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Inter-annual and seasonal trends in cetacean distribution, density and abundance off southern California



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ABSTRACT

Trends in cetacean density and distribution off southern California were assessed through visual line-transect surveys during thirty-seven California Cooperative Oceanic Fisheries Investigations (CalCOFI) cruises from July 2004–November 2013. From sightings of the six most commonly encountered cetacean species, seasonal, annual and overall density estimates were calculated. Blue whales (*Balaenoptera musculus*), fin whales (*Balaenoptera physalus*) and humpback whales (*Megaptera novaeangliae*) were the most frequently sighted baleen whales with overall densities of 0.91/1000 km² (CV=0.27), 2.73/1000 km² (CV=0.19), and 1.17/1000 km² (CV=0.21) respectively. Species specific density estimates, stratified by cruise, were analyzed using a generalized additive model to estimate long-term trends and correct for seasonal imbalances. Variances were estimated using a non-parametric bootstrap with one day of effort as the sampling unit. Blue whales were primarily observed during summer and fall while fin and humpback whales were observed year-round with peaks in density during summer and spring respectively. Short-beaked common dolphins (*Delphinus delphis*), Pacific white-sided dolphins (*Lagenorhynchus obliquidens*) and Dall's porpoise (*Phocoenoides dalli*) were the most frequently encountered small cetaceans with overall densities of 705.83/1000 km² (CV=0.22), 51.98/1000 km² (CV=0.27), and 21.37/1000 km² (CV=0.19) respectively. Seasonally, short-beaked common dolphins were most abundant in winter whereas Pacific white-sided dolphins and Dall's porpoise were most abundant during spring. There were no significant long-term changes in blue whale, fin whale, humpback whale, short-beaked common dolphin or Dall's porpoise densities while Pacific white-sided dolphins exhibited a significant decrease in density across the ten-year study. The results from this study were fundamentally consistent with earlier studies, but provide greater temporal and seasonal resolution.

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1. Introduction

Long-term assessments of density and distribution are central to evaluating potential effects of anthropogenic activities and ecosystem variability on cetacean populations (Fiedler and Reilly, 1994; Krebs, 2001; Morris and Doak, 2002; Rodrigues et al., 2006). The California Current Ecosystem (CCE) is a productive and dynamic habitat (Hayward and Venrick, 1998; Chhak and Di Lorenzo, 2007) that supports a diverse community of cetacean species as well as an array of human activities including commercial fishing, shipping and naval operations. The intersection

between cetacean and human use of the CCE has resulted in entanglements in fishing gear (Julian and Beeson, 1998; Carretta et al., 2004), ship strikes (Berman-Kowalewski et al., 2010; Redfern et al., 2013) and disturbance from anthropogenic sound (McDonald et al., 2006; Hildebrand, 2009; Goldbogen et al., 2013).

Cetacean density and distribution off southern California during summer and fall has been estimated for several cetacean species using ship-based line-transect surveys and mark-recapture photo-identification methods (Calambokidis and Barlow, 2004; Barlow and Forney, 2007). Limited sampling during winter and spring months (e.g. Forney and Barlow, 1998) as well as multi-year gaps between ship-based surveys (e.g. Barlow and Forney, 2007; Barlow, 2010) restricts the ability to quantify long-term cross-seasonal and inter-annual trends in cetacean density and distribution. Cetacean distribution and abundance patterns based

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on a subset of the data used in the current study (July 2004–April 2008) were recently reported by Douglas et al. (2014). The present study provides new and current estimates of cetacean density for the six most commonly encountered cetacean species off southern California based on sighting data collected during 37 quarterly CalCOFI cruises from 2004 to 2013. The current study resulted from a high survey repetition rate that allowed for the examination of inter-annual and seasonal trends in density as well as temporal and spatial patterns of distribution for six common cetacean species off southern California: blue whales, fin whales, humpback whales, short-beaked common dolphins, Pacific white-sided dolphins, and Dall's porpoise.

2. Methods

2.1. Data collection

Visual monitoring for cetaceans on CalCOFI cruises incorporated standard line-transect marine mammal survey protocol (Buckland et al., 1993; Barlow, 1995; Barlow and Forney, 2007). Two trained marine mammal observers utilized 7×50 Fujinon binoculars to sight all cetaceans encountered during daylight transits between CalCOFI stations (Fig. 1). Information on all cetacean sightings was logged systematically, including species, group size, reticle of cetacean position relative to the horizon, relative angle from the bow, latitude, longitude, ship's heading, behavior, sighting cue, sea state, swell height, visibility and comments. Survey effort was curtailed in sea state Beaufort 6 or higher, or when visibility was reduced to less than 1 km. The vessel did not alter course for species identification or group size estimates; however, either 25×150 or 18×50 power binoculars were available to better assess these metrics after the initial sighting was made using the 7×50 binoculars (Soldevilla et al., 2006).

Surveys were conducted using five research vessels: the Scripps Institution of Oceanography (SIO) 84-m RV *Roger Revelle*

(2 surveys) and the 52-m RV *New Horizon* (20 surveys); and National Oceanic and Atmospheric Administration (NOAA) ships the 52-m RV *David Starr Jordan* (8 surveys), the 63-m RV *Bell M. Shimada* (4 surveys), and the 62-m RV *McArthur II* (1 survey). Survey speeds ranged from 18.5 to 22.2 km/h and observer heights above sea level ranged from 8.1 to 17 m. Surveys were conducted quarterly; however, there was some temporal variation in the timing of the cruises across the nine-year study. Winter cruises were conducted during the months of January and February, spring surveys occurred during March, April and May, summer cruises occurred in June, July and August, and fall surveys were conducted during the months of October and November. Surveys were conducted during all four seasons of each year from 2004 to 2013 inclusive, with the exception of winter and spring 2004, and spring 2010.

Line-transect marine mammal surveys have typically been conducted using either “passing” or “closing” modes. “Passing mode” surveys necessitate that the vessel stay on the track line without diverting course for a closer investigation of groups detected, while “closing mode” surveys allow the vessel to divert course to the vicinity of a visual detection (Barlow, 1997). Due to the experimental design of the oceanographic sampling component of the CalCOFI program, all marine mammal survey effort in the current study was conducted in “passing mode,” which provides less biased estimates of encounter rates (because effort is continuous) but results in more unidentified or mis-identified groups, more biased estimates of group size, and less precise species percentages than closing mode (Barlow, 1997). Buckland et al. (2001) noted that while closing mode surveys allow for better resolution of species identification and group size, closing mode surveys can create a negative bias in density estimates.

Density and abundance estimates were calculated exclusively for the southern CalCOFI study area; this region encompasses the area delimited by six parallel survey lines running southwest to northeast from San Diego to north of Point Conception (Fig. 1). The lines increase in length from north to south (470–700 km), with stations occurring every 37 km in coastal and continental shelf waters inshore of the 2000 m isobath, and every 74 km offshore (Fig. 1). The lines are laid out such that they are roughly perpendicular to the coast and shelf. The study area is defined by a polygon around the six southern CalCOFI lines and extends one-half the distance between CalCOFI lines (32 km) south of line 93 and north of line 77, for a total area of 238,494 km² (Fig. 1).

Sightings were required to be both “on-effort” and “on-transect” to be included in the analyses of distribution, density and abundance. Sightings were classified as “on-effort” when two observers were actively searching in Beaufort sea state 0–5, with the vessel travelling a minimum of 11 km/h and having visibility of at least 1 km. Sightings were classified as “on-transect” only when the ship was transiting on one of the pre-defined parallel transect lines within the CalCOFI study area (Fig. 1). Sightings were classified as “off-transect” when they occurred during south/north coastal and offshore transits between the parallel lines, transits to San Diego or other ports and during deviations from the primary transect lines due to naval operations or bad weather.

To assess any potential bias associated with comparing annual or seasonal cetacean densities using models that have common detection function parameters, we tested for differences in two key variables that can potentially affect detection probabilities: sea state and group size (Barlow and Forney, 2007). For each variable, we used one-way ANOVA with season and year as factor covariates; for group size we used a log transformation and for sea state we weighted each season-year combination by the survey effort in each sea state. These analyses were conducted using the UNIANOVA command in SPSS version 17 (SPSS Inc. Chicago, IL).

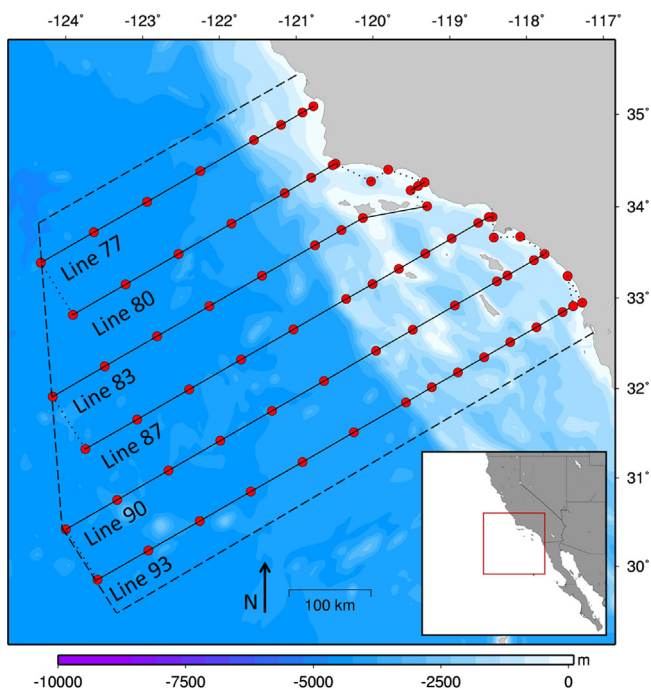


Fig. 1. CalCOFI transect lines and sampling stations in the southern CalCOFI study area. Dotted routes show “off-effort” connector lines between the six main transects. Dashed polygon represents entire study area of 238,494 km².

2.2. Estimation of density by survey

Distance sampling techniques (Buckland et al., 2001; Marques and Buckland, 2003; Marques et al., 2007) were used to estimate density and abundance by survey for six species: blue whales, fin whales, humpback whales, short-beaked common dolphins, Pacific white-sided dolphins and Dall's porpoise. The analyses involved five stages: (1) modeling the detection function and estimating effective strip width; (2) obtaining estimates of trackline detection probability; (3) estimating average school size; (4) estimating density (and abundance); and (5) estimating variance in density. All calculations were performed using the software Distance 6.2 (Thomas et al., 2010).

