged to obtain photographs if there was doubt about the identification of these or other species. Photographs were reviewed onboard, compared with identification guides (Reeves et al., 2002), and occasionally shared with experienced colleagues for species confirmation. Additionally, there are 2 forms of Pacific white-sided dolphins (*Lagenorhynchus obliquidens*) along the coast of California (Walker et al., 1986; Lux et al., 1997; Soldevilla et al., 2011); because these forms are indistinguishable from a distance, density and abundance for this species likely includes both forms.

Analytical methods

Sighting and effort data from the 16 CalCOFI cruises were split into 2 effort categories: 1) on-effort sightings on the 6 CalCOFI transect lines, the sightings that form the basis of all analyses and findings; and 2) opportunistic effort (sightings made off effort or when a vessel was not on a CalCOFI transect line), which is presented to show species diversity and presence or absence of species. We calculated encounter rates by season (number of on-effort sightings per 1000 km of transect line surveyed) for each species with 10 or more sightings. Distance r of the animal(s) sighted from the vessel and sighting position were determined from the reticle value (or estimated distance), height of observer platform, sighting angle (Δ) to animal from the bow of the vessel, and position of the vessel. To characterize the depth distribution of effort, sample points were created at 1-km intervals along transect lines within ArcGIS (vers. 9.2; Esri, Redlands, CA).

Sighting data also were plotted in ArcGIS, with sighting and effort data linked to a coastline shapefile and bathymetry data set from the ETOPO1 global relief model (Amante and Eakins, 2009) with 1850-m resolution (National Geophysical Data Center [NGDC], <http://www.ngdc.noaa.gov/mgg/global/global.html>); where highest resolution was not available from ETOPO1, the NGDC coastal relief model (NGDC, <http://www.ngdc.noaa.gov/mgg/coastal/crm.html>) provided 90-m resolution (73% of sighting depths and 49% of effort depths came from the 90-m resolution data set). Distance to the closest point of land, distance to the mainland, depth, and distance to the shelf break (200-m isobath) were also calculated for each sighting and effort location.

Using the cold (winter–spring, defined as January–April) and warm (summer–fall, defined as July–November) water distinctions in Forney and Barlow (1998), we tested for differences between the number of encounters of each positively identified species by

³ Barlow, J. 1997. Preliminary estimates of cetacean abundance off California, Oregon, and Washington based on a 1996 ship survey and comparisons of passing and closing modes. Southwest Fish. Sci. Cent. Admin. Rep. LJ-97-11, 25 p.

Table 2

Covariates and summary statistics for the best-fit detection function models by species group from analyses of data from line-transect surveys conducted off Southern California from 2004 to 2008. The distribution of perpendicular sighting distances for pooled species was used to parameterize the detection function models summarized here, where $f(0)$ is the probability density function evaluated at a perpendicular distance of zero, bin width (m) is the interval chosen to show the fraction of probability distribution, truncation value excludes the 5% of sightings by species group that were farthest from the transect line and therefore considered outliers, ESW is the effective strip (half)width for which the number of groups outside the ESW is equal to the number missed inside the ESW, and CV is the coefficient of variation. The hazard-rate key function was used in the best-fit model for all species groups. Species groups were selected on the basis of factors that influence sightability, such as common school sizes, body shape, and behavior. The species group of large whales consisted of the blue, fin, humpback, sperm, and killer whales. Delphinids included the short- and long-beaked common, northern right whale, Pacific white-sided, Risso's, and bottlenose dolphins and the Dall's porpoise. For detection function plots, see Figure 2.

Species groups for estimating $f(0)$	Number of observations	Covariates	Bin width (m)	Truncation (m)	Average ESW (m)	CV
Large whales	127	Perpendicular distance	500	2348	1294	0.11
Delphinids	211	Perpendicular distance, sea state, species, log(group size)	100	1098	298	0.10
Dall's porpoise	48	Perpendicular distance, sea state	100	1098	305	0.22

seasonal period (winter–spring and summer–fall) and between the distance from shore and depth by the season, with Systat (vers. 13; Systat Software, Chicago, IL). Because our data had a bimodal distribution, Kruskal-Wallis one-way ANOVAs and Mann-Whitney U -tests were run to examine variation in encounters by habitat, year, and season with Minitab software (vers. 15.1.30; Minitab, State College, PA).

We used line-transect methods (Buckland et al., 2001) with multiple covariates (Marques and Buckland, 2003) to estimate cetacean abundance for 2 seasonal periods and 2 depth categories (defined below) in Distance software (vers. 6.0; Research Unit for Wildlife Population Assessment, University of St. Andrews, UK; Thomas et al., 2010). Distance software uses the perpendicular distance of the encounter to the transect line rather than the straight line distance (observer to animal) made at the time of the sighting; therefore, we calculated perpendicular distance as $r \sin \theta$ before uploading these data into Distance. Small sample size by season precluded our ability to estimate abundance quarterly; therefore, we estimated abundance within 4 strata in the study area. The strata were defined by 2 seasonal periods, winter–spring (cold water) or summer–fall (warm water), and 2 depth categories, shallow (<2000.5 m and deep (\geq 2000.5 m). On the basis of known ecological differences between shelf or slope and basin, with greater density of cetaceans near the coast, we chose to look at these data in 2 depth categories. Additionally, a histogram of effort as a function of depth showed that depth in our study area was strongly bimodal and that the depth of 2000.5 m was an appropriate cutoff point. Sample units were specified by survey number, line number, season, and depth to ensure that each of the 6 transect lines from each

survey would be divided into a shallow and a deep sample unit.

To estimate density and abundance for a species, it is necessary to reliably estimate the detection function (the probability of seeing an animal at x distance from the transect line), and that requires a relatively large sample size (Buckland et al., 2001). The necessary sample sizes were not available for all species in this study; therefore, we pooled multiple species with similar surfacing characteristics (Barlow et al., 2001) and pooled (binned) sightings across season-and-depth strata to estimate the detection function (Table 2, Fig. 2). Pooled species groups were defined as 1) large whales, which included blue (*Balaenoptera musculus*), fin (*Balaenoptera physalus*), humpback (*Megaptera novaeangliae*), sperm (*Physeter macrocephalus*), and killer whales (*Orcinus orca*); 2) delphinids, which included short- and long-beaked common, northern right whale (*Lissodelphis borealis*), Pacific white-sided, Risso's (*Grampus griseus*), and common bottlenose (*Tursiops truncatus*) dolphins; and 3) Dall's porpoises (*Phocoenoides dalli*). Beaked whales and several other species of delphinids were encountered too infrequently to estimate abundance. Cetaceans that could not be identified to genus and species levels were not included in the pooled species groups for estimation of the detection function, and density and abundance levels were not estimated for them.

Potential covariates for building the detection function models included group size (a categorical variable that denotes whether sightings were greater or less than 20 individuals), cluster size (best estimate of group size), sea state (a numerical variable of 0–5), vessel, and species. Cut off points for group size were based on obvious breaks in histograms of group size for each species cat-

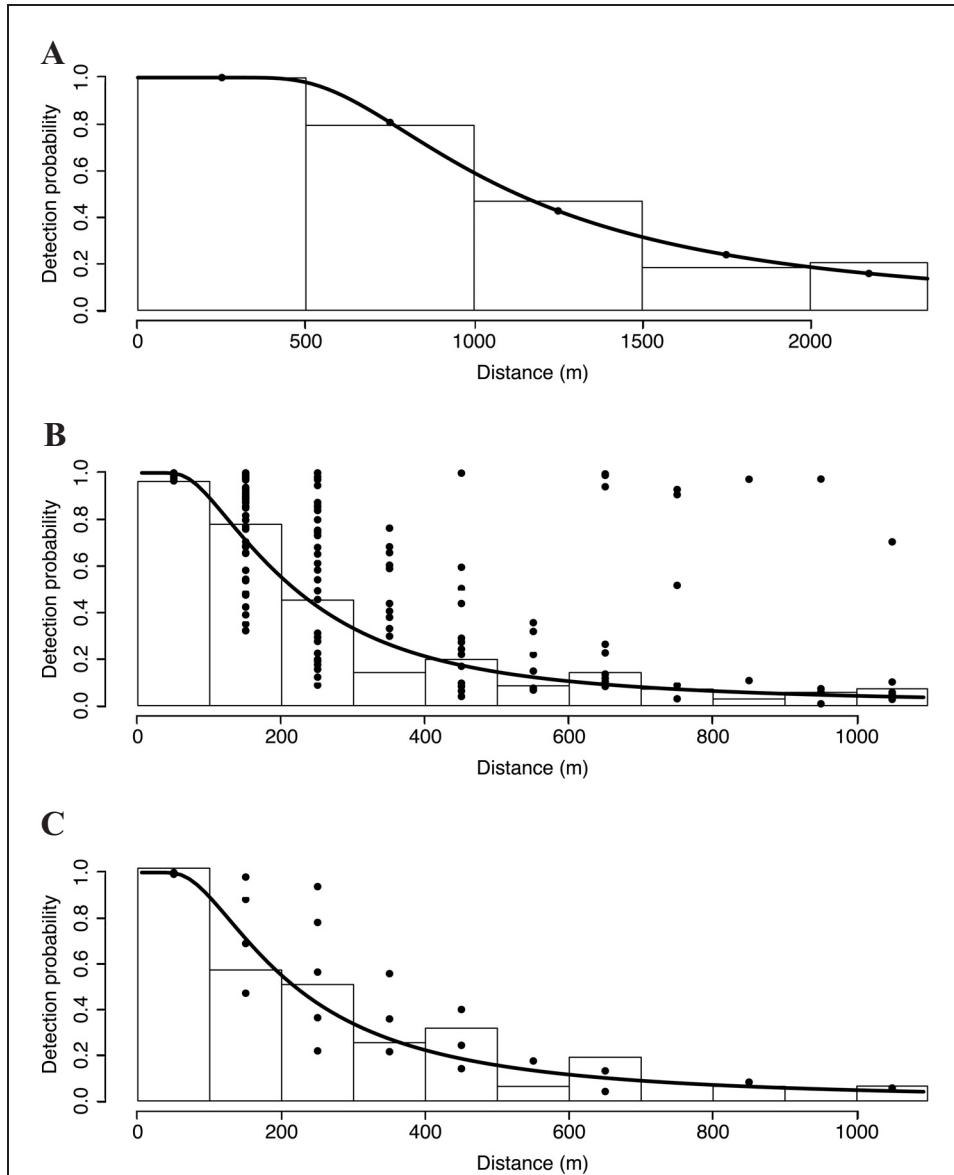


Figure 2

Detection function plots by species group ([A] large whales, [B] delphinids, and [C] Dall's porpoise [*Phocoenoides dalli*]) were created to visualize the correct detection functions to estimate density and abundance for the species most commonly encountered in the study area for line-transect surveys conducted off Southern California in 2004–08 during 16 quarterly California Cooperative Oceanic Fisheries Investigation cruises. The points are the probability of detection for each encounter dependent on its perpendicular distance and chosen covariate(s) for the best fit. The sighting data showed some evidence of heaping (i.e., rounding to certain distances) because of the limitations of the use of reticles to estimate distance. Therefore, sightings were binned to facilitate data analysis (Buckland et al., 2001). For detection function covariates and summary statistics, see Table 2.

egory. Selection of a detection function model was based primarily on the Akaike's information criterion (AIC) value (generated with Distance) and then confirmed by visual examination of detection plots (Burnham and An-

derson, 2002). Half-normal and hazard-rate key functions often provide a good fit to data used to model detection functions (Thomas et al., 2010). Although both were considered in the models tested, the hazard-rate

model was chosen for all 3 groups on the basis of AIC values and visual inspection (Thomas et al., 2010).

