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James V. Carretta

NOAA, U.S. National Marine Fisheries Service, Southwest Fisheries Science Center, NOAA, Jim.Carretta@noaa.gov

Susan J. Chivers

U.S. National Marine Fisheries Service, Southwest Fisheries Science Center, NOAA

Wayne L. Perryman

U.S. National Marine Fisheries Service, Southwest Fisheries Science Center, NOAA

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Cover Page Footnote

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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

James V. Carretta, Susan J. Chivers, and Wayne L. Perryman

*NOAA Fisheries, Southwest Fisheries Science Center, 3333 North Torrey Pines Court,
La Jolla, CA 92037*

Abstract.—The abundance of the long-beaked common dolphin (*Delphinus capensis*) is estimated from data collected during a 2009 ship-based line-transect survey. The survey was designed to provide fine-scale coverage of the known range of *D. capensis* along the California and west Baja California coasts. Estimates of *D. capensis* abundance presented are the highest to date for California waters and may reflect a combination of improved survey design for this species and increasing numbers of *D. capensis* in state waters. Estimates of *D. capensis* abundance within California waters are 183,396 (CV=0.41, 95% CI 78,149 – 379,325) animals. An additional 95,786 (CV=0.47, 95% CI 36,881 – 209,507) *D. capensis* were estimated in Baja California waters from the U.S./Mexico border south to the tip of Baja California. Total estimated abundance of *D. capensis* in California and Baja California west coast waters is 279,182 (CV=0.31, 95% CI 148,753 – 487,323) animals.

Introduction

In 2009, the Southwest Fisheries Science Center (SWFSC), a branch of the National Oceanic and Atmospheric Administration (NOAA), conducted a ship-based line-transect survey to estimate the abundance of long-beaked common dolphin (*Delphinus capensis*) in California waters and along the west coast of Baja California (Chivers *et al.* 2010). This was part of a larger mandate under the U.S. Marine Mammal Protection Act to collect data on marine mammal populations used to prepare marine mammal stock assessments published annually (Carretta *et al.* 2011). Surveys are conducted periodically to provide updates on marine mammal abundance and trends. Between 1991 and 2008, six coarse-scale vessel line-transect surveys were conducted along the U.S. west coast out to 300 nmi (Barlow 1995, Barlow 2003, Forney 2007, Barlow and Forney 2007, Barlow 2010). These surveys provided comprehensive estimates of abundance for short-beaked common dolphin (*Delphinus delphis*) in the California Current. However, transect coverage was not optimal for coastal species, such as *D. capensis*. Abundance estimates of *D. capensis* from previous coarse-scale surveys have been highly variable and characterized by small numbers of sightings and low statistical precision (Table 1). Part of this variability is because California waters represent the northern extent of the range of a *D. capensis* population which extends into Mexico. Gillnet bycatch of the California population of *D. capensis* has sometimes exceeded sustainable levels (“potential biological removal” or PBR) as defined under the Marine Mammal Protection Act (Wade and Angliss 1997). A lack of precise abundance estimates, in combination with human-caused mortality levels of this stock, prompted a more intensive, fine-scale survey of *D. capensis* coastal habitat in 2009 to provide improved estimates of abundance. Although this species also occurs in the Gulf of California, it was not practical to survey their entire range in 2009. Since

Table 1. Historic estimates of *D. capensis* abundance within California waters, from ship-based line-transect surveys. Multiple estimates in a given year reflect incorporation of new analysis methods to existing datasets, such as the use of covariates in line-transect analysis (Barlow and Forney 2007).

Survey year	Reference	<i>D. capensis</i> sightings (n)	Estimated abundance (CV)
1991	(Barlow 1995)	5	9,472 (0.68)
1991	(Barlow & Forney 2007)	5	16,714 (n/a)
1993	(Barlow & Forney 2007)	0	0
1996	(Barlow & Forney 2007)	6	49,431 (n/a)
2001	(Barlow 2003)	1	306 (1.02)
2001	(Barlow & Forney 2007)	2	20,076 (n/a)
2005	(Barlow & Forney 2007)	6	11,191 (n/a)
1991–2005 pooled	(Barlow & Forney 2007)	19	21,902 (0.50)
2005	(Forney 2007)	6	11,714 (0.99)
2008	(Barlow 2010)	7	62,447 (0.80)

management of the population is based only on abundance in U.S. waters and animals occur throughout their range year-round, the area surveyed in 2009 was adequate to assess the status of the U.S. population.