2.2.1. Effective strip width

Each of the six species analyzed met the recommended minimum of 60 “on-effort” and “on-transect” sightings (prior to truncation) for the development of a robust detection function, pooling sightings data across all surveys. The species-specific detection functions allowed for capturing species differences in detection probabilities inherent from differences in school size, body size, behavior, surfacing patterns, and potential reaction to the survey vessel (Buckland et al., 2001). Preliminary detection functions were fit using just perpendicular distance as a covariate (i.e., conventional distance sampling, CDS) and examined to determine, for each species, a truncation distance that utilized the least amount of truncation but maintained an estimated detection probability at the truncation point of approximately 0.1 or greater (Buckland et al., 2001). This process suggested similar truncation distances at $w=2400$ m for fin, blue and humpback whales while $w=600$ m was selected for common and Pacific white-sided dolphins and $w=700$ m for Dall's porpoise (Table 1).

Detection function modeling was then undertaken using the multiple covariate distance sampling (MCDS) framework (Marques and Buckland, 2003; Marques et al., 2007)—i.e., modeling probability of detection as a function of perpendicular distance and additional potential covariates. This allowed for variation in detectability between surveys, according to the covariate values. The covariates tried were Beaufort sea state (numerical: 0–5), ship (categorical), swell (numerical: wave height in m), school size (numerical), and, for short-beaked common dolphins, school size class (categorical) which was defined as greater or less than 20 individuals (Barlow and Forney, 2007). While there is the potential for differences between observers, because over 25 different observers participated in the current study, this potential covariate was excluded from analysis due to sample size limitations. The basic building blocks for modeling were the half-normal and hazard-rate key functions, with the additional covariates added in a forward stepwise fashion. Polynomial or cosine expansion terms were also considered for addition at each stage of the modelling. At each stage the model that minimized the value of

the Akaike Information Criterion (AIC, Akaike, 1974; Buckland et al., 2001) was selected, unless behavioral observations and/or the observed distribution of distances indicated a problem with vessel attraction, in which case the model that we felt best reflected the relationship between the probability of detection and distance for that species was subjectively selected. Goodness-of-fit was assessed by viewing quantile–quantile plots, and using Kolmogorov–Smirnov tests. Once a final detection function model was selected, it was used to the estimate effective strip width applying to each observation, as described by Marques et al. (2007).

For short-beaked common dolphins, the covariate school size class was retained in the model with the lowest AIC score. The current version of Distance does not allow stratification (i.e., estimation of density by survey) when a cluster size variable such as school size class is retained as a covariate. Therefore, we split the common dolphin sample into two analyses: small schools and large schools. Detection functions were fit separately for each school size class and density was estimated independently for small and large schools. Estimated densities for each class were then summed to give density for the species.

2.2.2. Trackline detection probability

Due to experimental design constraints, it was not possible to measure the probability of detection directly on the transect line, or g_0 , in the current study. Therefore g_0 values previously estimated for cetaceans in the CCE (Barlow and Forney, 2007) were applied to the current study: a value of 0.921 was used for blue, fin and humpback whales, 0.856 for Pacific white-sided dolphins, and 0.822 for Dall's porpoise; values of 0.856 and 0.970 were used for common dolphins of school size ≤ 20 and > 20 , respectively.

2.2.3. Average school size

In many cetacean surveys there is “size bias”—i.e., over-sampling of large schools because they are easier to detect than small schools. This was accounted for by including school size as a potential covariate in the detection function. Had school size been selected, an alternative density estimation formula would be required than the one we used (below)—see Marques et al. (2007). However, school size was not selected, and we therefore took the mean observed school size for each species, pooled over surveys, as an estimate of population average school size, except for common dolphins where we estimated mean school size separately for schools ≤ 20 and those > 20 .

2.2.4. Density and abundance

Density was estimated according to the equation

$$\hat{D}_v = \frac{\bar{s}}{2L_v \hat{g}_0} \sum_{i=1}^{n_v} \frac{1}{\hat{\mu}(z_i)}$$

Table 1

Truncation distance (w), fitted detection function model, covariates(Cov) retained in detection model, Kolmogorov–Smirnov goodness-of-fit test p -value (K–S p), trackline detection probability (g_0), mean effective strip width ($\hat{\mu}$) and corresponding percentage coefficient of variation for the species analyzed.

Species	w (m)	Model ^a	Cov ^b	K–S p	g_0	Mean $\hat{\mu}$ (m)	$\hat{\mu}CV$
Blue whale	2400	HnCos	ss	0.87	0.920	2400	0.09
Fin whale	2400	HnCos	ss	0.98	0.920	2498	0.06
Humpback whale	2400	HnCos	–	0.49	0.920	2586	0.08
SB common dolphin group size ≤ 20	600	HrSim	ss	0.88	0.970	409	0.07
SB common dolphin group size > 20	600	HrSim	ss	0.93	0.856	559	0.07
PWS dolphin	600	HnCos	–	0.11	0.856	608	0.09
Dall's porpoise	700	HnCos	–	0.25	0.822	800	0.09

^a Hn=half normal key; Hr=hazard rate key, Cos=cosine expansion term; Sim=simple polynomial expansion term.

^b ss=sea state.

where \hat{D}_v is the estimated density for a particular species for survey v ($v = 1, \dots, 37$), L_v is the total on-effort line length for the survey, \bar{s} is the mean observed school size, \hat{g}_0 is the estimated trackline detection probability, n_v is the number of sightings of the species in the survey, and $\hat{\mu}(z_i)$ is the estimated effective strip width (ESW) for the species given covariates z_i recorded on the i th detected group. For common dolphins, density was estimated separately for each school size class and then summed across classes to get a species total. Abundance, was estimated as density multiplied by the study area size of 238,494 km².

2.2.5. Variance estimation

Analytic expressions exist to estimate variance for density estimates by survey (Marques and Buckland, 2003) and are implemented in Distance. However, one goal of the analysis was to estimate average density over season and year (see the next section); this involves averaging the survey-specific estimates, which are not independent since they share common detection function parameters (as well as having the same mean school size and trackline detection probability). A straightforward and robust approach to variance and confidence interval estimation in such situations is a non-parametric bootstrap (Davison and Hinkley, 2006), also implemented in Distance. We therefore generated 5000 bootstrap resample datasets, using as the resampling unit all transects completed on a given day, and used these to estimate 5000 bootstrap density estimates for each survey. Data dependence between one sampling unit and the next is greatly reduced due to the cessation of observations during the overnight break (Buckland et al., 2001). These resamples were used to calculate variance and related quantities in averaged estimates of density, as detailed in the next section.

2.3. Estimation of average seasonal and annual densities and population trends

A statistical model was fit to the estimates of density by survey, and used to predict density by season and time, for two reasons. First simple averages of the estimates by season and year may be misleading if there are seasonal or annual patterns in density, since there were two years in which not all seasons were surveyed. Second, one goal of the analysis was to estimate long-term trends in density. All analyses were performed in R 3.1.0 (R project for statistical computing, <http://r-project.org/>). We used a generalized additive model (GAM, Wood, 2006) with estimated density as the response variable, assumed quasi-Poisson, a log link function, and explanatory variables season (as a factor) and year (as a smooth, specifically a penalized thin-plate regression spline with basis dimension 5—written $s(\text{year}, \text{bs} = "ts", k = 5)$ in the R mgcv package).

The fitted model was used to estimate mean density over all years, mean density by season over all years and pairwise differences in density between seasons. Estimated trend was displayed graphically by plotting the fitted smooth. It is also useful to summarize the trend as a single number, and this was done by calculating the average annual population change, expressed as a percentage—i.e., $\left(1 - \left[\frac{\hat{D}_{2013} - \hat{D}_{2004}}{9}\right]\right) \times 100$.

Variances and confidence intervals on all of the above quantities were calculated by repeating the modelling with each of the 5000 bootstrap density estimates. In each bootstrap replicate, we calculated mean density over all years, mean density by season over all years, pairwise differences in density between seasons and the estimated trend. Variance on each quantity was then estimated as the sample variance of the bootstrap estimates. Confidence intervals were calculated from the bootstrap estimates using the percentile method (Davison and Hinkley, 2006)—e.g., for a 95% confidence

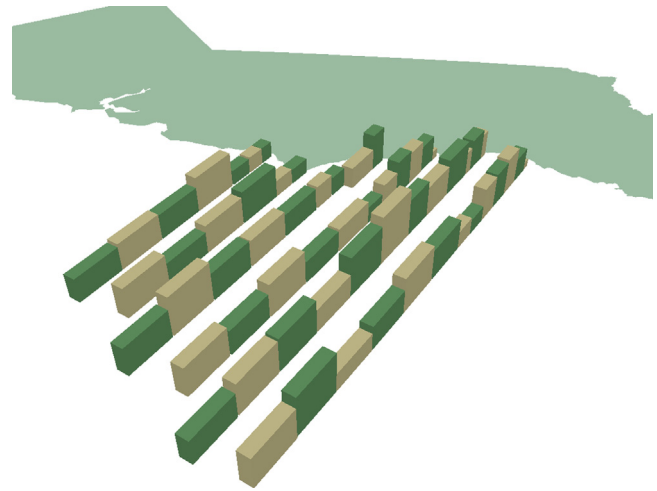


Fig. 2. Three-dimensional illustration of transect lines surveyed while “on-effort” during 37 CalCOFI cruises from July 2004 to November 2013. Alternating colors show the individual survey segments between sampling stations. Height of blocks depicts the number of times a given transect was surveyed over the course of the study with a range of 14–33 occasions. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

interval the 2.5th and 97.5th percentile of the bootstrap estimates was used.