Line-transect theory assumes that the probability of detecting an animal on the transect line, $g(0)$ equals 1.0 (perfect detectability), although this assumption is rarely true for marine mammals and can be relaxed if a correction factor is estimated. Estimation of a correction factor was beyond the scope of this study, and $g(0)$ is assumed to equal 1.0 and to be constant across sea states. The 5% of sightings made at the greatest distances to the vessel were assumed to be outliers and were truncated to improve the ability to fit the probability density function $f(0)$ (Buckland et al., 2001). Truncation distance was 2348 m for large whales and 1098 m for delphinids and porpoises. There were 7 whale, 11 dolphin, and 2 porpoise sightings recorded beyond the truncation distance and these were excluded from density and abundance analyses. We calculated density, D_i , for a given species within the study area i as

$$D_i = \frac{1}{2L_i} \sum_{j=1}^{n_i} \frac{f(0|z_j) * s_j}{g_j(0)}, \quad (1)$$

where L_i = the length of on-effort transect lines within the study area i ;

$f(0|z_j)$ = the probability density function at zero with associated covariates z for group;

s_j = the number of individuals of that species in group j ;

$g_j(0)$ = the transect line detection probability of group j ; and

n = the number of groups of that species encountered in the study area i .

Group abundance for each species in each stratum was estimated as

$$\widehat{N}_G = \frac{A}{2wL} \sum_{i=1}^n \frac{1}{\widehat{P}_1}, \quad (2)$$

where A = the area of the stratum;

L = the total search effort in the stratum;

n = the number of unique groups;

w = the truncation distance by species group; and

\widehat{P}_1 = the estimated probability of detecting group i obtained from the fitted detection model.

Results

Survey effort and sightings

Line-transect surveys were conducted during 16 cruises over 5 years, with 3 years of 4-season effort and 2 years of 2-season effort (Table 1). Including all survey effort from the southern CalCOFI transect lines, observers collected visual data on marine mammals over 267 days and searched 25,079 km of transect lines. Of that total distance of transect lines covered, 19,996 km was surveyed on the 6 southern CalCOFI lines

(hereafter referred to as “the study area”) in acceptable weather conditions (sea state of 0–5). Within the study area, on-effort transect line kilometers surveyed did not vary significantly by season (ANOVA, $F=0.078$, $P=0.97$). Sea states varied by season, with greatest sea states during spring and summer and lowest sea states during winter (Kruskal-Wallis one-way ANOVA, $P<0.001$). The median sea state was 3 in all seasons, except for summer, when it was 4. We found no significant difference in perpendicular distance to transect line for any species group by vessel (large whales, ANOVA, $F=2.08$, $P=0.16$; delphinids and porpoises ANOVA, $F=1.01$, $P=0.39$) or by vessel-season (large whales, ANOVA, $F=2.76$, $P=0.15$; delphinids and porpoises ANOVA, $F=0.36$, $P=0.56$).

As stated in the *Materials and methods* section, acceptable survey conditions required ≥ 0.9 km of estimated visibility on the transect line. Only 0.67% of effort was conducted with a visibility of ≤ 900 m, and that effort resulted in 4 sightings of common dolphins; because those dolphins were not identified to species level, their sightings were not used in the detection function. All encounters used in detection functions for the 3 species groups were made with at least 2.77 km visibility, with 93% of large whales, 94% of delphinids, and 100% of Dall’s porpoises encountered with visibility ≥ 7.4 km.

In the study area during the 16 survey cruises, 29 marine mammal species were encountered, including 22 cetaceans, 6 pinnipeds, and a single mustelid species (Table 3). There were 931 on-effort sightings in the study area, with California sea lions (154 recorded sightings) the most commonly encountered species, followed by short-beaked common dolphins (122 sightings), northern fur seals (*Callorhinus ursinus*, 59 sightings), and fin whales (53 sightings). The most commonly encountered large cetaceans in the study area were fin, humpback (34 sightings), blue (25 sightings), and sperm (20 sightings) whales (Fig. 3), and the most commonly encountered small cetacean species were short-beaked common dolphin, Pacific white-sided dolphin (46 sightings), and Dall’s porpoise (49 sightings) (Fig. 4). The ratio of on-effort sightings to opportunistic and off-effort sightings of cetaceans (1:0.76) in this study is higher than would be expected for other line-transect surveys where very little sighting effort is conducted off transect or in poor sea conditions. The large number of off-effort and opportunistic sightings in our study is mostly due to the large amount of opportunistic effort between the primary transect lines or at the water sampling stations along the coast.

Multispecies sightings were observed on 15 occasions for 7 dolphin species; the northern right whale dolphin and Pacific white-sided dolphin mixed most frequently (5 times), bottlenose dolphin and common dolphins mixed 3 times, Pacific white-sided dolphin and short-beaked common dolphin mixed 2 times, striped dolphin (*Stenella coeruleoalba*) and unidentified common dolphins mixed 2 times, and single occurrences

Table 3

Sighting data (number of encounters and estimated number of individuals) from 16 line-transect surveys conducted off Southern California from July 2004 to April 2008 on the 6 southern transect lines of quarterly California Cooperative Oceanic Fisheries Investigation (CalCOFI) cruises. Opportunistic effort is the category for sightings made off effort or when a vessel was not on a CalCOFI transect line.

Species	On effort		Opportunistic effort		Total	
	Number of encounters	Number of individuals	Number of encounters	Number of individuals	Number of encounters	Number of individuals
Humpback whale	34	60	6	13	40	73
Blue whale	25	34	20	27	45	61
Fin whale	53	100	9	10	62	110
Minke whale	10	10	8	9	18	19
Sei whale	0	0	1	1	1	1
Bryde's/sei whale	1	1	1	1	2	2
Gray whale	8	16	16	33	24	49
Sperm whale	20	36	11	18	31	54
Baird's beaked whale	1	20	0	0	1	20
Cuvier's beaked whale	3	3	1	3	4	6
Killer whale	2	9	0	0	2	9
Short-finned pilot whale	1	33	1	30	2	63
False killer whale	1	10	0	0	1	10
Short-beaked common dolphin	122	11,067	96	8677	218	19,744
Long-beaked common dolphin	17	3259	39	7652	56	10,911
Common dolphin (unknown Short- or long-beaked)	72	6532	75	12,443	147	18,975
Pacific white-sided dolphin	46	573	34	467	80	1040
Risso's dolphin	14	205	25	505	39	710
Bottlenose dolphin	12	220	18	221	30	441
Northern right whale dolphin	13	480	12	245	25	725
Rough-toothed dolphin	0	0	1	9	1	9
Striped dolphin	2	77	1	7	3	84
Harbor porpoise	0	0	1	2	1	2
Dall's porpoise	49	267	24	115	73	382
Unidentified large cetacean	123	153	74	98	197	251
Unidentified small cetacean	63	5496	61	3703	124	9199
Unidentified <i>Mesoplodon</i>	1	1	0	0	1	1
Total for cetaceans	693	28,662	535	34,289	1228	62,951
California sea lion	154	1318	85	606	239	1924
Northern fur seal	59	78	14	20	73	98
Guadalupe fur seal	0	0	2	2	2	2
Steller sea lion	1	1	0	0	1	1
Northern elephant seal	11	11	2	2	13	13
Harbor seal	0	0	3	3	3	3
Sea otter	0	0	1	1	1	1
Unidentified fur seal	1	1	0	0	1	1
Unidentified pinniped	12	19	4	4	16	23
Total for pinnipeds or mustelids	238	1428	111	638	349	2066
Grand total	931	30,090	646	34,927	1577	65,017
Total transect line surveyed (km)	19,996		5083		25,079	

were recorded of Pacific white-sided dolphin with unidentified common dolphins, Risso's dolphin with northern right whale dolphin, and Risso's dolphin with bottlenose dolphin.

Harbor porpoise (*Phocoena phocoena*) were encountered on a single survey north of Point Conception and

were excluded from analyses because the study area included only the very southern tip of the regular habitat of this species off California (Barlow, 1988; Forney et al., 1991). Rough-toothed dolphins (*Steno bredanensis*) and false killer whales (*Pseudorca crassidens*) were also encountered once each; both encounters were excluded

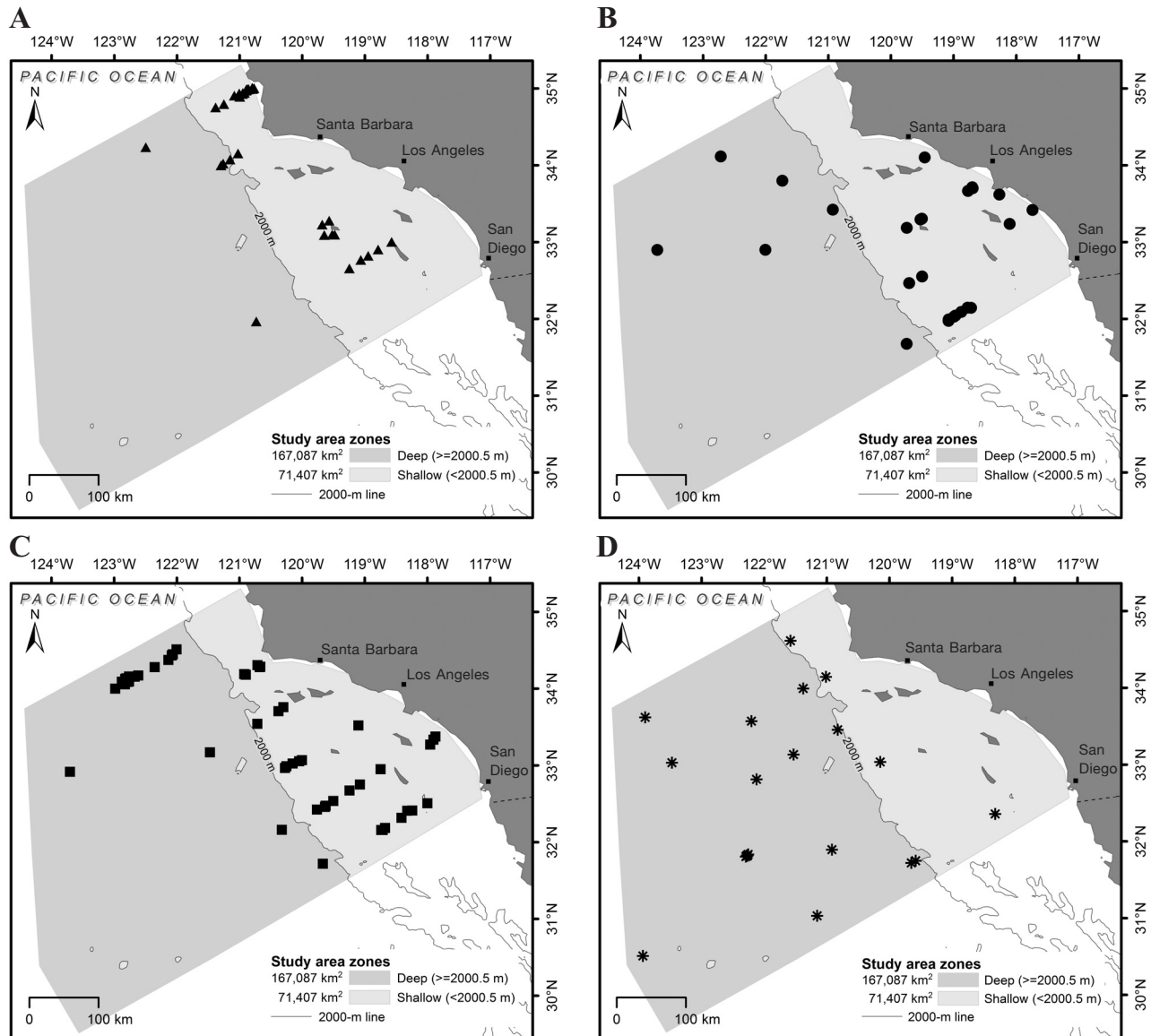


Figure 3

Maps of on-effort sightings of the 4 most commonly encountered species of large whales, the (A) humpback whale (*Megaptera novaeangliae*), (B) blue whale (*Balaenoptera musculus*), (C) fin whale (*B. physalus*), and (D) sperm whale (*Physeter macrocephalus*), recorded during the 16 shipboard line-transect surveys conducted quarterly during 2004–08 as part of the California Cooperative Oceanic Fisheries Investigation.

from analyses because the encounter records likely represent extralimital occurrences for both species.