Field Methods

A ship-based line-transect survey was conducted in 2009 on the 62 m NOAA vessel *McArthur II* from September to December (Chivers *et al.* 2010). Transect coverage of the study area was designed to encompass the known range of *D. capensis* in California waters and along the west coast of Baja California, based on examination of historic (SWFSC) sightings (Figure 1A).

The survey design included approximately 4,800 km of transect lines, with different coverage goals for each of three 25-day sea legs (Figure 1B). Leg 1 effort targeted inshore

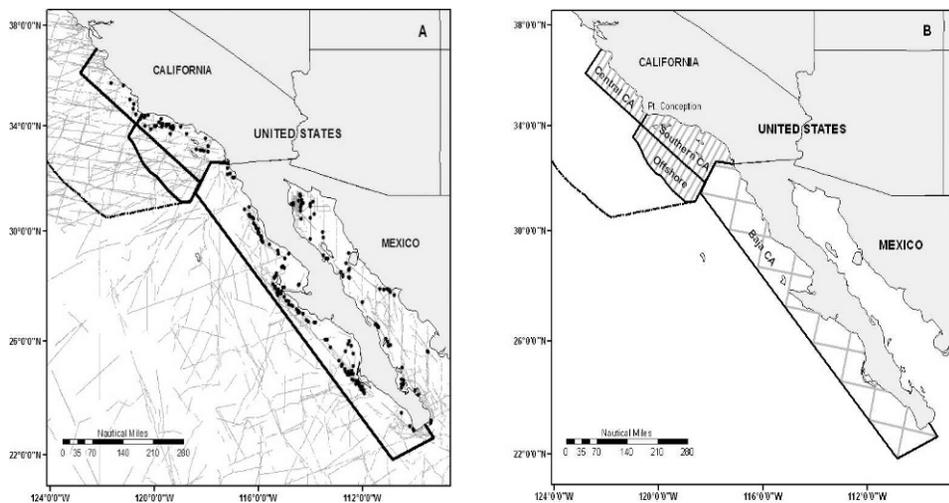


Fig. 1. (A) SWFSC ship survey line-transect effort and *Delphinus capensis* sightings prior to 2009. Solid black lines represent survey strata used to design transect coverage for the 2009 survey and dashed line represents a portion of the U.S. Exclusive Economic Zone (EEZ). Thin gray lines represent historic ship survey line-transect effort. (B) Planned transect coverage and geographic strata for the 2009 survey.

waters from Monterey Bay south to the U.S./Mexico border, with a series of 26 transects ranging from 40 to 170 km in length, up to 150 km offshore of the mainland. Leg 2 transects covered the waters of western Baja California, with a series of 15 transects in a saw-tooth pattern offshore to the shelf break, ranging from 85 to 195 km in length. Leg 3 transects included southern California transects from Leg 1, with additional offshore extensions of up to 250 km from the mainland. These additional offshore transects were not used to estimate abundance but were utilized to obtain additional data on stock structure of *D. delphis* in southern California offshore waters and to determine if the range of *D. capensis* was limited to inshore waters where it had been historically seen. Abundance and density were estimated for three strata: 'Central California', 'Southern California', and 'Baja California' (Figure 1). Areas for all strata were determined using ArcGIS 9.3 software, with a 'World Equal Area' map projection.

Line-transect methods were similar to previous SWFSC surveys described by Kinzey (2000) and Barlow and Forney (2007). The basic line-transect survey mode consisted of three experienced marine mammal observers searching from the flying bridge of the NOAA ship *McArthur II* at a height of 15.2 m above the water. Two observers searched port and starboard of the transect line using pedestal-mounted 25X binoculars, and a third observer acted as data recorder, searching the transect line primarily with naked eye and 7X binoculars. Surveys were conducted in 'closing mode' (Barlow and Forney 2007), whereby the ship diverts from the transect line to allow observers to better identify and count dolphin groups. Exceptions to closing mode occurred where navigational constraints prevented this or where closing mode made estimation of group size more difficult. For example, several dolphin groups (see Results) were too large and/or diffuse to effectively estimate group size in closing mode and therefore, passing mode was used. In passing mode, the ship maintains its course after animals are sighted and observers count animals as they pass on either side of the ship. Dolphin groups too large or diffuse to estimate group size in closing mode were known as 'mega-schools' and observers divided the task of estimating group size between the left and right sides of the ship as the ship passed through the school. Resulting group size estimates of 'mega-schools' represent the sum of estimates of two or more observers. Observers typically made three estimates of group size: a 'best', a 'high', and a 'low'. Only the observers' 'best' estimates were used in this study.