Density estimates and associated measures of uncertainty for the combined summer and fall seasons were calculated based on the mean of the summer and fall bootstrap estimates to facilitate direct comparisons with previous surveys conducted off southern California. A bootstrap resampling procedure (detailed below) was used to compare the estimated densities from the current study to the pooled 1991–2005 surveys (Barlow and Forney, 2007) as well as the pooled 1991–2008 surveys (Barlow, 2010) off southern California. We generated 5000 bootstrap density estimates by sampling from a lognormal distribution with log-mean equal to the natural logarithm of the relevant comparison density estimate, and log-variance derived from the reported coefficient of variation (CV) of the density estimate:

$$\text{var}(\ln(\hat{D})) = \ln(1 + \text{CV}^2)$$

The resulting values were back-transformed by first subtracting half the log-variance and then exponentiating. Each of the 5000 bootstrap comparison density estimates was paired with a bootstrap density estimate from the current study, and the differences computed. These differences were used to compute a confidence interval on the difference in estimated density between the current and comparative studies, again using the percentile method. If the 95% confidence interval on the difference did not contain zero, the comparison was statistically significant.

3. Results

3.1. Survey effort and summary of sightings

Thirty-seven surveys conducted between July 2004 and November 2013 produced 526 days where “on-effort” and “on-transect” criteria were met for a total of 42,874 km of active line-transect sampling along the track-lines (Fig. 2)¹. Overall on-effort survey effort was relatively consistent across the four seasons, totaling 9668 km over 131 days surveyed in winter, 8681 km across 107 days in spring, 14,052 km over 149 days in summer,

¹ Archived visual data can be accessed at oceaninformatics.ucsd.edu/datazoo.

and 139 days covering 10,473 km during fall surveys (Table 2). The mean sea state ranged from 2.86 to 3.76 for all seasons and years surveyed, and there was no statistically significant difference in sea state between any possible combination of seasons ($p=0.892$) or years ($p=0.978$, effort-weighted ANOVA) (Table 2).

Table 2

Annual and seasonal survey effort in lengths of lines surveyed in calm (sea state 0–2) and moderate (sea state 3–5) conditions and for both calm and moderate conditions pooled. Mean sea state and standard deviation weighted by effort for each year and season where cetacean densities were estimated.

Year/ season	Length of transects surveyed (km)			Weighted mean sea state	SD
	Calm sea state 0–2	Moderate sea state 3–5	Total sea state 0–5		
2004	385	1,989	2,374	3.65	1.21
2005	1,514	3,107	4,621	3.08	1.37
2006	2,100	3,516	5,616	3.09	1.41
2007	1,771	2,646	4,417	3.24	1.59
2008	1,863	2,295	4,158	2.86	1.49
2009	1,620	3,424	5,044	3.30	1.55
2010	586	2,594	3,181	3.24	1.17
2011	1,022	3,625	4,631	3.76	1.34
2012	1,007	3,152	4,159	3.51	1.36
2013	871	3,802	4,673	3.69	1.39
Winter	3,868	5,800	9,668	3.02	1.45
Spring	1,920	6,760	8,681	3.61	1.34
Summer	3,280	10,772	14,052	3.51	1.31
Fall	3,681	6,792	10,473	3.14	1.41

Table 3

Sighting data from the six most frequently sighted cetacean species in the southern CalCOFI study area across 37 surveys from summer 2004–fall 2013. n_s =number of sightings; n_i =number of individuals.

Species	On effort/on transect		Off effort/off transect		Total	
	n_s	n_i	n_s	n_i	n_s	n_i
Blue whale	79	122	57	113	136	235
Fin whale	177	331	85	131	262	462
Humpback whale	68	120	124	229	192	349
SB common dolphin	278	22,226	159	14,993	437	37,219
PWS dolphin	62	1128	45	896	107	2,024
Dall's porpoise	91	614	51	281	142	895
Total	755	24,541	519	16,404	1274	40,945

Table 4

Annual and seasonal mean group sizes by species for all groups after truncation. Mean group size (\bar{x}) and associated coefficient of variation (CV) for all species analyzed. For species with no more than one sighting in a given strata, CV could not be calculated.

Year/season	Species					
	Blue whale \bar{x} (CV)	Fin whale \bar{x} (CV)	Humpback whale \bar{x} (CV)	SB common dolphin \bar{x} (CV)	Pacific white-sided dolphin \bar{x} (CV)	Dall's porpoise \bar{x} (CV)
2004	1.3 (0.38)	1.9 (0.68)	1.9 (0.37)	73.3 (1.30)	9.2 (1.44)	– (–)
2005	1.4 (0.50)	2.3 (0.98)	3.2 (0.77)	118.8 (2.15)	9.0 (1.05)	6.3 (0.74)
2006	1.2 (0.36)	1.3 (0.48)	1.4 (0.38)	56.5 (1.36)	14.7 (1.33)	5.1 (0.57)
2007	– (–)	2.0 (0.00)	1.3 (0.38)	54.5 (1.34)	19.8 (1.13)	4.6 (0.61)
2008	1 (–)	1.4 (0.56)	1.9 (0.44)	22.5 (1.98)	12.6 (0.92)	4.8 (0.56)
2009	1.2 (0.35)	1.2 (0.35)	1.8 (0.22)	39.5 (1.58)	– (–)	5.8 (0.48)
2010	1.4 (0.38)	4.2 (1.84)	1.0 (0.00)	180.9 (1.78)	– (–)	– (–)
2011	3.0 (1.77)	1.4 (0.43)	1.7 (0.69)	89.1 (1.16)	16.4 (0.76)	11.4 (0.41)
2012	1.3 (0.37)	1.6 (0.58)	1.3 (0.40)	79.7 (1.42)	23.0 (0.00)	8.9 (0.94)
2013	1.8 (0.54)	1.6 (0.59)	1.8 (0.57)	101.2 (2.08)	127 (1.36)	7.7 (0.84)
Winter	– (–)	1.8 (0.54)	1.9 (0.60)	105.4 (2.02)	15.1 (1.21)	6.5 (0.68)
Spring	– (–)	1.5 (0.41)	1.7 (0.44)	73.6 (1.54)	12.0 (1.15)	6.0 (0.74)
Summer	1.6 (0.50)	1.9 (1.9)	1.5 (0.50)	56.2 (2.05)	35.0 (2.07)	– (–)
Fall	1.4 (1.45)	1.8 (0.64)	2.1 (0.80)	61.7 (1.37)	17.9 (1.11)	8.7 (0.83)
Overall	1.5 (2.13)	1.8 (1.54)	1.8 (0.59)	70.6 (2.10)	18.2 (1.96)	6.2 (0.72)

For the six focus species in the current study, a total of 1276 visual detections were made with 755 (59%) of them meeting both the “on-effort” and “on-transect” criteria for inclusion in the density analysis (Table 3). Comparisons of log-transformed group size values indicated there was a significant difference in common dolphin group size by year ($p=0.02$, $F=1.92$, ANOVA) but no other statistically significant differences for all species with all possible season and year combinations were revealed (Table 4).

Blue whales exhibited strong variations in seasonal occurrence with most sightings during the summer (Fig. 3). The summer distribution of blue whales extended throughout coastal, shelf and offshore waters, while fall distribution was primarily over the western portion of the continental shelf and in offshore regions. Blue whales also exhibited spatial variations in their distribution;

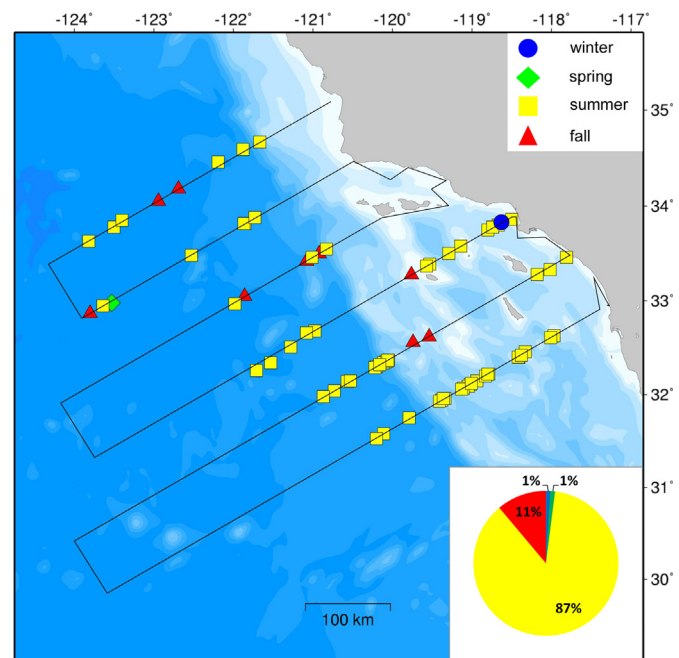


Fig. 3. On-effort visual detections of blue whales by season in the CalCOFI study area from 2004 to 2013. Pie chart shows percentage of sightings that occurred in each of the four defined seasons: winter=blue, spring=green, summer=yellow and fall=red. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

this species was observed throughout coastal, continental shelf and offshore waters in the southern half of the study area whereas, in the northern half of the study area, sightings were made exclusively in offshore waters (Fig. 3).

Fin whale occurrence varied seasonally with the majority of sightings in summer and fall; however, the species was present off southern California throughout the year (Fig. 4). The distribution of fin whales in the study area also varied with season. During winter and spring, the majority of sightings occurred in continental shelf waters within the southern half of the study area whereas summer and fall sightings were more widely distributed with the greatest concentrations offshore and in the northern portion of the study area along the northern-most survey line (Fig. 4).

Humpback whales were present in the study area throughout the year; however, occurrence varied as a function of season with greater numbers of sightings during spring and fall (Fig. 5). The distribution of sightings also changed seasonally. During spring, summer and fall cruises, humpback whales were generally distributed in coastal and shelf waters with the largest concentration occurring in relatively shallow waters, north of Point Conception. During winter cruises, the distribution of humpback sightings shifted to exclusively shelf and offshore waters with several sightings in deep pelagic waters, more than 200 km from shore (Fig. 5).

Short-beaked common dolphins were present in the study area throughout the year; however, occurrence patterns varied as a function of season with the greatest number of sightings during summer and relatively few sightings during spring (Fig. 6). The distribution of sightings also changed seasonally. Short-beaked common dolphins were seen throughout the study area during summer and fall, with the exception of coastal waters off Point Conception. The species distribution during winter and spring was limited to the southern half of the study area, with the majority of winter sightings occurring in pelagic waters off the continental shelf (Fig. 6).