Abundance estimates from line-transect data

Significant covariates for estimation of detection functions varied by species and species group (Table 2). On the basis of AIC values and visual examinations of test models, we selected sea state as a significant covariate for both the delphinid and Dall's porpoise group. Additionally, group size and dolphin species were chosen for

the delphinid detection model. Average effective strip width (ESW) was 1294 m for large whales, 298 m for delphinids, and 305 m for porpoises.

Baleen whales We encountered 6 or possibly 7 species of baleen whales (one encounter was undetermined; it was not possible to distinguish whether it was a Bryde's or sei whale [*Balaenoptera edeni brydei*, *B. e. edeni*, or *B. borealis*]), and sample sizes by species were sufficient to calculate seasonal abundance and density estimates for 3 of those species. Fin whales had the

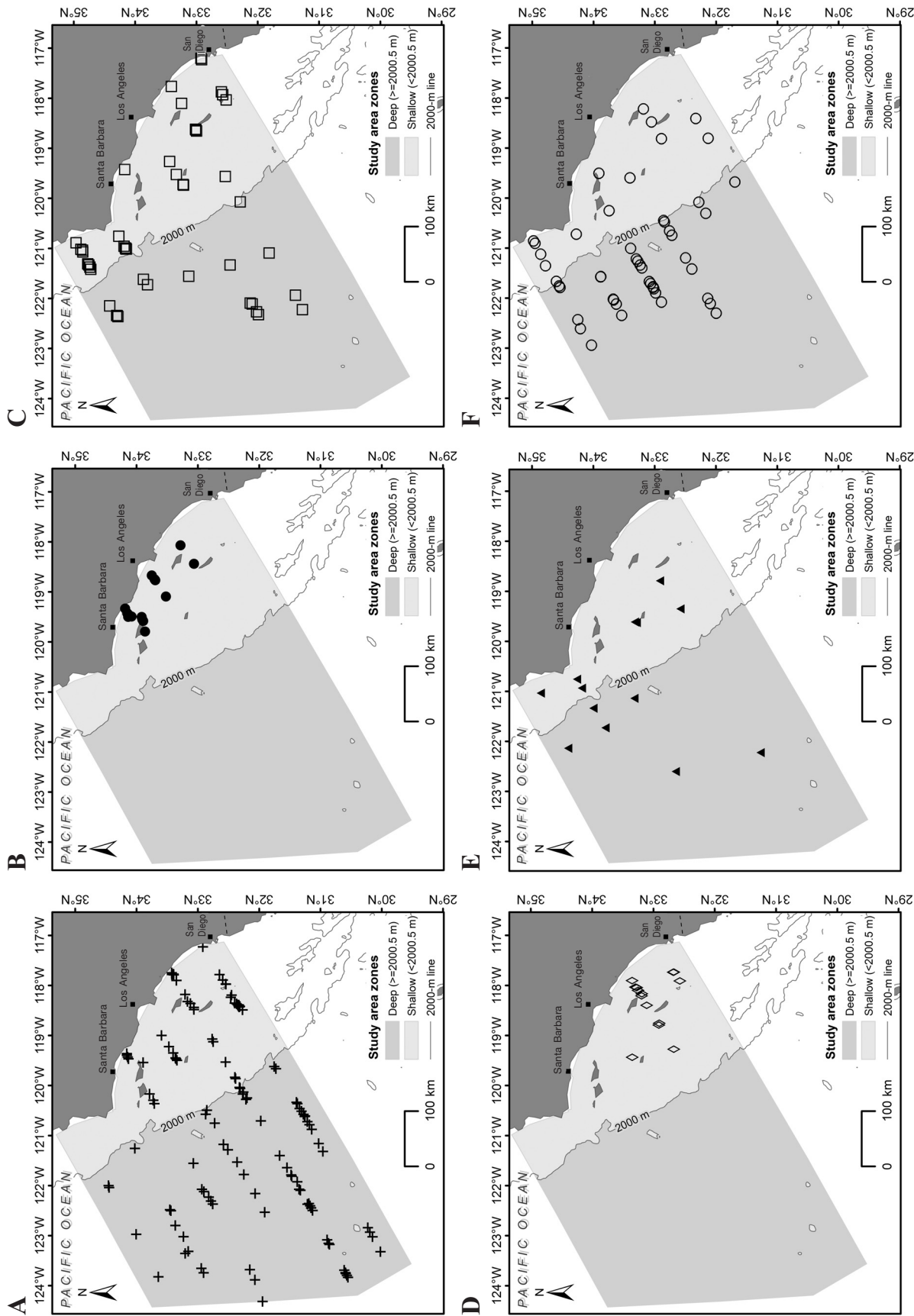


Figure 4

Map of on-effort sightings of the 5 most commonly encountered dolphin species, the (A) short-beaked common dolphin (*Delphinus delphis*), (B) long-beaked common dolphin (*D. capensis*), (C) Pacific white-sided dolphin (*Lagenorhynchus obliquidens*), (D) Risso's dolphin (*Grampus griseus*), and (E) northern right whale dolphin (*Lisiodelphis borealis*), and of the (F) Dall's porpoise (*Phocoenoides dalli*) recorded during the 16 shipboard line-transect surveys conducted quarterly during 2004–08 as part of the California Cooperative Oceanic Fisheries Investigation.

Table 4

Encounter rate, the number of encounters (Enc) per 1000 km, and number of sightings n of cetacean species by season on the 6 southern transect lines during 16 quarterly California Cooperative Oceanic Fisheries Investigation (CalCOFI) cruises conducted from 2004 to 2008 off Southern California, for species seen on 10 or more occasions. The value under each season represents the combined length of the transect lines surveyed.

Species	Winter	Spring	Summer	Fall	All seasons
	(4165 km) Enc/1000 km, n	(4904 km) Enc/1000 km, n	(6211 km) Enc/1000 km, n	(4716 km) Enc/1000 km, n	(19,996 km) Enc/1000 km, n
Humpback whale	0, 0	2.2, 11	1.6, 10	2.7, 13	1.7, 34
Blue whale	0, 0	0, 0	3.1, 19	1.3, 6	1.3, 25
Fin whale	0.7, 3	1.0, 5	3.7, 23	4.7, 22	2.7, 53
Minke whale	0, 0	1.4, 7	0.3, 2	0.2, 1	0.5, 10
Sperm whale	1.0, 4	0.4, 2	1.9, 12	0.4, 2	1.0, 20
Short-beaked common dolphin	7.2, 30	0.8, 4	9.5, 59	6.1, 29	6.1, 122
Long-beaked common dolphin	0.2, 1	0.2, 1	1.3, 8	1.5, 7	0.9, 17
Common dolphin (unknown short- or long-beaked)	2.6, 11	1.6, 8	5.5, 34	4.0, 19	3.6, 72
Pacific white-sided dolphin	2.6, 11	4.7, 23	1.1, 7	1.1, 5	2.3, 46
Risso's dolphin	0.7, 3	1.6, 8	0.2, 1	0.4, 2	0.7, 14
Bottlenose dolphin	0.5, 2	1.0, 5	0.2, 1	0.8, 4	0.6, 12
Northern right whale dolphin	0.2, 1	1.8, 9	0, 0	0.6, 3	0.7, 13
Dall's porpoise	2.6, 11	7.1, 35	0.2, 1	0.4, 2	2.5, 49

highest encounter rate (Table 4) and were the most abundant of large whales in the study area (Table 5), with the greatest density estimate from summer–fall surveys in shallow water, 3.67 individuals/1000 km² (CV=0.30) (Tables 6 and 7), and with the greatest abundance during the summer–fall surveys in deep water. Fin whales were the only whale species that showed a significant difference in depth, distance to land, and distance to shelf by seasonal period (Table 7; Figs. 5 and 6). Humpback whale density was highest during the summer–fall surveys in shallow water with 3.08 individuals/1000 km² (CV=0.36) (Table 5). Least abundant of the large whales, blue whales were encountered only during the summer–fall surveys, with the greatest density and abundance in shallow water, 3.20 individuals/1000 km² and 228 individuals (CV=0.26) (Table 5).

Odontocetes Although sperm whales were most abundant during the summer–fall surveys in deep water, 158 individuals (CV=0.36) (Table 5), density was similar for both shallow areas (0.94 individuals/1000 km² [CV=0.44]) and deep areas (0.95 individuals/1000 km² [CV=0.36]) for that seasonal period. Short-beaked common dolphins were the most abundant cetacean species, encountered in all seasons and at all depths; the highest encounter rate was observed in the summer months (Table 4) and the greatest density estimate was obtained from summer–fall surveys in shallow water, 1319.69 individuals/1000 km² (CV=0.24) (Table 5). Long-beaked common dolphins were the second-most abundant cetacean species; however, this species was encountered only in shallow water and, seasonally,

there was a dramatic shift in density with 22 times more long-beaked common dolphins observed during the summer–fall surveys than during the winter–spring surveys (Table 5). Because of the difficulty of distinguishing between short- and long-beaked common dolphins from a survey conducted in passing mode, 72 out of 211 on-effort common dolphin sightings were not identified to species (Table 3). Densities of Pacific white-sided, northern right whale, and Risso's dolphins were greatest during the winter–spring period in shallow water, and Dall's porpoises were most abundant during the winter–spring seasonal period in deep water; these species were least abundant during the summer–fall period. Abundance of Dall's porpoises varied strongly by seasonal period but not by depth. Beaked whales were encountered on 6 occasions, with Cuvier's beaked whale (*Ziphius cavirostris*) the most commonly encountered (3 occasions).

Discussion

Monitoring and management of marine mammal species off Southern California has often relied heavily on abundance estimates generated from line-transect surveys conducted during the summer and fall, despite year-round anthropogenic activities and significant seasonal spatial movements of many species (Forney and Barlow, 1998). Our observations from the 16 CalCOFI surveys conducted between 2004 and 2008 provide the most current and consistent data set on seasonal shifts in movements and abundance for the most commonly

Table 5

Density and abundance of cetaceans by species and season-and-depth stratum. The total area of the study area was 238,494 km², with 71,407 km² in shallow depths (<2000.5 m) and 167,087 km² in deep depths (≥2000.5 m). Coefficients of variation (CV) apply to both density and abundance estimates, and “NA” indicates that no CV was available because of a sample size equal to zero. Asterisks indicate mean values derived from the separate stratified densities for shallow and deep waters. See Table 2 for covariates used to estimate density by species group.