Observers aboard research vessels tend to underestimate dolphin group sizes because animals are diving and not available to be seen and because counting large groups of dolphins is a difficult task (Barlow *et al.* 1998, Gerrodette *et al.* 2002). Thus, estimates of group size require correction factors to address these biases. A NOAA Twin Otter aircraft was utilized during the 2009 survey to coordinate with the NOAA ship *McArthur II* to obtain digital aerial photographs of dolphin groups to calibrate observer estimates of group size. Photographs were taken using three Canon EOS-1 DS Mark III digital cameras mounted in the belly of the aircraft (Chivers *et al.* 2010). Digital aerial images of sufficient quality were obtained for 12 calibration groups (10 *D. capensis* and 2 *D. delphis*) where all six marine mammal observers aboard the *McArthur II* also obtained estimates of group size. Observer group size calibration coefficients were developed as described in the Analytical Methods section.

Analytical Methods

Standard line-transect methods were used to estimate the density and abundance of *D. capensis* and *D. delphis* (Buckland *et al.* 2001), using the program Distance 6.0

(Thomas *et al.* 2009). Only ‘standard effort’ transect data (effort on planned transect lines, excluding ‘deadhead’ effort between lines) where Beaufort sea state was between zero and 4, visibility was at least 3.5 nmi, and no fog or rain were recorded were used to estimate density and abundance. Dolphin density (\hat{D}) within a stratum was calculated as:

$$\hat{D}_i = \sum_{j=1}^2 \frac{n_{i,j} \cdot f(0) \cdot S_{i,j}}{2 \cdot L_i \cdot g(0)_j} \quad (1)$$

where

$n_{i,j}$ = number of dolphin groups of size j detected in stratum i ,
 $f(0)$ = probability density function (km^{-1}) evaluated at zero perpendicular distance
 $S_{i,j}$ = mean group size of dolphin groups of size category j in stratum i ,
 L_i = length of transect line (in km) surveyed in stratum i ,
 $g(0)_j$ = probability of detecting a dolphin group of size j on the transect line.

Values for $g(0)$ used in this analysis are based on those reported by Barlow and Forney (2007) for delphinid group sizes of ≤ 20 animals (0.856, CV=0.056) and > 20 animals (0.970, CV=0.017), respectively. Half-normal and uniform models with simple polynomial adjustment terms were fit to the perpendicular sighting distance data to estimate $f(0)$ and the effective strip width (ESW) for all geographic and group size strata pooled. The ESW is defined as that perpendicular distance from the transect line at which the number of objects detected beyond this distance equals the number missed within the same distance. Perpendicular sighting distances were right-truncated at 4.0 km (excluding 5–10% of the largest distances) to avoid fitting extreme values near the tail of the distribution. The model fit with the lowest Akaike’s Information Criterion (AIC) was selected by the program Distance to estimate dolphin density. Because observers are less likely to detect small groups of dolphins at greater distances, this may introduce a positive bias into overall mean group size. The program Distance includes the option of correcting mean group size based on regressing the logarithm of observed group size versus perpendicular sighting distance. If the regression is significant at an alpha-level of 0.15, then the ‘expected group size’ based on the regression is used in place of the observed group size (Thomas *et al.* 2009). We implemented this Distance program option in our analysis. It should be noted that regression-based corrections to mean group size address the bias that observers are more likely to miss small groups. This is independent of observer calibrations from aerial photographs used to correct the bias of undercounting of detected groups, which we discuss below.