Pacific white-sided dolphins were present in the study area throughout the year; however, occurrence patterns varied as a function of season with the majority of sightings occurring in winter and spring (Fig. 7). The distribution of sightings also changed seasonally. Pacific white-sided dolphins were seen throughout the study area during winter and spring, while

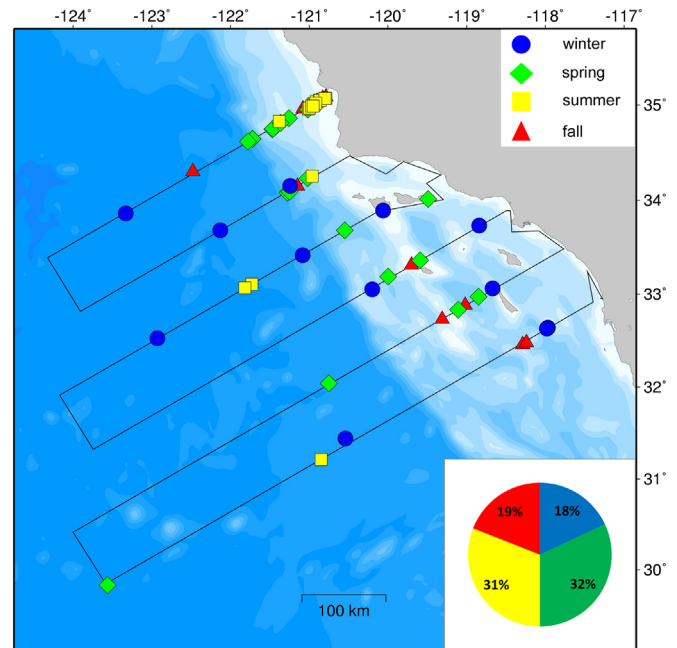


Fig. 5. On-effort visual detections of humpback whales by season in the CalCOFI study area from 2004 to 2013. Pie chart shows percentage of sightings that occurred in each of the four defined seasons: winter=blue, spring=green, summer=yellow and fall=red. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

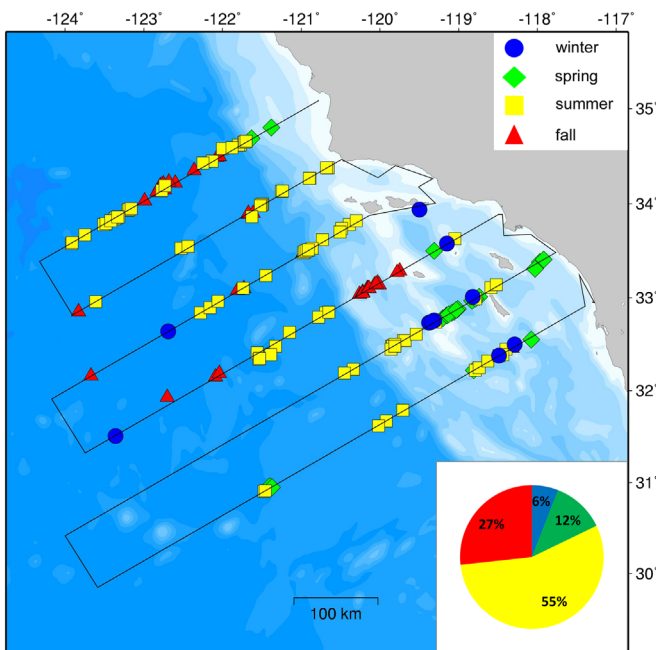


Fig. 4. On-effort visual detections of fin whales by season in the CalCOFI study area from 2004 to 2013. Pie chart shows percentage of sightings that occurred in each of the four defined seasons: winter=blue, spring=green, summer=yellow and fall=red. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

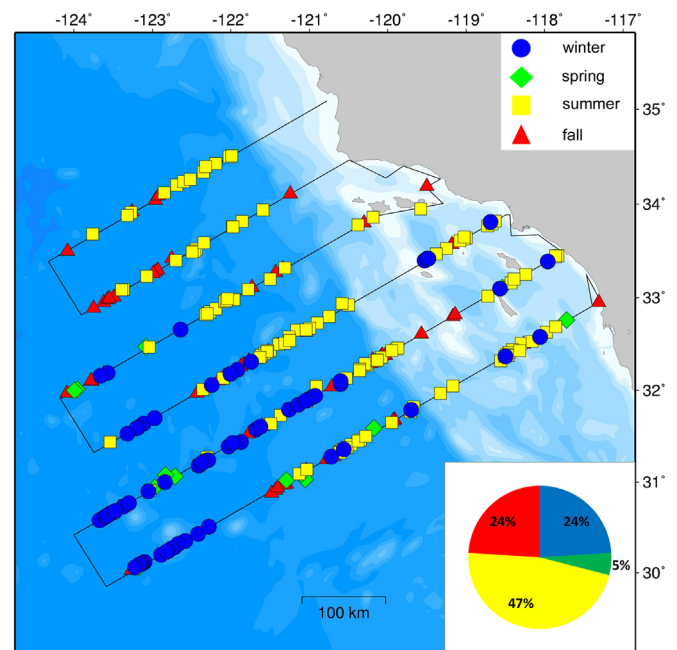


Fig. 6. On-effort visual detections of short-beaked common dolphins by season in the CalCOFI study area from 2004 to 2013. Pie chart shows percentage of sightings that occurred in each of the four defined seasons: winter=blue, spring=green, summer=yellow and fall=red. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

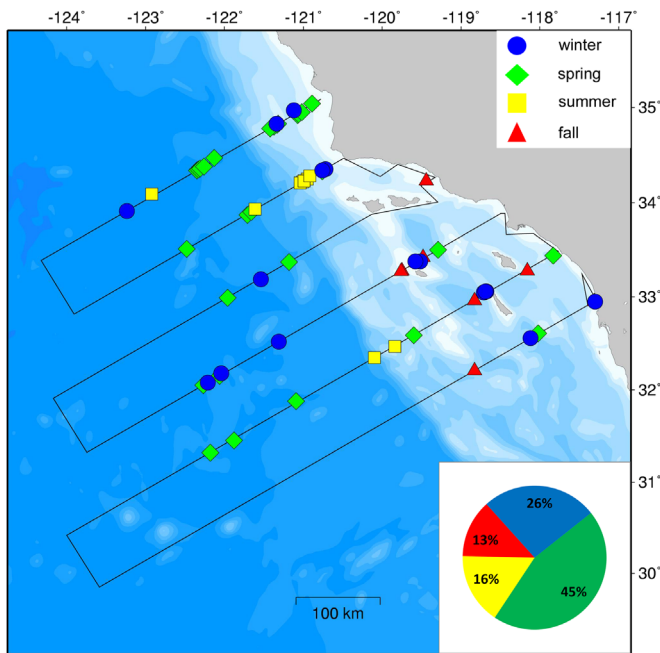


Fig. 7. On-effort visual detections of Pacific white-sided dolphins by season in the CalCOFI study area from 2004 to 2013. Pie chart shows percentage of sightings that occurred in each of the four defined seasons: winter=blue, spring=green, summer=yellow and fall=red. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

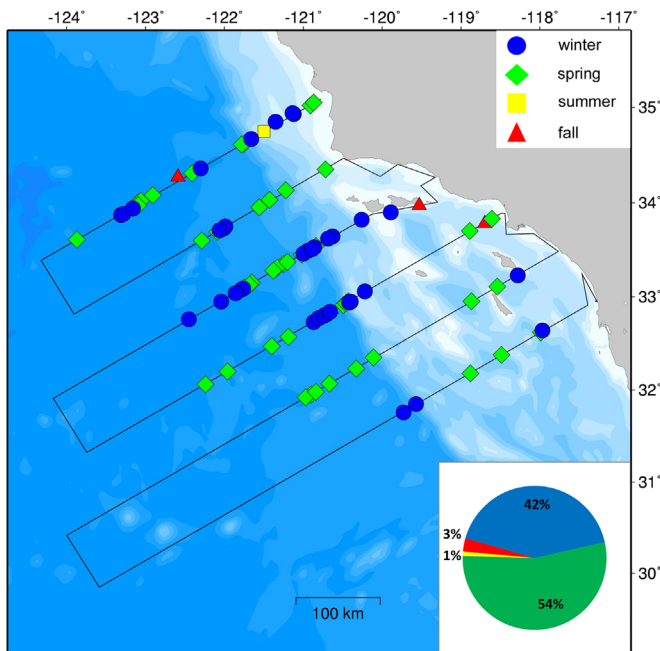


Fig. 8. On-effort visual detections of Dall's porpoise by season in the CalCOFI study area from 2004 to 2013. Pie chart shows color coded percentage of sightings that occurred in each of the four defined seasons: winter=blue, spring=green, summer=yellow and fall=red. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

distribution during fall was limited to coastal and shelf waters in the southern half of the study area; the majority of summer sightings occurred near the shelf edge and in pelagic waters (Fig. 7).

Dall's porpoise displayed distinct differences in seasonal occurrence patterns with the great majority of sightings occurring during winter and spring (Fig. 8). There was no apparent difference in the distribution of sightings between winter and spring.

Overall, Dall's porpoise distribution extended from coastal waters out to approximately 250 km from shore with a lower concentration of sightings in the southern portion of the study area, and few sightings along the southern-most survey line (Fig. 8).

3.2. Density and abundance estimation

The lowest AIC detection function for blue, fin and humpback whales was a half-normal with a cosine adjustment and with sea state as an additional covariate for blue and fin whales (Table 1, Fig. 9); for short-beaked common dolphins, hazard rate with a simple polynomial adjustment term and with sea state and group size class as additional covariates (Table 1, Fig. 9). The lowest AIC model for Pacific white-sided dolphin and Dall's porpoise was the hazard-rate model with simple polynomial adjustment. However, these fits gave unrealistic detection functions with a sharp "spike" in detectability at small distances, and detection probability declining to 0.5 at 50 m and 150 m, respectively. The pattern in observed distances causing these fits to be selected may be due to responsive movement for these two species which has been observed in previous studies (e.g. Turnock and Quinn, 1991; Williams and Thomas, 2007) and we follow other authors (e.g., Williams and Thomas, 2007) in restricting the candidate model set to half-normal models in these cases. Previous studies off southern California (Gerrodette and Focada, 2005; Barlow and Forney, 2007) have demonstrated that half-normal models are more robust and tend to have fewer convergence issues.