Species Season, depth	Number of groups	Mean group size	Density (individuals/ 1000 km ²)	Uncorrected abundance	CV
Blue whale					
Winter–spring, shallow	0	0.0	0.00	0	NA
Winter–spring, deep	0	0.0	0.00	0	NA
Summer–fall, shallow	19	1.4	3.20	228	0.26
Summer–fall, deep	5	1.2	0.36	59	0.33
Summer–fall, all depths	24	1.4	1.21*	288	0.23
Fin whale					
Winter–spring, shallow	7	2.0	2.33	166	0.30
Winter–spring, deep	0	0.0	0.00	0	NA
Summer–fall, shallow	22	1.4	3.67	262	0.30
Summer–fall, deep	21	2.0	2.49	417	0.42
Summer–fall, all depths	43	1.6	2.84*	679	0.25
Humpback whale					
Winter–spring, shallow	8	2	2.66	190	0.33
Winter–spring, deep	3	1.7	0.34	56	0.58
Winter–spring, all depths	11	1.9	1.03*	246	0.29
Summer–fall, shallow	19	1.4	3.08	220	0.36
Summer–fall, deep	2	4.5	0.53	89	0.58
Summer–fall, all depths	21	1.7	1.29*	309	0.32
Sperm whale					
Winter–spring, shallow	1	5	0.83	59	0.70
Winter–spring, deep	5	1.2	0.40	67	0.40
Summer–fall, shallow	3	2.7	0.94	67	0.44
Summer–fall, deep	10	1.6	0.95	158	0.36
Short-beaked common dolphin					
Winter–spring, shallow	11	57.6	307.83	21,981	0.33
Winter–spring, deep	22	127.8	609.86	101,900	0.45
Winter–spring, all depths	33	104.3	519.43*	123,881	0.21
Summer–fall, shallow	33	104.8	1319.69	94,235	0.24
Summer–fall, deep	51	37.5	454.35	75,916	0.20
Summer–fall, all depths	84	63.9	713.44*	170,151	0.14
Long-beaked common dolphin					
Winter–spring, shallow	1	60	30.90	2207	0.78
Winter–spring, deep	0	0.0	0.00	0	NA
Summer–fall, shallow	14	217.2	687.87	49,118	0.52
Summer–fall, deep	0	0.0	0.00	0	NA
Pacific white-sided dolphin					
Winter–spring, shallow	19	13.2	110.57	7896	0.38
Winter–spring, deep	14	14	41.91	7002	0.35
Winter–spring, all depths	33	13.5	62.46*	14,898	0.21
Summer–fall, shallow	11	6.6	29.24	2088	0.34
Summer–fall, deep	1	3	0.6967	116	0.72
Summer–fall, all depths	12	6.3	9.24*	2204	0.35
Risso’s dolphin					
Winter–spring, shallow	9	19	35.65	2546	0.36
Winter–spring, deep	0	0.0	0.00	0	NA
Summer–fall, shallow	3	8.6	3.90	279	0.55
Summer–fall, deep	0	0.0	0.00	0	NA

table continued

Table 5 (continued)

Species Season, depth	Number of groups	Mean group size	Density (individuals/ 1000 km ²)	Uncorrected abundance	CV
Bottlenose dolphin					
Winter–spring, shallow	4	11.2	22.12	1580	0.54
Winter–spring, deep	1	2	0.97	161	0.79
Summer–fall, shallow	5	13.6	40.32	2879	0.69
Summer–fall, deep	0	0.0	0.00	0	NA
Northern right whale dolphin					
Winter–spring, shallow	5	39	107.31	7662	0.50
Winter–spring, deep	4	13.5	20.30	3392	0.49
Summer–fall, shallow	1	6	6.72	480	0.78
Summer–fall, deep	2	25	11.10	1855	0.68
Dall's porpoise					
Winter–spring, shallow	13	4.8	45.50	3249	0.32
Winter–spring, deep	32	5.3	48.65	8128	0.28
Winter–spring, all depths	45	5.1	47.71*	11,378	0.26
Summer–fall, shallow	2	3	2.11	151	0.58
Summer–fall, deep	1	17	2.73	456	0.78

encountered marine mammal species in the Southern California region. Although seasonal variation was seen in cetacean encounters, large numbers of whales and dolphins were observed year-round off Southern California, both on and between transect lines (Table 4; Figs. 3 and 4).

Abundance and density of cetaceans: overall comparisons with previous surveys

Although our analyses of relative density by seasonal period and depth are robust for the most commonly encountered species, absolute densities and uncorrected abundances reported here may differ from values reported by the NOAA Southwest Fisheries Science Center (SWFSC) for its previous studies in Southern California; those differences primarily are due to 5 factors. First, our study relied on data collected by the naked eye or with 7× binoculars, hence ESWs by species group in our study were calculated as half (or less) of the ESWs used for the same species groups from 5 years of pooled SWFSC sighting data, which were collected with 25× binoculars as the primary search method (Barlow and Forney, 2007). Second, we assumed that detection on the transect line was certain, or $g(0)=1$; this decision likely had the greatest negative impact on density of cryptic or long-diving species, like sperm whales. Third, we had a relatively high proportion of sightings that were not identified to species, and we did not prorate unidentified cetaceans, thinking that it would be better to compute a best estimate of cetaceans positively identified to species than to make assumptions about the detectability of unidentified and identified species. Fourth, we used uncalibrated group-size estimates—an

approach different from the one for SWFSC cruises in which observers make group-size estimates independently and each observer is “calibrated” with the use of photogrammetry of select sightings (Gerrodette and Perrin⁴). Carretta et al. (2011b) stated that uncalibrated group-size estimates could result in estimated counts that were 50% lower than actual group sizes. Fifth, we did not correct for reactions to vessel approach by small cetaceans—an issue that is primarily a concern with the Dall's porpoise and vessel-attracted dolphin species, like the short-beaked common dolphin. Lastly, the SWFSC southern stratum, with an area of 318,500 km², is larger than the study area of the CalCOFI surveys by 25%. We compared density and abundance of species from these 2 studies because the 2 areas overlap by 75% and the CalCOFI study area occurs completely inside the SWFSC southern stratum. That said, our study provides the most recent and best replicated shipboard assessment of seasonal densities for 11 species of cetaceans off Southern California, including 3 species of baleen whales, the sperm whale, 6 species of delphinids, and the Dall's porpoise.

Baleen whales The most commonly occurring large whales that used this area for feeding were fin, humpback, and blue whales; because of their presence along the coast in greater numbers during the summer and fall, compared with other seasons, these species have been well represented in previous line-transect and

⁴ Gerrodette, T., and C. Perrin. 1991. Calibration of shipboard estimates of dolphin school size from aerial photographs. Southwest Fish. Sci. Cent. Admin. Rep. W-91-36, 73 p.

Table 6

Analysis of seasonal habitat use by cetacean species encountered on the 6 southern transect lines of 16 California Cooperative Oceanic Fisheries Investigation (CalCOFI) cruises conducted from 2004 to 2008 off Southern California. Values of mean depth, mean distance from land (Mean Dist Land), and mean distance to the mainland (Mean Dist Mainland) are for all cetacean species for which there were 10 or more on-effort encounters on the 6 CalCOFI transect lines; an exception was made for striped dolphins, where $n=2$. For sample sizes, see Table 4. Standard deviations (SD) of mean depths and mean distances from land are shown in parentheses. SDs were not available (NA) if only a single sighting was made during a season. The value under each season represents the combined length of the transect lines surveyed.

Species	Winter (4165 km)			Spring (4904 km)			Summer (6211 km)			Fall (4716 km)			All Seasons (19,996 km)		
	Mean Depth (SD)(m)	Mean Dist Land (km)	Mean Dist Mainland (km)	Mean Depth (SD)(m)	Mean Dist Land (km)	Mean Dist Mainland (km)	Mean Depth (SD)(m)	Mean Dist Land (km)	Mean Dist Mainland (km)	Mean Depth (SD)(m)	Mean Dist Land (km)	Mean Dist Mainland (km)	Mean Depth (SD)(m)	Mean Dist Land (km)	Mean Dist Mainland (km)
Whales															
Humpback	-	-	-	1395 (1369)	50 (47)	87	179 (127)	18 (16)	18	911 (1140)	36 (44)	78	852 (1132)	35 (40)	63
Blue	-	-	-	-	-	1551 (1342)	82 (78)	130 (1708)	1710 (1708)	72 (66)	127 (1401)	1589 (1401)	79 (74)	129	139
Fin	761 (620)	26 (18)	88	965 (530)	45 (31)	66	1790 (1434)	82 (70)	133	3105 (1529)	144 (67)	170	2200 (1593)	102 (74)	48
Minke	-	-	-	708 (353)	34 (12)	53	250 (80)	7 (4)	55	53 (NA)	2 (NA)	2	551 (388)	25 (17)	238
Sperm	3729 (353)	236 (173)	304	2460 (1889)	116 (103)	194	3367 (1172)	199 (103)	227	2587 (2353)	174 (166)	223	3270 (1209)	195 (118)	231
Delphinids															
Short-beaked common	2942 (1613)	258 (186)	315	2470 (1955)	297 (204)	373	2517 (1579)	127 (101)	184	2807 (1624)	172 (115)	219	2689 (1600)	176 (143)	29
Long-beaked common	51 (NA)	12 (NA)	12	1232 (NA)	11 (NA)	68	215 (227)	9 (6)	96	453 (427)	18 (8)	18	363 (398)	12 (7)	117
Pacific white- sided	1836 (1859)	87 (104)	134	2126 (1772)	113 (98)	133	1430 (937)	66 (28)	81	291 (288)	12 (5)	54	1751 (1660)	89 (90)	63
Risso's	663 (230)	31 (21)	81	902 (387)	29 (15)	64	795 (NA)	19 (NA)	34	920 (151)	11 (3)	46	846 (318)	26 (15)	80
Bottlenose	949 (448)	11 (3)	83	1015 (1602)	74 (128)	128	260 (NA)	4 (NA)	54	400 (210)	5 (1)	24	736 (1034)	34 (84)	128
Northern right whale	640 (NA)	64 (NA)	153	2023 (1770)	98 (112)	138	-	-	-	2666 (1581)	86 (46)	86	2065 (1663)	92 (94)	326
Striped	-	-	-	-	-	-	4075 (54)	294 (159)	326	-	-	-	4075 (54)	294 (159)	151
Porpoise															
Dall's porpoise	2700 (1598)	108 (68)	141	2933 (1444)	120 (68)	158	1135 (NA)	93 (NA)	93	2134 (2718)	92 (125)	107	2811 (1501)	115 (68)	151

Table 7

Summary of results from Kruskal-Wallis and Mann-Whitney tests of seasonality for depth, distance from vessel to land, and distance from vessel to shelf break for cetaceans encountered on the transect lines of the California Cooperative Oceanic Fisheries Investigation (CalCOFI) surveys conducted from 2004 to 2008 across all 4 seasons. Probability values that indicate significant results are shown in bold type. Asterisks indicate species for which tests were run with a limited number of sightings for one or more seasons; see Table 4 for number of sightings.

Species	Depth (<i>P</i> -value)	Distance to land (<i>P</i> -value)	Distance to shelf break (<i>P</i> -value)
Humpback whale	0.007	0.149	0.191
Blue whale	0.799	0.611	0.484
Fin whale*	0.003	<0.000	0.001
Minke whale	0.079	0.040	0.143
Sperm whale*	0.783	0.729	0.732
Short-beaked common dolphin*	0.122	0.005	0.008
Long-beaked common dolphin	0.247	0.037	0.015
Common dolphin (unknown short- or long-beaked)	0.773	0.422	0.587
Pacific white-sided dolphin	0.014	0.005	0.008
Risso's dolphin*	0.581	0.136	0.087
Bottlenose dolphin*	0.256	0.223	0.252
Northern right whale dolphin*	0.518	0.518	0.518
Dall's porpoise*	0.889	0.941	0.929

photoidentification studies. The large whales represented here are highly visible from a distance and often occur in small groups; therefore, confidence levels on group-size estimates are higher and abundance estimates likely are more accurate for them than for the smaller cetaceans that occur in large and more variable size groups. Group sizes for fin, humpback, and blue whales (Table 5) were similar to group sizes reported by Barlow (2010) and Barlow and Forney (2007). The number of unidentified large cetacean encounters (123) is to be expected from a survey conducted in passing mode. Although we did not apportion encounters of unidentified species in our analyses, on the basis of the proportion of large whale species positively identified, it is likely that fin, humpback, and blue whales made up the majority of these sightings.