Total abundance was estimated as the sum for all three geographic strata (Central California, Southern California, and Baja California) as:

$$\hat{N}_i = \sum_i^3 \hat{D}_i \cdot A_i \quad (2)$$

where \hat{N}_i is estimated abundance in stratum i and A_i is the area of the stratum. Encounter rate (n/L) variance was estimated empirically within the program Distance from the individual survey effort segments. We tested a range of effort segment lengths as sampling units (5 km to 100 km), to see if resulting coefficients of variation (CV) in abundance

estimates were significantly affected by segment length choice. An initial sensitivity analysis suggested that segment lengths of 20 km provided the greatest precision for this particular dataset (in exploratory analyses, CVs for all strata combined ranged from 0.43 to 0.51 using segment lengths of 5 to 100 km). Within a stratum i , the CV of the abundance estimate for groups of size j was calculated as the square root of the sum of the squared CVs of the parameters group size, encounter rate, detection function, and trackline sighting probability:

$$CV(\hat{N}_{i,j}) = \sqrt{CV^2(S_{i,j}) + CV^2\left(\frac{n_{i,j}}{L_i}\right) + CV^2(f(0)) + CV^2(g(0)_j)} \quad (3)$$

The variance and CV of the combined abundance (across all group size categories j within stratum i) was calculated as:

$$Var(\hat{N}_i) = \sum_{j=1}^2 (CV(N_{i,j}) \cdot N_{i,j})^2 \quad (4)$$

and

$$CV(\hat{N}_i) = \frac{\sqrt{Var(\hat{N}_i)}}{\hat{N}_i} \quad (5)$$

Variances for combined estimates of abundance (multiple strata) were also calculated as shown in Equation 5. Ninety-five percent confidence intervals for abundance estimates were estimated by simulating a log-normal distribution from each point estimate and associated CV and taking the 2.5th and 97.5th percentiles respectively, as the lower and upper limits of the confidence interval.

Group size calibration

Group size calibration coefficients were developed from digital aerial photographs of 12 dolphin groups (10 *Delphinus capensis* and 2 *Delphinus delphis*) and corresponding observer 'best' estimates of group size from the research vessel. Three counters independently counted dolphin numbers from aerial photographs of the 12 calibration groups and the 'true group size' for each sighting was calculated as the mean of the three photo counts (Table 2). We calculated individual observer calibration coefficients by fitting a log-transformed, linear regression (intercept = 0) to the 12 photo calibration groups and 'best' estimates of group size. The calibration coefficient, β_0 , for a given observer is:

$$\ln \bar{S}_{best} = \beta_0 \cdot \ln S_{photo} \quad (4)$$

where

S_{best} = the observer's best estimate of group size

and

\bar{S}_{photo} = mean 'true group size' determined from aerial photographs.

Estimates of group size for individual observers were corrected as follows:

$$\ln S_{corrected} = \ln S_{best} / \beta_0 \quad (5)$$

In cases where multiple observers estimated separate portions of a mega-school, a single

Table 2. Dolphin counts from digital aerial photographs of 12 *Delphinus* groups obtained in 2009 and used for group size calibration. Uncorrected field estimates of mean group size and corrected estimates of group size, based on 2009 and ETP calibration coefficients are shown.

Sighting Number	Species	Mean Photo Count	Uncorrected Mean Best Estimate	Corrected Mean Best Estimate (2009 coefficients)	Corrected Mean Estimate (ETP correction factor)
161	<i>D. capensis</i>	569	310	590	360
290	<i>D. delphis</i>	272	155	269	180
291	<i>D. capensis</i>	634	353	681	411
292	<i>D. capensis</i>	1394	396	778	461
293	<i>D. capensis</i>	776	283	530	329
320	<i>D. capensis</i>	48	33	46	39
322	<i>D. capensis</i>	35	20	27	23
512	<i>D. capensis</i>	475	613	1166	713
514	<i>D. capensis</i>	284	289	561	336
526	<i>D. capensis</i>	1281	404	795	470
528	<i>D. capensis</i>	574	303	553	352
705	<i>D. delphis</i>	122	159	278	185

calibration coefficient was used and calculated as the mean of all individual observer calibration coefficients. For comparison, we also report estimates of abundance obtained using uncorrected group sizes (calibration coefficients = 1.00) and those obtained by applying a mean group size correction factor for 52 observers calibrated during line-transect surveys in the Eastern Tropical Pacific (ETP) (Gerrodette *et al.* 2002, Gerrodette and Forcada 2005). The ETP correction factor is based on the mean ratio of observer best estimates to photo counts (0.860), with a mean of 38 calibration groups per observer (Gerrodette *et al.* 2002, Gerrodette and Forcada 2005). Estimates of dolphin density and abundance presented in the Results section utilize the calibration coefficients developed from 12 calibration schools photographed in 2009.