Blue whales were the second most frequently encountered baleen whale species with an overall density estimate of 0.91 animals per 1000 km² (CV=0.27) (Table 5). Annual estimates of blue whale densities from 2004 to 2013 ranged from a low of 0.11 (CV=1.19) in 2007 to a peak of 1.70 (CV=0.71) in 2009 (Table 6, Fig. 10). Despite the variations in annual density estimates, the mean annual population change rate of -2.88% (95% CI = -17.72% +8.72%) was not significant, indicating stable numbers in the study area over the 10-year period (Fig. 10). Seasonally, blue whales were significantly more abundant in summer than fall, as well as winter or spring when the species was virtually absent from the study area (Table 7, Fig. 11—dashed lines join seasonal estimates where 95% confidence intervals on the difference in density between seasons span zero). The summer/fall density estimate of 1.74/1000 km² (CV=0.26) blue whales in the CalCOFI study area was not statistically significantly different from the estimate of 2.64/1000 km² (CV=0.20) from pooled 1991–2005 surveys (Barlow and Forney, 2007) (difference -0.90/1000 km², 95% CI = -3.20–0.48), or the estimate and 2.33/1000 km² (CV=0.27) reported from pooled 1991–2008 surveys off southern California (Barlow, 2010) (difference -0.59/1000 km², 95% CI = -3.68–0.60).

Fin whales were the most frequently encountered and the most abundant baleen whale in the CalCOFI study area with an overall density estimate of 2.73 animals per 1000 km² (CV=0.19) (Table 5). Annual estimates of fin whale densities from 2004 to 2013 ranged from a low of 0.98 (CV=0.59) in 2007 to a peak of 5.31 (CV=0.32) in 2011 (Table 6, Fig. 10). The mean annual population change rate of +6.8% (95% CI = -0.3%–20.6%) suggested a positive increase; however, this change was not significant because the 95% confidence interval spanned zero (Fig. 10). Seasonally, fin whales were significantly more abundant during summer and fall versus winter and summer versus spring (Table 7, Fig. 11). The summer/fall density estimate of 4.24/1000 km² (CV=0.21) fin whales in the CalCOFI study area is significantly greater than both the estimate of 1.13/1000 km² (CV=0.40) from pooled 1991–2005 surveys (Barlow and Forney, 2007) (difference 3.11/1000 km², 95% CI = 1.10–3.69), and the estimate and 1.56/1000 km² (CV=0.27) reported from pooled

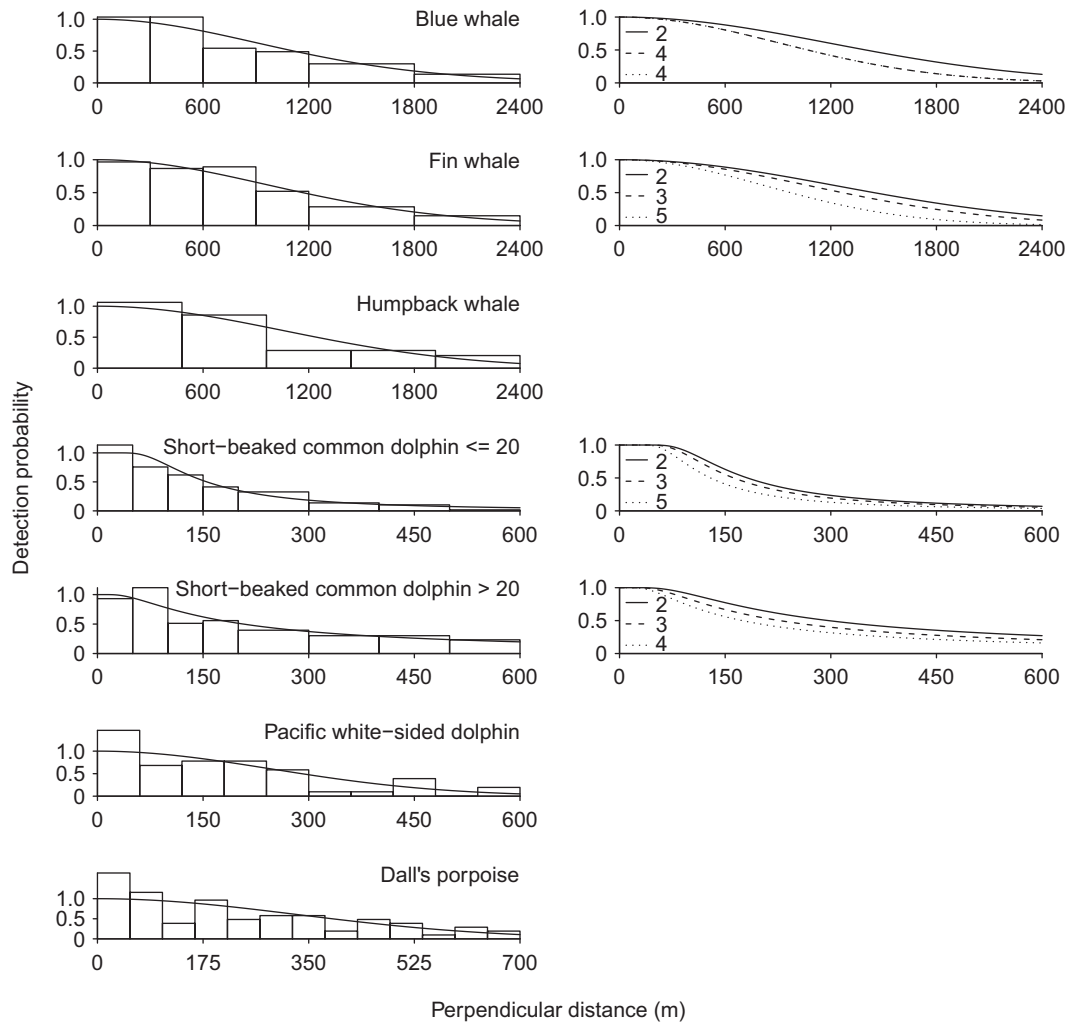


Fig. 9. Average estimated detection functions superimposed over scaled histograms of observed perpendicular distances (left side) for models used to calculate density estimates, and example detection functions plotted at the 25th, 50th and 75th percentile of the sea state covariates for models that include sea state (right side) for each of the six species analyzed. Short-beaked common dolphins were divided into small (≤ 20) or large (> 20) group size classes.

Table 5
Average abundance and density estimates for each of the six species analyzed, calculated as the means of predicted values for all years and seasons from the GAM analysis. Total numbers of sightings after truncation (n), density/1000 km² (D), 95% confidence interval of density estimate, cetacean abundance (N), 95% confidence interval of abundance. Coefficients of variation (CV) are the same for abundance and density estimates.

Species	n	D	95%CI(D)	N	95%CI(N)	CV
Blue whale	73	0.91	0.58–1.54	217	139–366	0.27
Fin whale	166	2.73	1.90–3.95	650	452–940	0.19
Humpback whale	66	1.17	0.66–1.65	278	157–392	0.21
SB common dolphin	239	705.83	430.30–1039.62	167,988	102,340–247,282	0.22
PWS dolphin	52	51.98	22.71–77.07	12,371	5,404–18,342	0.27
Dall's porpoise	77	21.37	12.20–27.94	5,086	2,903–6650	0.19

1991–2008 surveys off southern California (Barlow, 2010) (difference 2.68/1000 km², 95% CI=1.30–3.63).

Humpback whales were the third most frequently encountered baleen whale in the CalCOFI study area with an overall density estimate of 1.17 per 1000 km² (CV=0.21) (Table 5). Annual estimates of humpback whale densities from 2004 to 2013 ranged from a low of 0.43/1000 km² (CV=0.59) in 2011 to a peak of 2.62/1000 km² (CV=0.50) in 2013 (Table 6, Fig. 10). The mean annual population change of 0.5% (95% CI=−15%–+20%) was not significant, indicating stable density over the 10-year study (Fig. 10). Humpback whale densities were not significantly different for any

seasonal combination; however, density estimates were highest during spring and lowest in fall (Table 7, Fig. 11). The summer/fall density estimate of 0.91/1000 km² (CV=0.29) humpback whales in the CalCOFI study area was significantly higher than both the estimate of 0.11/1000 km² (CV=0.51) reported from pooled 1991–2005 surveys off southern California (Barlow and Forney, 2007) (difference 0.80/1000 km², 95% CI=0.58–0.85) and the estimate of 0.15/1000 km² (CV=0.43) from the pooled 1991–2008 surveys (Barlow, 2010) (difference 0.76/1000 km², 95% CI=0.61–0.85).

Short-beaked common dolphins were the most frequently encountered cetacean in the study area with an overall density

Table 6

Annual density estimates by species. Estimated cetacean density/1000 km² (*D*), and associated coefficients of variation (CV) are presented for each of ten years pooled across seasons from 2004 to 2013. Values in bold were predicted from the GAM because they are from years where not all seasons were sampled and therefore do not have any associated variance.