Fin whales were the most commonly encountered and most abundant large whale in the study area. As has been documented by Forney and Barlow (1998), fin whales were encountered during all seasons, but the encounter rate for this species increased during the summer and fall seasons. Our abundance of 679 individuals (CV=0.25) in the study area during the summer–fall seasonal period is similar to Barlow's (2010) estimate of 499 individuals (CV=0.27) from a 2008 survey for Southern California and higher than the abundance estimate of 359 individuals (CV=0.40) from surveys conducted in 1991–2005 (Barlow and Forney, 2007). Given the differences in survey design, we would have expected our abundance estimate to have been lower than the values presented in Barlow (2010);

however, annual variability, which we do not address in this study of multiyear CalCOFI surveys, may account for the difference in abundance estimates. Broadly, these patterns of increasing abundance are consistent with the recently documented trend of an increasing population for fin whales (Moore and Barlow, 2011). Although there were few encounters during winter, fin whales used nearshore waters in the winter and spring and shifted into offshore waters in the summer and fall (Tables 6 and 7; Figs. 5 and 6); this movement seems to coincide with the observed coldest temperatures in nearshore waters recorded in winter and spring and with a slight increase of zooplankton biomass that occurs in the spring (Munger et al., 2009).

Although humpback whales were the second-most frequently encountered large cetacean, none were sighted during the winter. Our abundance estimate of 309 individuals (CV=0.32) for the summer–fall period is almost 6 times larger than the estimates of 49 individuals (CV=0.43) from the 2008 survey (Barlow, 2010) and of 36 whales (CV=0.51) from pooled 1991–2005 surveys (Barlow and Forney, 2007); however, just over half of our on-effort humpback sightings came from the 2007 summer cruise near Point Conception, where and when zooplankton abundance was notably high (Munger et al., 2009), indicating that an unusually large proportion of the population shifted into this area to take advantage of available prey. Because Southern California represents the southern end of the humpback whale's feeding range, such annual variation in available prey could strongly affect the abundance of

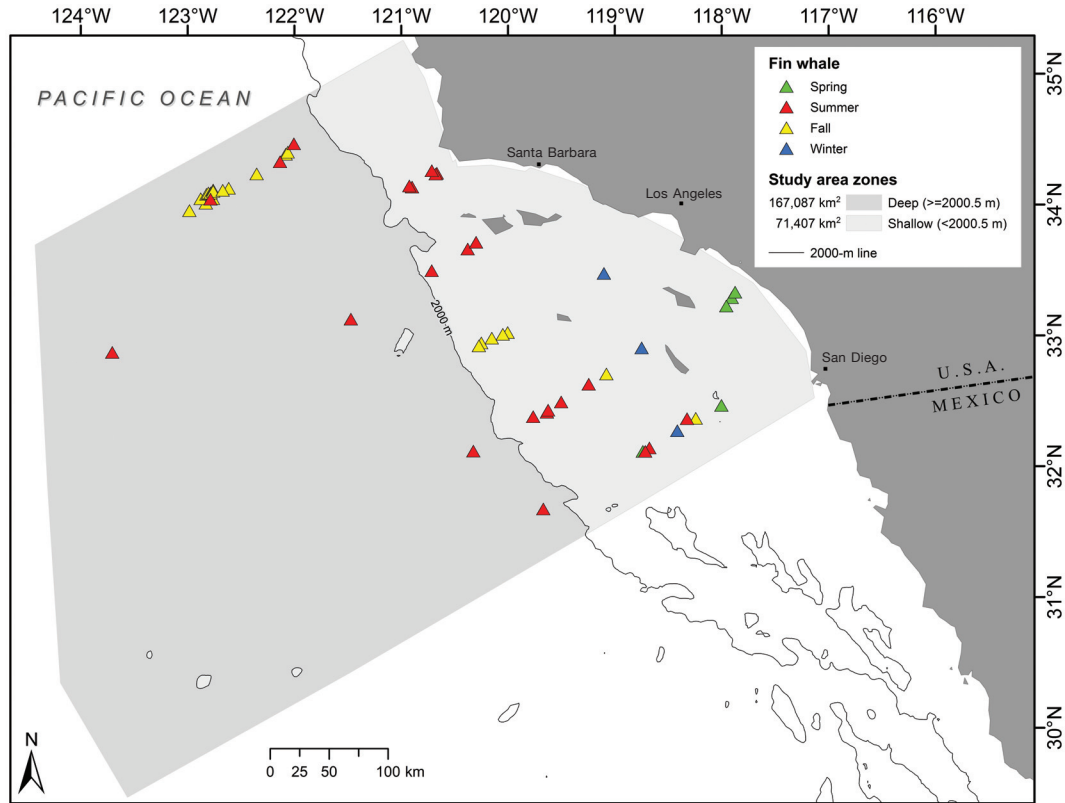


Figure 5

Map of on-effort encounters with the fin whale (*Balaenoptera physalus*) by season, recorded during the 16 shipboard line-transect surveys conducted quarterly during 2004–08 as part of the California Cooperative Oceanic Fisheries Investigation. The color of the triangle indicates the season: blue=winter, green=spring, red=summer, and yellow=fall.

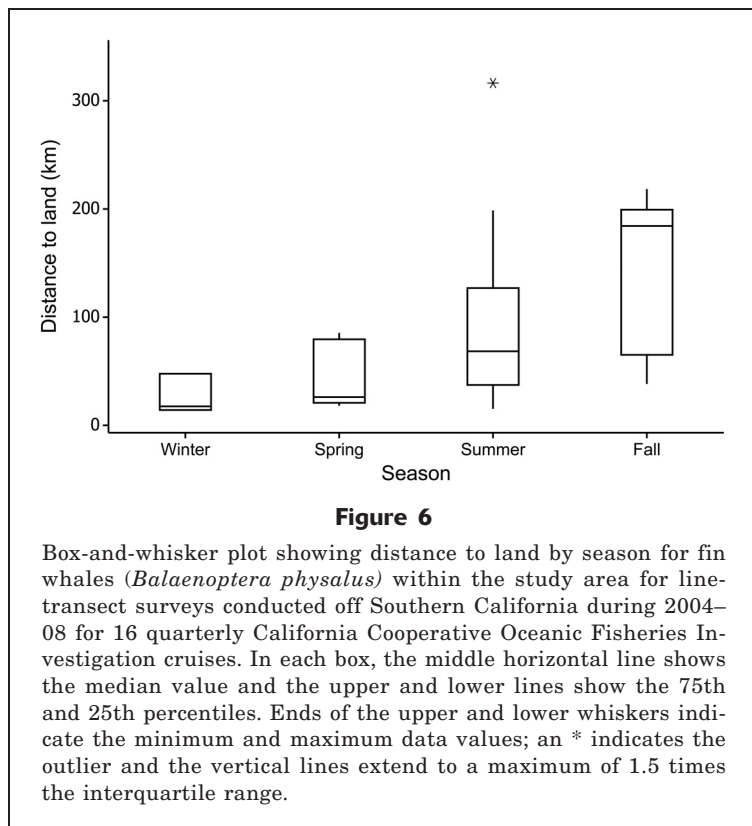
this species in our study area. Humpback whales off California, Oregon, and Washington migrate seasonally to wintering grounds off Baja, California, mainland Mexico, and Central America (Steiger et al., 1991; Calambokidis et al., 2000; Urbán et al., 2000). Clapham et al. (1997) and Forney and Barlow (1998) noted that in waters off California, a significantly greater proportion of the humpback whale population was found farther offshore in winter than in summer. We also found that more humpback whales occurred farther offshore and in deeper water in spring than during the summer–fall seasonal period (Table 6).

The thirdmost frequently encountered and abundant baleen whale within the study area, the blue whale, showed a distinct seasonal presence, a result that concurs with the findings from year-round aerial and ship-based surveys off Southern California. Forney and Barlow (1998) and Larkman and Veit (1998) found the greatest abundance of blue whales during August–October. Our abundance estimate of 288 blue whales (CV=0.23) was much lower than Barlow and Forney's (2007) estimate of 842 individuals (CV=0.20) off Southern California. The discrepancy between these estimates is likely due to a few factors, including interan-

nual differences in proportion of the population found within the study area and our lack of a correction factor for transect-line detection probability. Barlow and Forney's (2007) estimate included surveys completed in 1991, 1993, and 1996, all years when much of the blue whale population was thought to be feeding along the California coast; however, in more recent years, evidence has indicated that blue whales are using more northerly, southerly, and offshore waters (Calambokidis and Barlow, 2004; Barlow and Forney, 2007; Calambokidis et al., 2009). No blue whales were encountered in the study area during the winter–spring period—a finding that corresponds to their known migration pattern of feeding off California from May to November and migrating south to spend winter and spring off Mexico (Calambokidis et al., 1990; Mate et al., 1999; Stafford et al., 1999) and as far south as 6°N at the Costa Rica Dome (Wyrski, 1964).

Although known to be present year-round (Dohl et al.⁵; Forney et al., 1995; Barlow³), minke whales

⁵ Dohl, T. P., R. C. Guess, M. L. Duman, and R. C. Helm. 1983. Cetaceans of central and northern California, 1980–1983: status, abundance, and distribution. Part of investigator's fi-



(*Balaenoptera acutorostrata*) are difficult to sight even in very good sea conditions. The sample size of this species in the 6 CalCOFI surveys was insufficient for an abundance estimate, but it is worth noting that we encountered minke whales in low numbers from spring to fall, and a peak in encounter rates occurred during the spring (Table 4) that cannot be explained by better sea conditions in spring. Although sei whales were historically the fourth-most commonly captured whale along coastal California during whaling activity in the 1950s and 1960s (Rice, 1974), they now are considered rare in California waters (Dohl et al.⁵; Mangels and Gerrodette, 1994; Forney et al., 1995; Barlow³). Our results support findings that they are not commonly encountered off southern California with only a single sighting of a sei whale and a sighting of one other individual that was either a sei whale or a Bryde's whale.

Odontocetes We encountered 16 species of odontocetes, with sufficient sightings of 8 species to calculate seasonal abundance and density and examine seasonal trends. The most commonly encountered odontocete species along Southern California are present year-

round, although some of them undergo seasonal shifts in abundance; the Dall's porpoise and Risso's dolphin have been recognized as moving seasonally into Southern California waters during the winter months. Such seasonal shifts of abundance out of Southern California waters during winter months increases the likelihood that these species were regionally underrepresented in previous estimates (Barlow and Forney, 2007; Carretta et al., 2011b) of density and abundance that were generated from sighting data collected during summer–fall ship-based surveys.

Sufficient sample size allowed for density and abundance estimation of sperm whales; however, mean group size (2.7 individuals) was significantly lower than the 8.1 individuals reported off Southern California from pooled sightings collected over 5 years of SWFSC surveys (Barlow and Forney, 2007). In our study, group-size estimates were very likely negatively biased by the constraints of conducting a survey in passing mode, instead of using the protocol for the SWFSC line-transect surveys of conducting multiple counts over 90 min to enumerate asynchronously diving whales (Barlow and Taylor, 2005; Barlow and Forney, 2007). We encountered sperm whales year-round and in both depth categories, but we observed this species primarily during the summer–fall period in depths

>2000.5 m—findings similar to earlier analyses of year-round survey effort (Dohl et al.⁵; Barlow, 1995; Forney et al., 1995).