Results

Over 5,000 km of standard line-transect effort was conducted during the 2009 survey in Beaufort sea states 0 through 5 (Table 3; Figure 2). The length of completed transects slightly exceeds the length of the designed transect grid because Southern California stratum transects were surveyed on both Legs 1 and 3. Standard effort sightings included 88 groups of *D. capensis* (Figure 3). The observed distribution of *D. capensis* sightings in 2009 did not differ appreciably from historic sighting distributions (Figures 1 and 3). No sightings of *D. capensis* were made in the Offshore stratum, though some groups were sighted near the boundary of the Offshore and Southern California strata. Observers underestimated group size for the 12 calibration schools, as evidenced by the mean ratio of observer best estimates to aerial photo counts (=0.669, Table 2). Four out of six observers had group size correction coefficients of less than one and the degree of underestimation increased with group size (Tables 2 and 4; Figure 4). After correcting observer best estimates with linear regression, the mean ratio of corrected counts to aerial photo counts was 1.20 (Table 2). A half-normal model provided the best fit to the perpendicular distance data over competing uniform models, based on the lowest AIC values (Figure 5). The mean ESW for *D. capensis* was 2.81 km (CV=0.13), which is similar to previous estimates reported by Barlow and Forney (2007) and Barlow (2010), who reported values of 2.85 km and 2.62 km, respectively.

Table 3. Stratum sizes and length of transect lines surveyed during standard survey effort. Estimates of density and abundance in this report do not include survey effort and sightings within the 'Offshore' stratum.

Stratum	Study Area (km ²)	Length of transects surveyed (km)			
		Beaufort 0-3	Beaufort 4	Beaufort 5	Total (Beaufort 0-5)
Central California	23,259	233	82	68	383
Southern California	42,263	1,059	740	340	2,139
Offshore	32,094	291	292	180	763
Baja California	175,493	580	1,016	142	1,738
TOTAL	273,109	2,163	2,130	730	5,023

Mean group size of *D. capensis* (corrected for undercounting bias) was 454 animals (Table 5). This is larger than that reported by Barlow and Forney (2007), who reported a mean group size of 315 animals, but smaller than the mean of 535 animals recently reported by Barlow (2010) from a 2008 survey. Approximately 279,000 *D. capensis* were estimated for all geographic strata combined, with approximately 180,000 animals in U.S.