Year	Species					
	Blue whale <i>D</i> (CV)	Fin whale <i>D</i> (CV)	Humpback whale <i>D</i> (CV)	SB common dolphin <i>D</i> (CV)	Pacific white-sided dolphin <i>D</i> (CV)	Dall's porpoise <i>D</i> (CV)
2004	0.91	1.91	2.42	1029.91	138.12	24.92
2005	1.15 (0.77)	2.75 (0.65)	0.78 (0.71)	711.59 (0.52)	92.84 (0.45)	23.85 (0.39)
2006	1.03 (0.37)	1.66 (0.48)	1.04 (0.49)	818.57 (0.32)	87.68 (0.56)	18.93 (0.47)
2007	0.11 (1.19)	0.98 (0.58)	0.78 (0.81)	747.22 (0.32)	44.70 (0.61)	32.47 (0.41)
2008	0.31 (0.63)	2.78 (0.31)	1.35 (0.91)	419.10 (0.34)	76.85 (0.44)	38.45 (0.37)
2009	1.69 (0.71)	1.67 (0.43)	1.02 (0.47)	789.50 (0.29)	7.07 (0.97)	24.26 (0.38)
2010	1.05	3.24	0.65	331.87	22.17	15.37
2011	1.13 (0.41)	5.31 (0.31)	0.43 (0.59)	415.76 (0.44)	36.30 (0.60)	14.14 (0.57)
2012	1.19 (0.46)	3.95 (0.46)	0.78 (0.68)	491.32 (0.37)	4.65 (1.12)	15.77 (0.57)
2013	0.57 (0.59)	3.07 (0.32)	2.62 (0.50)	1025.24 (0.33)	17.15 (1.05)	7.26 (0.74)

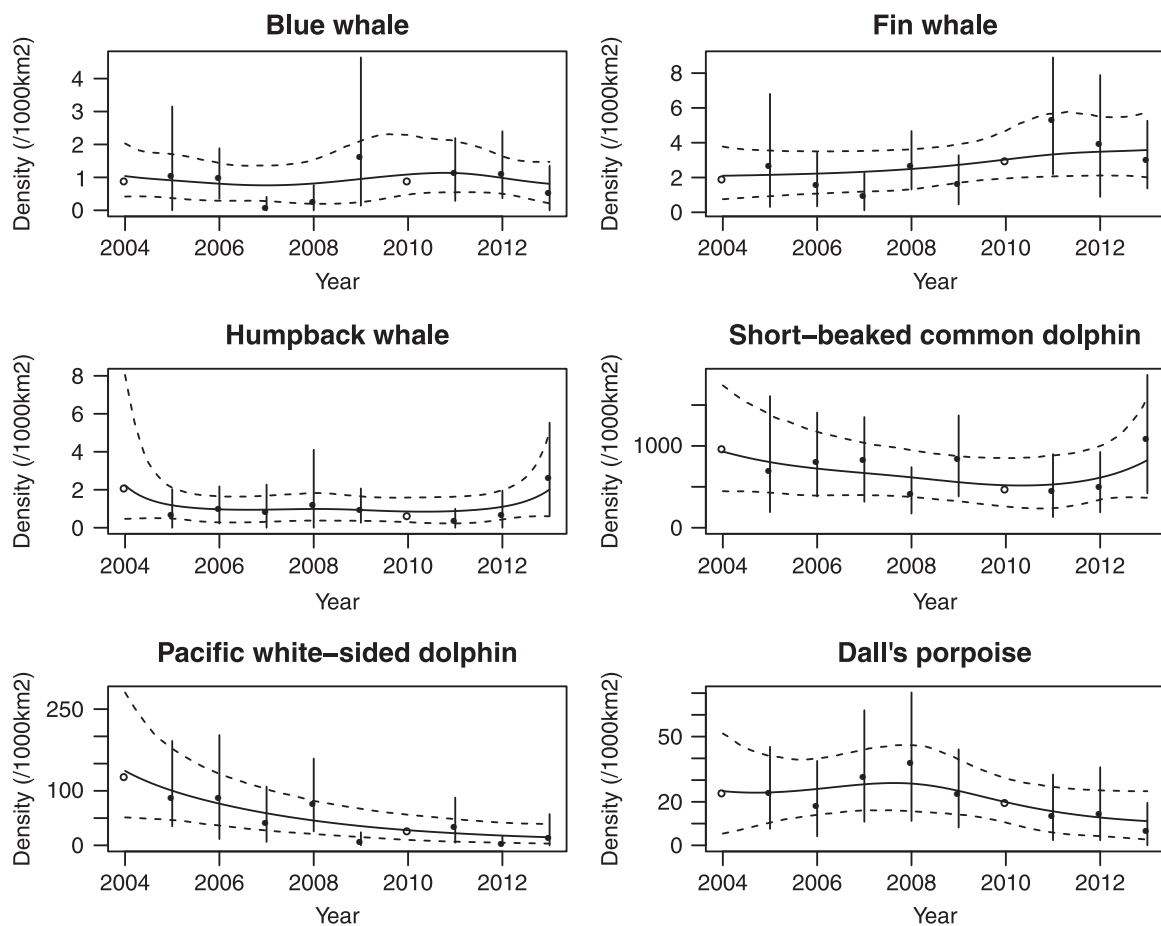


Fig. 10. Annual and long-term trend in density by species. Dots are the mean over seasons of the annual density estimates by year and vertical lines show 95% bootstrap confidence intervals, except for 2004 and 2010 where the dots are the mean of the seasonal estimates where available and the predicted values from the GAM in seasons where no survey was performed. Solid line represents the predicted long-term trend from the GAM and dashed lines represent lower and upper 95% confidence intervals.

estimate of 706 per 1000 km² (CV=0.22) (Table 5). Estimates of annual densities were calculated for each of the ten calendar years sampled and ranged from a peak of 1025/1000 km² (CV=0.34) in 2013 to a low of 419/1000 km² (CV=0.34) in 2008 (Table 6, Fig. 10). The long-term trend line suggested a decrease in short-beaked common dolphin densities from 2004 to 2009 followed by an increase from 2010 to 2013. The mean annual population change of -1.4% (95% CI = -9.61% – $+6.90\%$) was not significant, suggesting stable density for this species over the course of the ten

year study (Fig. 10). Seasonally, short-beaked common dolphins exhibited significantly higher densities in winter, summer and fall versus spring (Table 7, Fig. 11). The summer/fall density estimate of 857/1000 km² (CV=0.22) short-beaked common dolphins in the CalCOFI study area was not significantly different from either the estimate of 519/1000 km² (CV=0.19) reported from pooled 1991–2005 surveys off southern California (Barlow and Forney, 2007) (difference 338/1000 km², 95% CI = -109.50 – 599.41) or the estimate of 477/1000 km² (CV=0.17) from the pooled

Table 7
Seasonal density estimates by species. Total numbers of sightings after truncation (n), estimated cetacean density/1000 km² (D), and coefficients of variation (CV) are presented for each season pooled across ten years from 2004 to 2013.

Species	Winter			Spring			Summer			Fall		
	n	D	CV	n	D	CV	n	D	CV	n	D	CV
Blue whale	1	0.07	1.20	1	0.07	0.97	62	3.01	0.27	9	0.56	0.34
Fin whale	9	0.65	0.42	19	1.81	0.46	94	5.39	0.23	44	3.13	0.33
Humpback whale	12	1.07	0.41	22	1.92	0.51	20	1.03	0.50	12	0.82	0.43
SB common dolphin	60	947.40	0.32	11	155.70	0.45	111	902.77	0.25	59	708.12	0.28
PWS dolphin	14	70.10	0.44	23	100.56	0.36	8	18.73	0.61	7	24.93	0.51
Dall's porpoise	27	27.10	0.32	46	55.84	0.22	1	0.62	0.93	3	2.89	0.59

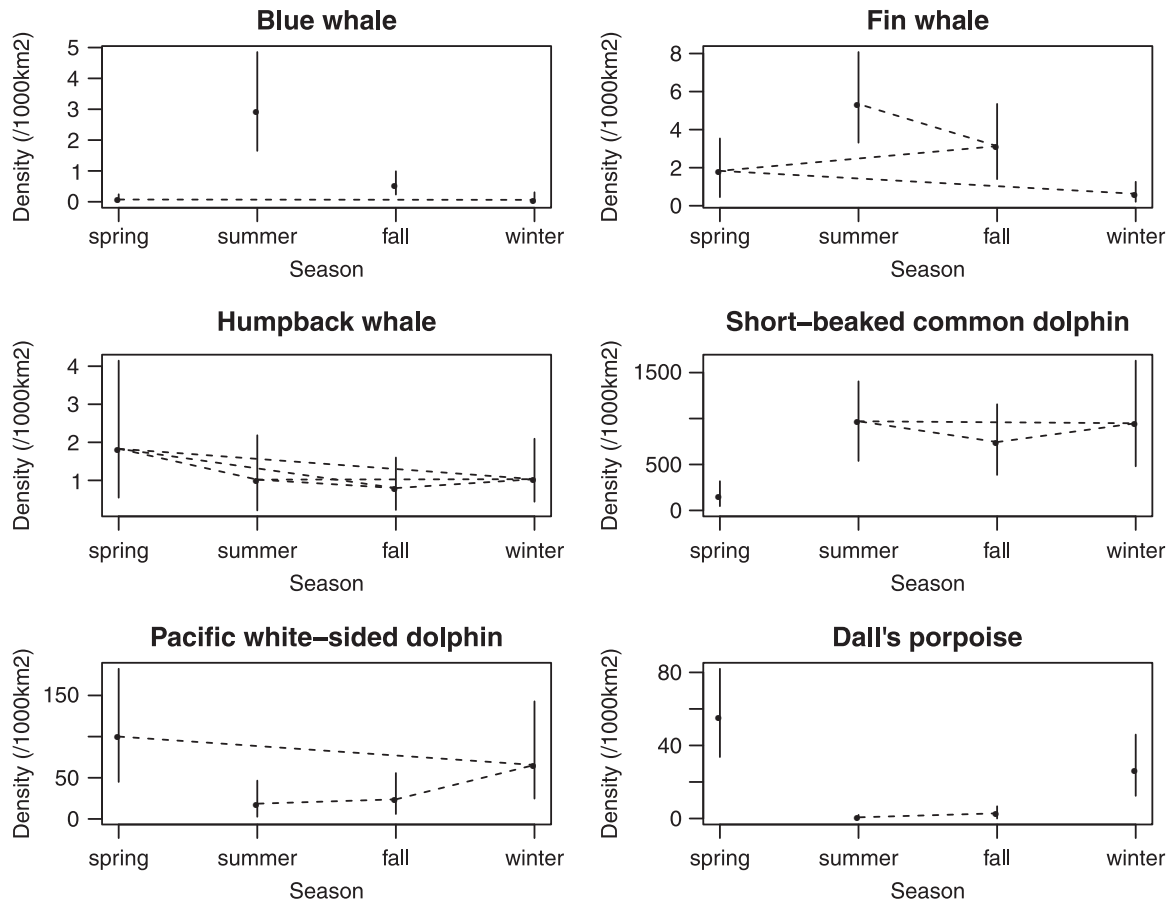


Fig. 11. Seasonal density estimates by species. Dots are the mean predicted density by season from the GAM, and vertical lines show 95% bootstrap confidence intervals. The dots are joined by a dashed line when a 95% bootstrap confidence interval on the difference in mean density between seasons includes zero.

1991–2008 surveys (Barlow, 2010) (difference 380/1000 km², 95% CI = -66.52–592.18).