Even with our relatively high number of common dolphin sightings that could not be identified to species, we found that short-beaked common dolphins were the most abundant and widely distributed cetacean in our study area—a finding that is consistent with previously published results from cetacean survey effort off Southern California (Leatherwood et al., 1982; Dohl et al., 1986; Smith et al., 1986; Barlow, 1995; Forney et al., 1995). Moreover, our stratified abundance estimates provide clear evidence of seasonal shifts in habitat use. We found that, during the summer–fall period, short-beaked common dolphins were fairly evenly spread throughout the study area, and, during the winter–spring period, there was a surge in abundance of this species into offshore waters (mean group size: 127.7 individuals; abundance: 101,900 individuals [CV=0.45]). The greatest seasonal abundance estimate (170,151 individuals [CV=0.14]) was from the summer–fall period, a level that is very close to Barlow and Forney's (2007) estimate for that seasonal period of 165,400 individuals (CV=0.19). From aerial and ship-based line-transect surveys, the abundance of short-beaked common dolphins off California has been shown to change on seasonal and interannual times scales (Dohl et al., 1986; Barlow, 1995; Forney et al., 1995).

nal report, Marine Mammal and Seabird Study, central and northern California, Contract No. 14-12-0001-29090. Prepared by Center for Marine Sciences, Univ. California, Santa Cruz, for the Pacific OCS Region, Minerals Management Service, OCS Study MMS 84-0045, 284 p.

Long-beaked common dolphins were the fourthmost commonly encountered and secondmost abundant small cetacean in the study area. Distribution of long-beaked common dolphins was limited to waters near the California coast or Channel Islands—a result that is consistent with findings that this species is commonly found within ~93 km of the coast and ranges from Baja California to central California, with the highest densities observed during warm-water events throughout their range (Heyning and Perrin, 1994). The uncorrected abundance estimate from summer–fall surveys at shallow depths for long-beaked common dolphins (49,118 individuals [CV=0.52]) was about 3 times higher than Barlow's (2010) abundance estimate determined from pooled data from line-transect surveys conducted during 1991–2008, but our mean group size (217.2 individuals [CV=0.52]) and abundance estimate were much lower than his mean group size and abundance estimates from the 2009 line-transect survey, where corrected mean group size was 481.0 individuals and abundance was 111,738 individuals (CV=0.44) (Carretta et al., 2011a). Our estimates are likely negatively biased, given the relatively large number of common dolphin sightings that were not identified to species. However, the 2009 estimates were much greater than the results from earlier surveys, and there was an indication that the moderate El Niño event in 2009 may have caused an influx of dolphins from the south. Our surveys, conducted during 2004–08, show that this species is present year-round but increases 22-fold in abundance during the summer–fall period, indicating that dolphins are shifting south for the winter and spring.

Although the number of sightings was insufficient from the winter–spring period to quantify year-round seasonality of long-beaked common dolphins, this study is the first to provide evidence of seasonal habitat use for the 2 common dolphin species found along Southern California. For previous publications that have documented seasonality, aerial surveys were used for cold-water seasonal surveys; however, at the time of those studies, there was not an effective method for distinguishing the 2 species from an aerial platform (Dohl et al., 1986; Forney et al., 1995; Forney and Barlow, 1998). In marked contrast to the ratio of encounters of short- and long-beaked common dolphins reported here (6:1), Carretta et al. (2011a) encountered the 2 species at a 1:1 ratio in 2009; their observation supports the hypothesis of a dramatic shift or pronounced interannual variability from the preceding years off Southern California.

Pacific white-sided dolphins were encountered in all seasons, with the greatest abundance estimate (14,898 individuals [CV=0.21]) from both depth categories combined in the winter–spring seasonal period. Although density was markedly different between the shallow and deep categories during the winter–spring season, abundance was fairly constant throughout the entire study area. During the summer–fall period, we found that density and abundance (9.24 individuals/1000 km²;

2204 individuals [CV=0.35]) decreased by almost 15% from the previous winter–spring period, with greater abundance in shallow waters than in deep waters. Barlow and Forney (2007) published a similar pooled abundance estimate of 2196 individuals (CV=0.39) for surveys conducted in all depths during the summer–fall period during 1991–2005. From the data on encounters by season, we found that a significant shift into deep water occurred during the winter–spring period (Table 7, Fig. 7). Along the coast of California, the 2 forms of Pacific white-sided dolphins are primarily found in waters over the continental shelf and slope (Forney, 1994). The northern form is thought to enter coastal Southern California waters during the winter months and to congregate with the southern form (Walker et al., 1986; Lux et al., 1997; Soldevilla et al., 2011). Because we were unable to differentiate between the 2 forms, it is possible that the increase in observed abundance during the winter–spring season was a result of capturing both forms that use the study area rather than capturing only the southern form.

Risso's dolphins were encountered year-round in shallow water, with abundance estimates of 2546 individuals (CV=0.36) for the winter–spring period and of 279 individuals (CV=0.55) for the summer–fall period. Our findings agreed with those from visual surveys that found high seasonal variability in occurrence and distribution of this species off California (Shane, 1994; Forney and Barlow, 1998; Kruse et al., 1999; Benson et al., 2002; Barlow and Forney, 2007) and that their abundance along the California coast could be an order of magnitude higher during the winter than during the summer (Forney and Barlow, 1998). However, further research is needed to understand our results in relation to the findings of Soldevilla et al. (2010), who found peak Risso's dolphin echolocation activity off Southern California in the fall.

On the basis of genetics and morphology, bottlenose dolphins along the coast of California and elsewhere worldwide are split into offshore and coastal populations (Hansen, 1990; Carretta et al., 1998; Defran and Weller, 1999; Bearzi et al., 2009; Perrin et al., 2011). The Southern California coastal population typically is encountered within 500 m of shore (this species was sighted within that boundary 99% of the time during a previous study; Hanson and Defran [1993]), and the offshore population is found outside of a few kilometers from the mainland. The mean distance from a land mass that bottlenose dolphins were recorded in this study was 34 km; the minimum distance was just over 2 km. The study area did not include nearshore waters sufficiently to encounter coastal bottlenose; therefore, we assume that our abundance estimate is for the offshore bottlenose dolphin population. For our stratum of the summer–fall period and shallow depth, the abundance estimate (2879 individuals [CV=0.69]) is greater than Barlow and Forney's (2007) abundance estimate (1831 individuals [CV=0.47]) for this population off Southern California during the same period.

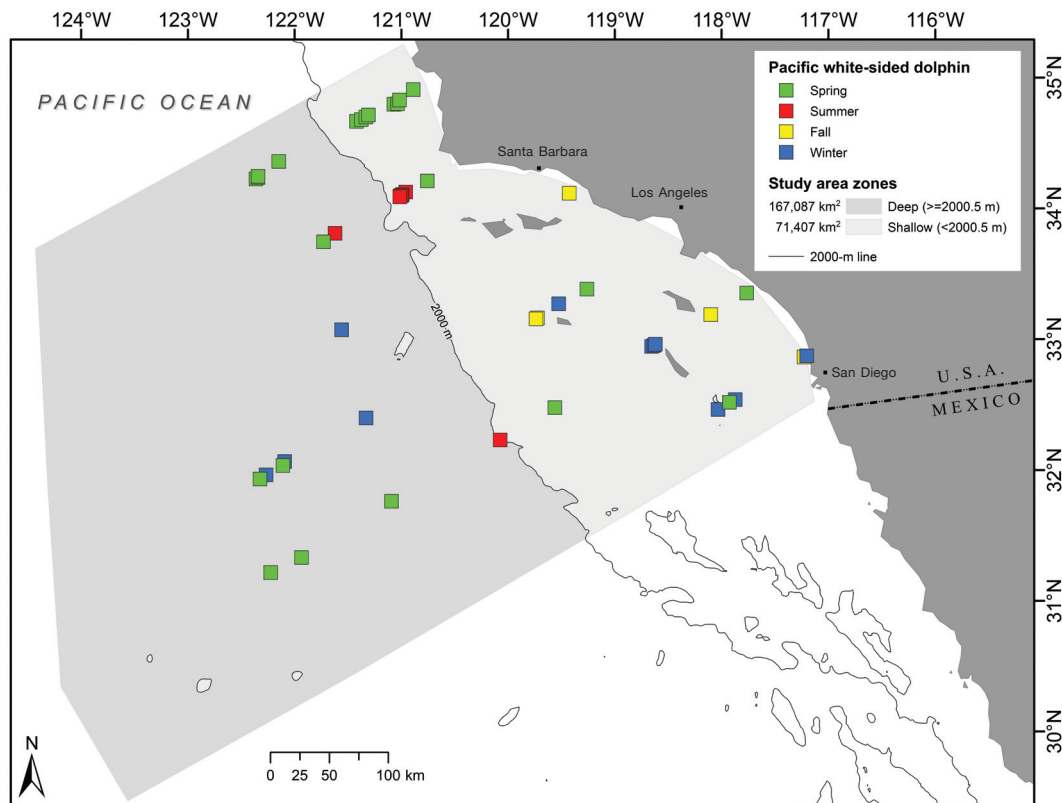


Figure 7

Map of on-effort encounters with the Pacific white-sided dolphin (*Lagenorhynchus obliquidens*) by season during the 16 shipboard line-transect surveys conducted quarterly during 2004–08 as part of the California Cooperative Oceanic Fisheries Investigation. The color of the triangle indicates the season: blue=winter, green=spring, red=summer, and yellow=fall.

In addition to the high CV value associated with our abundance estimate, a likely cause of this discrepancy between the 2 studies is the difference in estimated group size, where we observed an average of 40.5 individuals in a group and Barlow and Forney (2007) reported 13.4 individuals in a group.

The Northern right whale dolphin and Dall's porpoise are known to favor cold waters, and we found both species to have the greatest abundance estimates during the winter–spring period over all depths. Although encounters with northern right whale dolphins in the summer–fall period were few, an increase in density during the winter–spring surveys in shallow water was observed—a finding that is consistent with earlier records that found this species beyond the continental slope for warm-water seasons and in shelf waters of the Southern California Bight for the cold-water season (Barlow, 1995; Forney et al., 1995; Forney and Barlow, 1998).

Although seasonally abundant, Dall's porpoises are often initially sighted when they react to survey vessels, thereby biasing abundance estimates upward. To compensate for vessel attraction, Barlow and Forney (2007) included only Dall's porpoise sightings made in sea states of 0–2—an approach that they noted limited

sample size. On the basis of the detection model for Dall's porpoises (Fig. 2), which showed an even tapering of sightings with distance from the vessel, we included sightings in sea states of 0–5, assuming that it would be better to have a greater number of sightings than an insufficient number to estimate abundance. Spatially, our analysis of encounters with Dall's porpoises in the CalCOFI study area agrees with the finding of Morejohn (1979) that Dall's porpoises were commonly seen in small groups along the shelf and slope and in offshore waters. Dall's porpoises were consistently found in recently upwelled waters near shore (Peterson et al., 2006). In the CalCOFI study area, the highest encounter rates of Dall's porpoises occurred in spring, when upwelling waters were active.

As with the Dall's porpoise, many of the delphinids are known to react to a vessel before visual observers can detect them; this behavior is especially a concern when the naked eye and low-power binoculars are used in the search method, as they were in the CalCOFI surveys used in this study. Although reaction to vessel cannot be ruled out as a factor in our results, our decision to keep all on-effort sightings in the analyses was based on the detection model for delphinids (Fig.

3) that showed an even tapering of sightings with distance from vessel.

Our results on seasonal occurrence of the 6 frequently occurring delphinid species and the Dall's porpoise are consistent with prior findings. The bottlenose dolphin, long-beaked common dolphin, and short-beaked common dolphin generally favor warm-water (summer–fall) periods along the California coast (Dohl et al., 1986; Barlow, 1995; Forney et al., 1995). Dall's porpoise, the Pacific white-sided dolphin, the northern right whale dolphin, and Risso's dolphin commonly are found during the cold-water (winter–spring) periods off Southern California, and these species tend to migrate north into central California or Oregon and Washington during the warm-water periods (Forney, 1994; Forney and Barlow, 1998). These species have exhibited abundance shifts associated with oceanographic variability on both seasonal and interannual time scales (Perrin et al., 1985; Heyning and Perrin, 1994; Forney, 1997; Forney and Barlow, 1998; Becker, 2007).