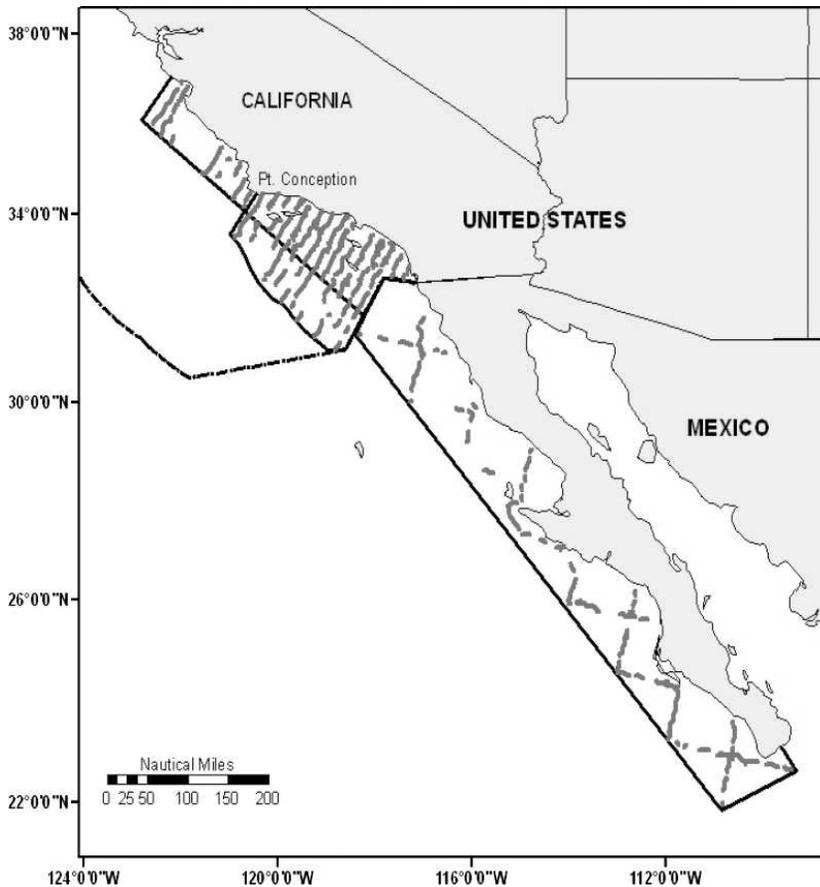


Fig. 2. All standard survey effort completed during Legs 1-3 (07 September - 09 December 2009).

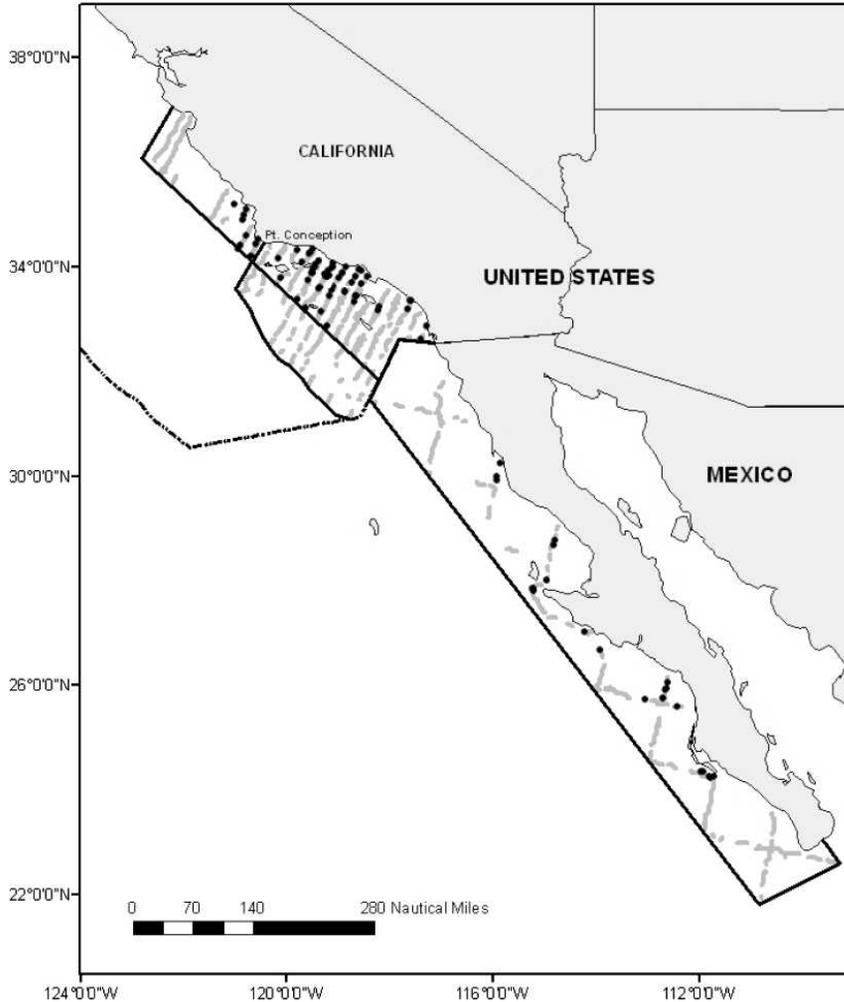


Fig. 3. Sighting locations of long-beaked common dolphin (*D. capensis*, n=88) during standard survey effort (gray lines).

west coast waters (Table 6). These estimates are based on using observer calibration coefficients calculated from 12 *Delphinus* groups photographed in 2009. Corrected estimates were on average, nearly double that of estimates not corrected for underestimation of group size (Figure 6). Estimates of density and abundance for *D. capensis* are provided in Table 6.