Pacific white-sided dolphins were the third most frequently encountered odontocete in the study area with an overall density estimate of 52 per 1000 km² (CV=0.27) (Table 5). Estimates of annual density from 2004 to 2013 ranged from a peak of 93/1000 km² (CV=0.56) in 2005 to a low of 4.6/1000 km² (CV=1.07) in 2012 (Table 6, Fig. 10). The mean annual population change was -22.5% (95% CI = -35%–-9%), indicating a significant decrease in the number of Pacific white-sided dolphins estimated to be utilizing the study area over the last decade (Fig. 10). Seasonally, spring density was significantly higher than summer or fall (Table 7, Fig. 11). The summer/fall density estimate of 21/1000 km² (CV=0.46) Pacific white-sided dolphins in the CalCOFI study area was significantly greater than the estimate of 6.9/1000 km² (CV=0.71) reported from pooled

1991–2005 surveys off southern California (Barlow and Forney, 2007) (difference 14.3/1000 km², 95% CI = 5.15–18.69) and the estimate of 6.00/1000 km² (CV=0.39) from the pooled 1991–2008 surveys (Barlow, 2010) (difference 15.17/1000 km², 95% CI = 6.76–18.30).

Dall's porpoise were the second most frequently encountered small cetacean in the study area with an overall density estimate across all four seasons of 21.4 per 1000 km² (CV=0.19) (Table 5). Estimates of annual density ranged from a peak of 38.4/1000 km² (CV=0.39) in 2008 to a low of 7.3/1000 km² (CV=0.74) in 2013 (Table 6, Fig. 10). The mean annual population change of -8.3% (95% CI = -22.3%–+6.3%), was not significant, suggesting relatively stable density for this species over the course of the ten year study (Fig. 10). Seasonally, Dall's porpoise exhibited significantly higher densities in winter and spring versus summer and fall (Table 7, Fig. 11). The summer/fall density estimate of

1.7/1000 km² (CV=0.52) Dall's porpoise in the CalCOFI study area was not significantly different than the estimate of 2.3/1000 km² (CV=0.99) reported from pooled 1991–2005 surveys off southern California (Barlow and Forney, 2007) (difference $-0.55/1000$ km², 95% CI = -3.18 – 1.28) and the estimate of 2.0/1000 km² (CV=0.52) from the pooled 1991–2008 surveys (Barlow, 2010) (difference 0.73/1000 km², 95% CI = -2.97 – 1.25).

4. Discussion

Environmental impact assessments and management protocols for the protection of cetaceans, particularly endangered species, off southern California have primarily relied upon ship-based line-transect density estimates generated from relatively few surveys (generally every 4–5 years) conducted only during summer and fall (Barlow and Forney, 2007). The current study examines seasonal and inter-annual patterns in density, abundance and distribution with a higher rate of sampling than previous cetacean surveys off the California coast, particularly for the winter and spring periods, when there have been few recent surveys (e.g. Carretta and Forney, 1993; Carretta et al., 1993). As such, the results provided here are thought to offer a complementary and more robust baseline for management purposes and, importantly, for informing mitigation of anthropogenic disturbance (e.g. shipping and Naval operations).

Distance sampling techniques rely on a set of assumptions that, if not met, can introduce bias in resulting density estimates. One of the key assumptions is that groups present on the transect line will be detected with certainty. Due to the inherent diving behavior of cetaceans, this assumption cannot be reasonably achieved under most circumstances, resulting in the need for a correction factor that accounts for groups that were missed during the survey. Our field protocol did not allow for calculation of trackline detection probability – or g_0 – directly on the transect line; therefore, values previously calculated for ship-based surveys of cetaceans in the CCE (Barlow, 1995) were applied to the current study. While the application of previously calculated g_0 values likely reduced the bias associated with the assumption that all animals on the trackline were detected, the correction factors applied were from a different study where a team of three observers, two of which used $25 \times$ binoculars were used. Because CalCOFI surveys utilized only two observers using $7 \times$ binoculars, it is likely that our actual g_0 values are lower than those utilized from previous studies (Barlow, 1995); therefore, our resulting estimates are likely negatively biased.

Distance sampling also relies on the assumption that animals are detected at their original location relative to the trackline versus being detected after any potential responsive movement from the survey vessel. Previous marine mammal line-transect studies have suggested that small cetaceans (*i.e.* dolphins and porpoise) may show responsive movement to the survey vessel, manifested by either positive (approaching the vessel) or negative reactions (vessel avoidance) which will result in, respectively, positive or negative bias in the estimates of density (Buckland et al., 2001). Sighting cues and behavioral events collected during CalCOFI visual detections as well as the distribution of sighting distances indicated that, of the three small cetacean species described in the current study, Pacific white-sided dolphins and Dall's porpoise exhibited responsive movement in the form of vessel attraction; this behavior likely positively biased the density/abundance estimates for this species.

For Pacific white-sided dolphin and Dall's porpoise, the lowest AIC model in Distance was not selected because behavioral observations and/or the observed distribution of distances indicated a problem with attraction. In both cases, we selected the

half-normal model over the hazard-rate model due to unrealistic pdf curves. This will have helped to reduce the positive bias, by avoiding under-estimating the effective strip width; however it is likely that the count of schools was increased by animals moving within detection range, and hence some positive bias remains in our estimates for these species.

Differences in study area boundaries and field methodology during CalCOFI surveys versus earlier surveys may have been factors in some of the observed differences in density estimates. The CalCOFI study area differs in size from the southern California region utilized in earlier studies (e.g. Barlow and Forney, 2007; Barlow, 2010). The CalCOFI study area extends from 75 km north of Point Conception to 330 km offshore in the northern portion and 700 km offshore in the southern portion for a total of 238,494 km². The southern California strata utilized for previous density estimates has a similar southern border, yet the northern boundary is 75 km south of the CalCOFI boundary and the study area extends further offshore, for a total of 318,500 km², resulting in a stratum area that is 25% larger than the CalCOFI study region. The northern CalCOFI boundary, which extends north of Point Conception, may favor species that prefer cooler waters such as Pacific white-sided dolphins and Dall's porpoise. Only density estimates (versus abundance) from the summer and fall CalCOFI cruises were used for comparisons with previous studies to avoid inherent bias associated with making incongruent temporal or spatial comparisons. CalCOFI surveys strictly incorporate passing mode for all cetacean visual observations while the earlier surveys were primarily conducted using closing mode. While closing mode allows for better resolution of species identification and group size estimation, closing mode surveys can create either a negative or positive bias in encounter rates and related density and abundance estimates (Barlow, 1997; Buckland et al., 2001). The detection range and associated ESW was greater on the earlier surveys as observers utilized 25×150 binoculars for searching and detection while CalCOFI cruises used hand-held 7×50 binoculars. While the greater detection range and ESW acquired from higher powered binoculars results in a greater number of sightings, if groups are randomly distributed relative to the transect line, the overall density estimates should be similar regardless of absolute detection range as long as other key assumptions are also met.

Blue whale density peaked in summer followed by a five-fold decrease in fall; the species was only seen once during the winter and once during spring. Aerial surveys conducted during the 1980s and 1990s as well as continuous, year-round acoustic monitoring carried out since 2000 off southern California corroborate that blue whales are present in summer and fall and rare or absent at other times of year (Dohl et al., 1980; Carretta et al., 1993; Forney and Barlow, 1998; Burtenshaw et al., 2004; Oleson et al., 2007). The seasonal density patterns for blue whales observed in the current study also corresponds to the well described migration pattern for this species with an influx of feeding whales off California from May to October followed by movement to more southerly waters off Mexico and Central America during winter and spring (Calambokidis et al., 1990; Mate et al., 1999).

Blue whale densities for summer/fall were not significantly different than the estimates reported for the pooled 1991–2005 surveys (Barlow and Forney, 2007) and the pooled 1991–2008 surveys (Barlow, 2010), despite the fact that these earlier estimates included surveys completed in 1991, 1993 and 1996 (Barlow and Forney, 2007), when dense concentrations of feeding blue whales occurred off southern California (Fiedler et al., 1998; Barlow and Forney, 2007). More recent survey data suggest blue whales in the North Pacific utilize more northerly, southerly and offshore waters (Calambokidis and Barlow, 2004; Barlow and Forney, 2007; Calambokidis et al., 2009). Blue whale density estimates from

the entire state of California as well as the Oregon/Washington region from the last 3 decades provide further support for the hypothesized northward shift in blue whale distribution; estimates for California were more than 3 times greater during surveys in 1991, 1993 and 1996 than in 2001 and 2005. Concurrent to the decreases in the numbers of blue whales observed off California, increased blue whale abundance was observed in Oregon and Washington with an change from 0 in 1996 to 1987 in 2001, and 141 in 2005 (Barlow and Forney, 2007; Barlow, 2010). The long-term trend in density as well as the mean annual population change for blue whales in the current study indicates that, after the change in blue whale distribution in the late 1990s, the number of blue whales using the waters off southern California over the last ten years has remained relatively stable (Fig. 10).

Fin whales were the most frequently encountered and most abundant baleen whale in the CalCOFI study area with variations in both annual and seasonal densities across the study period. In contrast to blue whales, fin whales were present year round off southern California with peak density in summer, followed by a decrease in fall. This pattern is consistent with previous studies that have indicated year-round occurrence of fin whales off southern California with a seasonal influx of larger numbers of the species during summer and fall (Dohl et al., 1980; Carretta et al., 1993; Forney and Barlow, 1998; Oleson, 2005; Munger et al., 2009; Sirovic et al., 2013). The year-round presence of fin whales off southern California may be linked to the less selective and more varied diet of this species versus blue whales (Perry et al., 1999a). The relatively wider range of prey items consumed by fin whales, including krill, copepods, cephalopods, and small schooling fish such as sardines, herring and anchovies (Mizroch et al., 1984), suggests that this species may utilize prey resources available throughout the year versus the focused krill foraging behavior associated with the presence of blue whales in summer and fall.

Fin whale densities for summer/fall were significantly greater than the estimates reported for the pooled 1991–2005 surveys (Barlow and Forney, 2007) and the pooled 1991–2008 surveys (Barlow, 2010). The significantly greater current estimate is consistent with the recently described long-term increase in fin whale abundance off California based on Bayesian state space model trend analysis (Moore and Barlow, 2011). The annual rate of change in the current study is very consistent with that estimated by Moore and Barlow (2011). Given the increase in fin whale population size documented by Moore and Barlow (2011) between 1991 and 2008 – from about 1000 individuals to nearly 3000 individuals off California – it is not surprising that the recent estimate in this study is markedly greater than the pooled 1991–2005 and 1991–2008 estimates. More recent density estimates derived for 2005–2008 by Moore and Barlow (2011) for the partially overlapping areas of southern and central California are much closer to those estimated in the current study.