There were only 6 sightings of beaked whales, but all 3 genera (*Ziphius*, *Berardius*, and *Mesoplodon*) known to be present off Southern California were detected. The single sighting of a *Mesoplodon* could not be confirmed to species. A single encounter with a group of Baird's beaked whales (*Berardius bairdii*) near the shelf break during a survey in the summer is consistent with other sightings of this species in continental slope waters from late spring to early fall (Balcomb, 1989; Carretta et al., 2011b).

Of the 11 dolphin species encountered, 5 species were represented by only 1–3 sightings per species: killer whale, false killer whale, short-finned pilot whale (*Globicephala macrorhynchus*), rough-toothed dolphin, and striped dolphin. Of these 5 species, only the killer whale is commonly found year-round off Southern California, with 2 U.S. stocks (Eastern North Pacific Transient and Eastern North Pacific Offshore [Carretta et al., 2011b]) that use the area. We were unable to confirm which stocks were represented in the 2 sightings of this species. The rough-toothed dolphin and false killer whale are considered rare off California, with no known current or historical populations along the West Coast of the United States; therefore, our sightings likely represent extralimital movements from populations farther south.

There were too few encounters with striped dolphins in the study area to look at seasonal shifts in habitat; however, it is worth noting that the 3 sightings of this species occurred in surveys conducted in the summer–fall period, in the deepest mean water depth, and at the greatest mean distance to land of any species observed in the study area (Table 6). Season, distance to shore, and depth of striped dolphin encounters correspond with those of previous surveys conducted in summer and fall and with habitat models that revealed the presence of striped dolphins in tropical to warm-temperate pelagic waters, with a continuous distribution outside upwelling coastal waters of California (Perrin et al., 1985; Jefferson et al., 1993; Mangels and

Gerrodette, 1994; Archer and Perrin, 1999; Becker et al., 2012; Forney et al., 2012).

Short-finned pilot whales were encountered commonly off Southern California before the El Niño event in 1982–83 (Dohl et al.¹); on the basis of numerous surveys, including this one, it is apparent that this species now uses these waters only infrequently (Carretta and Forney, 1993; Shane, 1994; Barlow³; Forney, 2007). The single encounter of false killer whales in the study area occurred during the 2008 winter cruise at a depth of 300 m and within 5 km of Santa Rosa Island. False killer whales are normally found in tropical to warm-temperate oceans; however, sightings have been made occasionally in cold-temperate areas as well (Stacey and Baird, 1991; Baird, 2008).

Conclusions

We collected sighting data from seasons and years that have not been reported previously, generated density and abundance estimates for 11 species of cetaceans off Southern California, and documented shifts in seasonal distribution for fin whales and Pacific white-sided dolphins. In recent years, interest has increased in the development of predictive models to forecast near real-time marine mammal distribution as a way to inform, mitigate, and decrease the effect of potentially harmful human activities in the marine environment (Becker et al., 2012; Forney et al., 2012; Thompson et al., 2012; Henderson et al., 2014). Although our data set spans a 5-year period that ends in 2008, visual and acoustic data on detections of marine mammals continue to be collected with corresponding oceanographic data, both physical and biological, during CalCOFI cruises. As the CalCOFI data set grows, it potentially could become one of the most valuable collections of data both for monitoring and creating year-round habitat models of cetacean species and their environment off Southern California.

Acknowledgments

F. Stone, E. Young, and L. Petitpas and the Office of Naval Research provided funding and project management. We appreciate the efforts of all who were involved in the CalCOFI surveys in 2004–08: the captains and crews of the *New Horizon*, *David Starr Jordan*, and *Roger Revelle* and the scientists, especially D. Wolgast, J. Wilkinson, A. Hays, R. Baird, S. Yin, M. Smith, A. Miller, L. Morse, V. Iriarte, E. Vázquez, N. Rubio, K. Merckens, J. Burtenshaw, E. Oleson, and E. Henderson. We also thank K. Forney and R. Baird for manuscript review. Finally, the authors would like to honor S. Claussen, whose presence and laughter is greatly missed.

Literature cited

- Amante, C., and B. W. Eakins.
2009. ETOPO1 1 Arc-Minute Global Relief Model: procedures, data sources and analysis. NOAA Tech. Memo. NESDIS-NGDC-24, 19 p.
- Archer, F. I., II, and W. F. Perrin.
1999. *Stenella coeruleoalba*. Mamm. Species 603:1-9.
- Baird, R. W.
2008. False killer whale, *Pseudorca crassidens*. In Encyclopedia of marine mammals, 2nd ed. (W. F. Perrin, B. Würsig, and J. G. M. Thewissen, eds.), p. 405-406. Academic Press, Amsterdam.
- Balcomb, K. C., III.
1989. Baird's beaked whale *Berardius bairdii* Stejneger, 1883: Arnoux's beaked whales *Berardius arnuxii* Duvernoy, 1851. In Handbook of marine mammals, vol. 4: river dolphins and the larger toothed whales (S. H. Ridgway and R. Harrison, eds.), p. 261-288. Academic Press, New York.
- Barlow, J.
1988. Harbor porpoise, *Phocoena phocoena*, abundance estimation in California, Oregon, and Washington: I. Ship surveys. Fish. Bull. 86:417-432.
1995. The abundance of cetaceans in California waters. Part I: Ship surveys in summer and fall of 1991. Fish. Bull. 93:1-14.
2010. Cetacean abundance in the California Current estimated from a 2008 ship-based line-transect survey. NOAA Tech. Memo. NMFS-SWFSC-456, 19 p.
- Barlow, J., and K. A. Forney.
2007. Abundance and population density of cetaceans in the California Current ecosystem. Fish. Bull. 105:509-536.
- Barlow, J., T. Gerrodette, and J. Forcada.
2001. Factors affecting perpendicular sighting distances on shipboard line-transect surveys for cetaceans. J. Cetacean Res. Manage. 3:201-212.
- Barlow, J., and B. L. Taylor.
2005. Estimates of sperm whale abundance in the north-eastern temperate Pacific from a combined acoustic and visual survey. Mar. Mamm. Sci. 21:429-445.
- Bearzi, M., C. A. Saylan, and A. Hwang.
2009. Ecology and comparison of coastal and offshore bottlenose dolphins (*Tursiops truncatus*) in California. Mar. Freshw. Res. 60:584-593.
- Becker, E. A.
2007. Predicting seasonal patterns of California cetacean density based on remotely sensed environmental data. Ph.D. diss., 303 p. Univ. California, Santa Barbara, CA.
- Becker, E. A., D. G. Foley, K. A. Forney, B. Barlow, J. V. Redfern, and C. L. Gentemann.
2012. Forecasting cetacean abundance patterns to enhance management decisions. Endang. Species Res. 16:97-112.
- Benson, S. R., D. A. Croll, B. B. Marinovic, F. P. Chavez, and J. T. Harvey.
2002. Changes in the cetacean assemblage of a coastal upwelling ecosystem during El Nino 1997-98 and La Nino and La Nina 1999. Prog. Oceanogr. 54:279-291.
- Berman-Kowalewski, M., F. M. D. Gulland, S. Wilkin, J. Calambokidis, B. Mate, J. Cordaro, D. Rotstein, J. St. Leger, P. Collins, K. Fahy, and S. Dover.
2010. Association between blue whale (*Balaenoptera musculus*) mortality and ship strikes along the California coast. Aquat. Mamm. 36:59-66.
- Bograd, S. J., D. A. Checkley, and W. S. Wooster.
2003. CalCOFI: a half century of physical, chemical, and biological research in the California Current System. Deep Sea Res. (II Top. Stud. Oceanogr.) 50:2349-2353.
- Buckland, S. T., D. R. Anderson, K. P. Burnham, J. L. Laake, D. L. Borchers, and L. Thomas.
2001. Introduction to distance sampling: estimating abundance of biological populations, 448 p. Oxford Univ. Press, Oxford, UK.
- Buckland, S. T., D. R. Anderson, K. P. Burnham, and J. L. Laake.
1993. Distance sampling: estimating abundance of biological populations, 446 p. Chapman and Hall, London.
- Burnham, K. P., and D. R. Anderson.
2002. Model selection and multimodel inference: a practical information-theoretic approach, 2nd ed., 488 p. Springer-Verlag, New York.
- Calambokidis, J., and J. Barlow.
2004. Abundance of blue and humpback whales in the eastern North Pacific estimated by capture-recapture and line-transect methods. Mar. Mamm. Sci. 20:63-85.
- Calambokidis, J., J. Barlow, J. K. B. Ford, T. E. Chandler, and A. B. Douglas.
2009. Insights into the population structure of blue whales in the eastern North Pacific from recent sightings and photographic identifications. Mar. Mamm. Sci. 25:816-832.
- Calambokidis, J., G. H. Steiger, J. C. Cabbage, K. C. Balcomb, C. Ewald, S. Kruse, R. Wells, and R. Sears.
1990. Sightings and movements of blue whales off central California 1986-88 from photo-identification of individuals. Rep. Int. Whal. Comm. (special issue) 12:343-348.
- Calambokidis, J., G. H. Steiger, K. Rasmussen, J. Urbán R., K. C. Balcomb, P. Ladrón de Guevara P., M. Salinas Z., J. K. Jacobsen, C. S. Baker, L. M. Herman, S. Cerchio, and J. D. Darling.
2000. Migratory destinations of humpback whales that feed off California, Oregon and Washington. Mar. Ecol. Prog. Ser. 192:295-304.
- Carretta, J. V., S. J. Chivers, and W. L. Perryman.
2011a. Abundance of the long-beaked common dolphin (*Delphinus capensis*) in California and western Baja California waters estimated from a 2009 ship-based line-transect survey. Bull. South. Calif. Acad. Sci. 110:152-164.
- Carretta, J. V., and K. A. Forney.
1993. Report of the two aerial surveys for marine mammals in California coastal waters utilizing a NOAA DeHavilland twin otter aircraft March 9-April 7, 1991 and February 8-April 6, 1992. NOAA-TM-NMFS-SWFSC-185, 77 p.
- Carretta, J. V., K. A. Forney, and J. L. Laake.
1998. Abundance of southern California coastal bottlenose dolphins estimated from tandem aerial surveys. Mar. Mamm. Sci. 14:655-675.
- Carretta, J. V., K. A. Forney, E. Oleson, K. Martien, M. M. Muto, M. S. Lowry, J. Barlow, J. Baker, B. Hanson, D. Lynch, L. Carswell, R. L. Brownell, J. Robbins, D. K. Mattila, R. L. Brownell Jr., J. Robbins, D. K. Mattila, K. Ralls, and M. C. Hill.
2011b. U.S. Pacific marine mammal stock assessments: 2011. NOAA Tech. Memo. NMFS-SWFSC-488, 356 p.