Humpback whales exhibited annual and seasonal variations in density across the study period; however, both the long-term trend-line and the annual population change suggested a relatively stable population off southern California over the last decade. Seasonal occurrence patterns and density estimates of humpback whales indicate that the species is present off southern California year-round with an indication of greater concentrations during the spring; however the density differences were not significant. Continuous year-round acoustical monitoring off southern California identified similar patterns where humpback vocalizations, although most frequent in spring, are detected year round (Helble et al., 2013). This pattern is consistent with the notion that the peak density observed for humpback whales during spring represents both migrants travelling between wintering grounds south of southern California (i.e. Mexico and Central American) and summer feeding grounds north of southern California (i.e. US West Coast, British

Columbia and Alaska), as well as individuals that feed off southern California for an extended period of time (Calambokidis et al., 1996).

Humpback whale distribution during winter was exclusively in shelf and offshore waters; this may be the result of migrants travelling through pelagic waters to feeding areas in Alaska earlier in the season than individuals that forage off California (Calambokidis et al., 1996). Similar to fin whales, the year-round presence of humpback whales off southern California may be linked to the more varied diet of this species versus blue whales (Perry et al., 1999b). The year-round presence of humpback whales and the seasonal shift in distribution described in the current study also supports previous research where it was noted that along California, a significantly greater proportion of the humpback whale population was found farther offshore during winter than in summer (Clapham et al., 1997; Forney and Barlow, 1998).

Humpback whale densities for summer/fall were significantly greater than the estimates reported for the pooled 1991–2005 surveys (Barlow and Forney, 2007) and the pooled 1991–2008 surveys (Barlow, 2010). The significantly higher current estimate may be related to the higher rate of sampling off southern California, particularly in waters out to the 2000 m isobaths, where most of our summer/fall sightings occurred.

Short-beaked common dolphins were the most abundant and widely distributed cetacean observed during the current study, supporting findings from previous cetacean surveys off California (Dohl et al., 1986; Forney et al., 1995; Barlow and Forney, 2007; Barlow, 2010). Short-beaked common dolphins exhibited annual variations in density across the study period; however, the long-term trend-line across the entire study period and the null annual population change suggested a no significant long-term trend was observed off southern California over the last decade. The value of long-term, continuous monitoring of cetacean densities is exemplified by this species where an earlier analysis of short-beaked common dolphin densities from 2004 to 2010 suggested an approximately 6% annual decrease off southern California (Oedekoven et al., 2011). Data collected from 2011 to 2013 indicated that the density of common dolphins off southern California has recently been increasing; the addition of these three years of survey data changed the overall long term mean annual population change to near zero.

Seasonally, estimates of short-beaked common dolphin densities for summer, fall and winter were significantly higher than the estimate for spring. During summer and fall cruises, short-beaked common dolphins were observed throughout the study area, whereas during winter and spring cruises, sightings were restricted to the region south of 34°N. This distributional pattern suggests that, during the cold seasons of winter and spring, the majority of this species on the U.S. west coast is south of Point Conception. In the current study, the winter distribution of short-beaked common dolphins was centered in pelagic waters off the continental shelf, in the southern half of the study area. While this distributional pattern supports the north-south density gradient reported from recent habitat-based density modeling exercises (Becker et al., 2014), this species was distributed further offshore than predicted from the density modeling which suggested the majority of short-beaked common dolphins would be inside the 2000 m isobath (Becker et al., 2014).

The lower density observed during the spring season as well as the overall seasonal distribution patterns suggest that increased numbers of short-beaked common dolphins occur in the study area from summer through winter, followed by a return to warmer, southerly waters during spring. These findings support previous research in the region that described similar annual and seasonal changes in the distribution and density of this species in southern California waters from a range that extends well beyond the CalCOFI study area (Dohl et al., 1986; Henning and Perrin

(1994); Barlow, 1995; Forney et al., 1995; Forney and Barlow, 1998). Overall, short-beaked common dolphin density for summer/fall was not significantly different from the estimates reported for the pooled 1991–2005 surveys (Barlow and Forney, 2007) and the pooled 1991–2008 surveys (Barlow, 2010), providing further support for the long-term stability in density for this species off southern California.

Pacific white-sided dolphins exhibited notable variations in both annual and seasonal densities across the study. Previous ship-based and aerial surveys as well as continuous, year-round acoustic monitoring off southern California support previous observations that Pacific white-sided dolphins occur most frequently during winter and spring, but are present at other times of year (Forney and Barlow, 1998; Soldevilla et al., 2010). Pacific white-sided dolphins are classified as a cool-temperate species (Barlow and Forney, 2007), and annual and seasonal variations in the density this species off southern California have been attributed, in part, to variations in sea surface temperature (SST) (Barlow and Forney, 2007; Becker et al., 2014), with the species reported as being more abundant during cooler water seasons and years (Forney and Barlow, 1998). Climatic observations from the CCE over the last decade indicate that the system has remained in a cool, productive phase since 2007 underscored by moderate and strong La Niña events in 2007/2008 and 2011/2012 respectively (Wells et al., 2013); apparent changes in distribution and density of this species are inconsistent with these climate variations. Therefore, in the current study, the long-term, significant decreasing trend observed for this species over the last decade does not appear to be simply driven only by SST, but by a suite of variables including but not limited to SST. In addition, annual density estimates for Pacific white-sided dolphins may be complicated by separate northern and southern populations with southern California representing an area of overlap (Walker et al., 1986; Lux et al., 1997). The apparently counterintuitive patterns documented in this study (fewer animals in recent years, when water temperatures have been cooler), could arise if fewer animals belonging to the southern form are off southern California. Planned habitat modeling exercises incorporating dolphin densities with in-situ variables collected during CalCOFI cruises will allow us to develop a better understanding of the interaction between the distribution and density of Pacific white-sided dolphins and the CCE.

Pacific white-sided dolphin density for summer/fall was significantly greater than the estimates reported for the pooled 1991–2005 surveys (Barlow and Forney, 2007) and the pooled 1991–2008 surveys (Barlow, 2010) off southern California. In both the current and previous studies, as a result of the strong seasonal shift in distribution, relatively small samples were collected from this species during the summer/fall period off southern California. Despite the significant difference between the current and previous studies, the small sample sizes for summer/fall preclude a more informative statistical comparison.

Similar to Pacific white-sided dolphins, Dall's porpoise exhibited large variations in both seasonal and annual densities across the study period. Seasonally, Dall's porpoise were almost exclusively observed during the cool seasons of winter and spring with only four sightings of the species occurring in either summer or fall. The seasonal fluctuations in density observed for Dall's porpoise in the current study support similar findings from past research in waters off southern California indicating that Dall's porpoise are usually encountered in cooler, upwelling-modified water < 17 °C (Becker, 2007; Forney et al., 2012), and are more frequently sighted during the cooler water periods of winter and spring (Dohl et al., 1986; Barlow, 1995; Barlow and Forney, 2007; Becker et al., 2010). Previous studies off California have attributed the inter-annual variability in Dall's porpoise densities to annual fluctuations in SST, suggesting that a dramatically lower density of

the species was observed during a warmer water year versus a colder water year (Mangels and Gerrodette, 1994; Barlow and Gerrodette, 1996). Southern California represents the approximate southern extent of this species' range in the Eastern North Pacific and the variable seasonal and annual densities observed in the current and previous studies may reflect southward movement into California from waters off Washington and Oregon. In the current study, despite a negative average annual population change of –8.3%, the 95% confidence intervals crossed the value zero and therefore precluded a significant trend. Thus, despite the cool and productive state of the CCE since 2007 (Wells et al., 2013), we did not find any significant increases in the population during this time period. Similar to other species, we suggest that while some of the variation in Dall's porpoise distribution and densities in the CCE can be explained by variations in SST, extensive habitat modeling exercises which incorporate a suite of ecological variables will be required to better understand the relationship between cetacean densities and habitat variables in the CCE.

The summer/fall estimates of Dall's porpoise density in the current study were very similar to both the pooled 1991–2005 surveys (Barlow and Forney, 2007) and the pooled 1991–2008 surveys (Barlow, 2010) off southern California. Dall's porpoise estimates in the current study are likely positively biased as a result of vessel attraction and the related inclusion of sightings that occurred in Beaufort sea states between 0 and 5 versus the sea state criteria of 0–2 incorporated in previous studies (Barlow and Forney, 2007) as the inclusion of sightings that occurred in sea states 3–5 may preclude the observers' ability to document porpoise reactions or lack thereof to the approaching survey vessel.

5. Conclusions

Cetacean monitoring on CalCOFI cruises has been conducted over the last ten years to make overall, annual and seasonal estimates of cetacean density and abundance, and to investigate cetacean distribution patterns relative to habitat features. In the current study, we described the seasonal and annual trends in occurrence, distribution and density for the six most frequently sighted species of cetaceans off southern California, representing the first assessment of continuous long-term trends in cetacean density in the region. The overall findings in this study were generally consistent with previous studies, but provide greater temporal and seasonal resolution. Some of the identified differences between this and previous studies may be attributable to population increases; however, unexplained differences remain that warrant further investigation. The importance of long-term continuous monitoring of cetacean densities off southern California is exemplified in the current study where cetacean densities showed notable annual variations for a number of species, such as short-beaked common dolphins, which could have been misinterpreted without the longer time-series reported here. Several other cetacean species (e.g., Cuvier's beaked whales—*Ziphius cavirostris*) that were documented during the course of the ten-year study were not included in the current analysis due to small sample sizes; additional data collected from ongoing quarterly CalCOFI marine mammal surveys will allow for inclusion of this and other less frequently sighted species in future analyses.

The data set utilized for the current study is currently being integrated with other cetacean line-transect data collected off southern California, resulting in a more robust spatial and temporal data set from which improved habitat density modeling analysis can be conducted. This integrated dataset will provide the basis for new predictive models to forecast near real-time marine mammal distributions off southern California (e.g. Becker et al., 2012; Forney et al., 2012); the primary goal of that work is to inform planning of

operations by the US Navy with the hope of minimizing any adverse impacts on marine mammals in the region.

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