- Clapham, P. J., S. Leatherwood, I. Szczepaniak, and R. L. Brownell.
1997. Catches of humpback and other whales from shore stations at Moss Landing and Trinidad, California, 1919–1926. *Mar. Mamm. Sci.* 13:368–394.
- Defran, R. H., and D. W. Weller.
1999. Occurrence, distribution, site fidelity, and school size of bottlenose dolphins (*Tursiops truncatus*) off San Diego, California. *Mar. Mamm. Sci.* 15:366–380.
- Dohl, T. P., M. L. Bonnell, and R. G. Ford.
1986. Distribution and abundance of common dolphin, *Delphinus delphis*, in the Southern California Bight: a quantitative assessment based upon aerial transect data. *Fish. Bull.* 84:333–344.
- Forney, K. A.
1994. Recent information on the status of odontocetes in Californian waters. NOAA Tech. Memo. NMFS-SWF-SC-202, 87 p.
1997. Patterns of variability and environmental models of relative abundance for California cetaceans. Ph.D. diss., 260 p. Scripps Inst. Oceanography, Univ. California, San Diego, CA.
2007. Preliminary estimates of cetacean abundance along the U.S. West Coast and within four National Marine sanctuaries during 2005. NOAA Tech. Memo. NMFS-SWFSC-406, 27 p.
- Forney, K. A., and J. Barlow.
1998. Seasonal patterns in the abundance and distribution of California cetaceans, 1991–1992. *Mar. Mamm. Sci.* 14:460–489.
- Forney, K. A., J. Barlow, and J. V. Carretta.
1995. The abundance of cetaceans in California waters. Part II: aerial surveys in winter and spring of 1991 and 1992. *Fish. Bull.* 93:15–26.
- Forney, K. A., M. C. Ferguson, E. A. Becker, P. C. Fiedler, J. V. Redfern, J. Barlow, I. L. Vilchis, and L. T. Ballance.
2012. Habitat-based spatial models of cetacean density in the eastern Pacific Ocean. *Endang. Species Res.* 16:113–133.
- Forney, K. A., D. A. Hanan, and J. Barlow.
1991. Detecting trends in harbor porpoise abundance from aerial surveys using analysis of covariance. *Fish. Bull.* 89:367–377.
- Hansen, L. J.
1990. California coastal bottlenose dolphins. In *The bottlenose dolphin* (S. Leatherwood and R. R. Reeves, eds.), p. 403–420. Academic Press, San Diego, CA.
- Hanson, M. T., and R. H. Defran.
1993. The behaviour and feeding ecology of the Pacific coast bottlenose dolphin, *Tursiops truncatus*. *Aquat. Mamm.* 19:127–142.
- Henderson, E., K. A. Forney, J. P. Barlow, J. A. Hildebrand, A. B. Douglas, J. Calambokidis, and W. J. Sydeman.
2014. Effects of fluctuations in sea-surface temperature on the occurrence of small cetaceans off Southern California: implications for climate change. *Fish. Bull.* 112:159–177.
- Heyning J. E., and W. F. Perrin.
1994. Evidence for two species of common dolphins (genus *Delphinus*) from the eastern North Pacific. *Nat. Hist. Mus. Los. Ang. Cty., Contrib. Sci.* 442:1–35.
- Jefferson T. A., S. Leatherwood, and M. A. Webber.
1993. *Marine mammals of the world*. FAO species identification guide, 320 p. FAO, Rome.
- Jensen, A. S., and G. K. Silber.
2003. Large whale ship strike database. NOAA Tech. Memo. NMFS-OPR-25, 37 p.
- Julian, F., and M. Beeson.
1998. Estimates of marine mammal, turtle, and seabird mortality for two California gillnet fisheries: 1990–95. *Fish. Bull.* 96:271–284.
- Kinzey, D., and T. Gerrodette.
2003. Distance measurements using binoculars from ships at sea: accuracy, precision and effects of refraction. *J. Cetacean Res. Manage.* 5:159–171.
- Kruse, S., D. Caldwell, and M. Caldwell.
1999. Risso's dolphin. In *Handbook of marine mammals*, vol. 6: the second book of dolphins and porpoises (S. H. Ridgway and R. Harrison, eds.), p. 183–212. Academic Press, London.
- Laist, D. W., A. R. Knowlton, J. G. Mead, A. S. Collet, and M. Podesta.
2001. Collisions between ships and whales. *Mar. Mamm. Sci.* 17:35–75.
- Larkman, V. E., and R. R. Veit.
1998. Seasonality and abundance of blue whales off of Southern California. *CalCOFI Rep.* 39:236–239.
- Leatherwood, S., R. R. Reeves, W. F. Perrin, and W. E. Evans.
1982. Whales, dolphins and porpoises of the eastern North Pacific and adjacent Arctic waters: a guide to their identification. NOAA Tech. Rep. NMFS Circular 444, 245 p.
- Lux, C. A., A. S. Costa, and A. E. Dizon.
1997. Mitochondrial DNA population structure of the Pacific white-sided dolphin. *Rep. Int. Whal. Comm.* 47:645–652.
- Mangels, K. F., and T. Gerrodette.
1994. Report on cetacean sightings during a marine mammal survey in the eastern Pacific Ocean and the Gulf of California aboard the NOAA Ships *McArthur* and *David Starr Jordan*, July 28–November 6, 1993. NOAA Tech. Memo. NMFS-SWFSC-211, 88 p.
- Marques, F. F. C., and S. T. Buckland.
2003. Incorporating covariates into standard line transect analyses. *Biometrics* 59:924–935.
- Mate, B. R., B. A. Lagerquist, and J. Calambokidis.
1999. Movements of North Pacific blue whales during the feeding season off southern California and southern fall migration. *Mar. Mamm. Sci.* 15:1246–1257.
- McDonald, M. A., J. A. Hildebrand, and S. M. Wiggins.
2006. Increases in deep ocean ambient noise in the northeast Pacific west of San Nicolas Island, California. *J. Acoust. Soc. Am.* 120:711–8.
- Moore, J. E., and J. Barlow.
2011. Bayesian state-space models of fin whale abundance trends from a 1991–2008 time series of line-transect surveys in the California Current. *J. Appl. Ecol.* 48:1195–1205.
- Morejohn, G. V.
1979. The natural history of Dall's porpoise in the North Pacific Ocean. In *Behavior of marine mammals*, vol. 3: cetaceans. Current perspectives in research (H. E. Winn and B. L. Olla, eds.), p. 45–83. Plenum Press, New York.
- Munger, L. M., D. Camacho, A. Havron, G. Campbell, J. Calambokidis, A. Douglas, and J. Hildebrand.
2009. Baleen whale distribution relative to surface temperature and zooplankton abundance off southern California, 2004–2008. *CalCOFI Rep.* 50:155–168.

- Ohman, M. D., and E. L. Venrick.
2003. CalCOFI in a changing ocean. *Oceanography* 16:76-85.
- Perrin, W. F., M. D. Scott, G. J. Walker, and V. L. Cass.
1985. Review of geographical stocks of tropical dolphins (*Stenella* spp. and *Delphinus delphis*) in the eastern Pacific. NOAA Tech. Rep. NMFS 28, 28 p.
- Perrin, W. F., J. L. Thieleking, W. A. Walker, F. I. Archer, and K. M. Robertson.
2011. Common bottlenose dolphins (*Tursiops truncatus*) in California waters: cranial differentiation of coastal and offshore ecotypes. *Mar. Mamm. Sci.* 27:769-792.
- Peterson, W. T., R. Emmet, R. Goericke, E. Venrick, A. Mantyla, S. J. Bograd, F. B. Schwing, R. Hewitt, N. Lo, W. Watson, J. Barlow, M. Lowry, S. Ralston, K. A. Forney, B. E. Lavaniegos, W. J. Sydeman, D. Hyrenbach, R. W. Bradely, P. Worzybok, F. Chavez, K. Hunter, S. Benson, M. Weise, and J. Harvey.
2006. The state of the California Current, 2005-2006: warm in the north, cool in the south. *CalCOFI Rep.* 47:30-74.
- Reeves, R. R., B. S. Stewart, P. J. Clapham, and J. A. Powell.
2002. Guide to marine mammals of the world, National Audubon Field Guide Series, 527 p. Alfred A. Knopf, New York.
- Reid, J. L., G. I. Roden, and J. G. Wyllie.
1958. Studies of the California Current system. Contributions from the Scripps Institution of Oceanography, New Series No. 998. *In Calif. Coop. Ocean. Fish. Invest. Prog. Rep.*, 1 July 1956 to 1 January 1958, p. 28-56. [Available from http://www.calcofi.org/publications/calcofireports/v06/CalCOFI_Rpt_Vol_06_1958.pdf]
- Rice, D. W.
1974. Whales and whale research in the eastern North Pacific. *In The whale problem: a status report* (W. E. Schevill, ed.), p. 170-195. Harvard Press, Cambridge, MA.
- Rosel, P. E., A. E. Dizon, and J. E. Heyning.
1994. Genetic analysis of sympatric morphotypes of common dolphins (genus *Delphinus*). *Mar. Biol.* 119:159-167.
- Shane, S. H.
1994. Occurrence and habitat use of marine mammals at Santa Catalina Island, California from 1983-1991. *Bull. South. Calif. Acad. Sci.* 93:13-29.
- Smith, R. C., P. Dustan, D. Au, K. S. Baker, and E. A. Dunlap.
1986. Distribution of cetacean and sea-surface chlorophyll concentrations in the California Current. *Mar. Biol.* 91:385-402.
- Soldevilla, M. S., S. M. Wiggins, and J. A. Hildebrand.
2010. Spatial and temporal patterns of Risso's dolphin echolocation in the Southern California Bight. *J. Acoust. Soc. Am.* 127:124-132.
- Soldevilla, M. S., S. M. Wiggins, J. Calambokidis, A. Douglas, E. M. Oleson, and J. A. Hildebrand.
2006. Marine mammal monitoring and habitat investigations during CalCOFI surveys. *CalCOFI Rep.* 47:79-91.
- Soldevilla, M. S., S. M. Wiggins, J. A. Hildebrand, E. M. Oleson, and M. C. Ferguson.
2011. Risso's and Pacific white-sided dolphin habitat modeling from passive acoustic monitoring. *Mar. Ecol. Prog. Ser.* 423:247-260.
- Stacey, P. J., and R. W. Baird.
1991. Status of the false killer whale, *Pseudorca crassidens*, in Canada. *Can. Field-Nat.* 105:189-197.
- Stafford, K. M., S. L. Nieukirk, and C. G. Fox.
1999. An acoustic link between blue whales in the eastern tropical Pacific and the northeast Pacific. *Mar. Mamm. Sci.* 15:1258-1268.
- Steiger, G. H., J. Calambokidis, R. Sears, K. C. Balcomb, and J. C. Cubbage.
1991. Movement of humpback whales between California and Costa Rica. *Mar. Mamm. Sci.* 7:306-310.
- Thomas, L., S. T. Buckland, E. A. Rexstad, J. L. Laake, S. Strindberg, S. L. Hedley, J. R. B. Bishop, T. A. Marques, and K. P. Burnham.
2010. Distance software: design and analysis of distance sampling surveys for estimating population size. *J. Appl. Ecol.* 47:5-14.
- Thompson, S. A., W. J. Sydeman, J. A. Santora, B. A. Black, R. M. Suryan, J. Calambokidis, W. T. Peterson, and S. J. Bograd.
2012. Linking predators to seasonality of upwelling: using food web indicators and path analysis to infer trophic connections. *Prog. Oceanogr.* 101:106-120.
- Urbán R., J., A. Jaramillo L., A. Aguayo L., P. Ladrón de Guevara P., M. Salinas Z., C. Alvarez F., L. Medrano G., J. K. Jacobsen, K. C. Balcomb, D. E. Claridge, J. Calambokidis, G. H. Steiger, J. M. Straley, O. von Ziegesar, J. M. Waite, S. Mizroch, M. E. Dahlheim, J. D. Darling, and C. S. Baker.
2000. Migratory destinations of humpback whales wintering in the Mexican Pacific. *J. Cetacean Res. Manage.* 2:101-110.
- Walker, W. A., S. Leatherwood, K. R. Goodrich, W. F. Perrin, and R. K. Stroud.
1986. Geographical variation and biology of the Pacific white-sided dolphin, *Lagenorhynchus obliquidens*, in the north-eastern Pacific. *In Research on dolphins* (M. M. Bryden and R. Harrison, eds.), p. 441-465. Clarendon Press, Oxford, UK.
- Weilgart, L. S.
2007. The impacts of anthropogenic ocean noise on cetaceans and implications for management. *Can. J. Zool.* 85:1091-1116.
- Wyrтки, K.
1964. Upwelling in the Costa Rica Dome. *Fish. Bull.* 63:355-372.