Discussion

Estimated abundance of *D. capensis* in California waters in 2009 ($\approx 180,000$ animals) is the highest of any ship line-transect survey to date. Nearly 40% of the estimate ($\approx 70,000$) comes from the Central California stratum, where relative survey effort was low, group sizes were large, and precision of the estimate was poor ($CV=0.79$). The ratio of *D. capensis* to *D. delphis* sightings during standard transect effort was nearly 1:1 (88 and 90 sightings, respectively) within our strata. Previous SWFSC line-transect surveys from 1986–2008 within the same strata had a ratio of 1:3.6 (73 and 262 standard-effort

Table 4. Individual group size correction coefficients based on 'best' estimates of group size for 12 calibration groups photographed in 2009.

Observer	Group size correction coefficient (2009)
A	0.859
B	0.943
C	0.874
D	0.909
E	0.880
F	0.931
Mega-school aggregate	0.900

sightings, respectively) *D. capensis* to *D. delphis* sightings (SWFSC unpublished data). The difference in relative sighting numbers of each species may reflect differences between fine-scale and coarse-scale transect coverage between previous surveys and ours, but it may also reflect increasing trends in abundance of *D. capensis*.

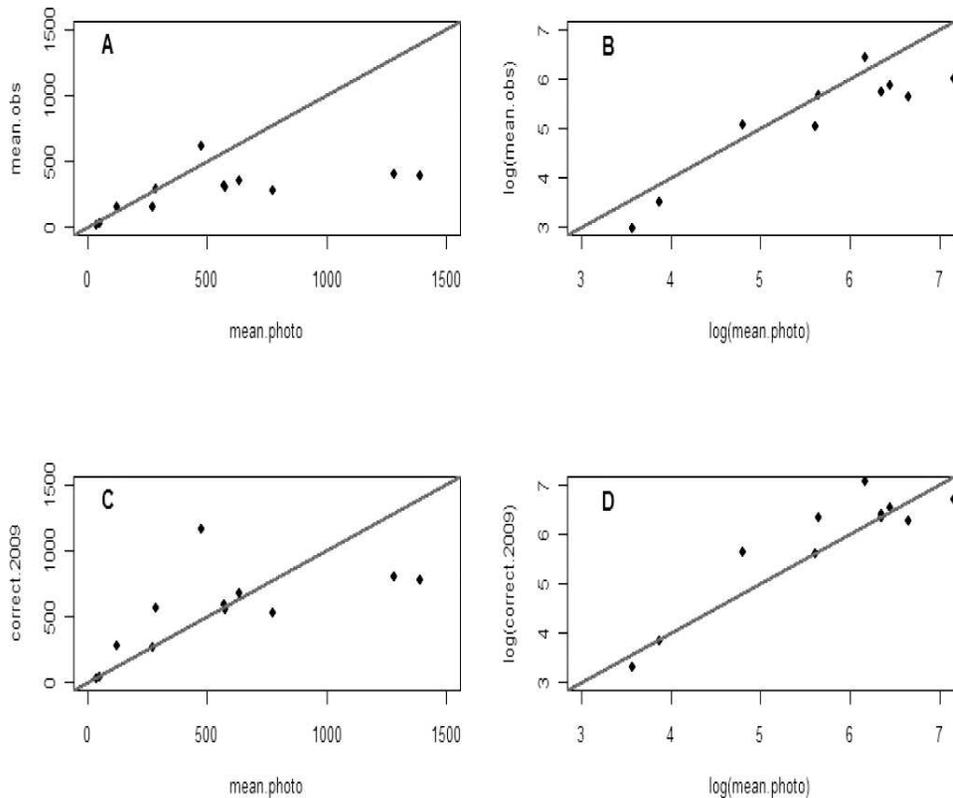


Fig. 4. Top Row: Mean photo counts and mean observer estimates (mean of six 'best' observer estimates) for 12 calibration groups of common dolphin photographed during 2009. Both raw (A) and log-transformed values (B) are shown. Bottom row: Corrected observer estimates based on the linear relationship between observer estimates and 'true group size' from aerial photographs. Both raw (C) and log-transformed (D) values are shown. Diagonal lines represent a 1:1 relationship between uncorrected/corrected observer estimates and counts from aerial photographs. In the absence of estimation error, all points would fall on the diagonal line.

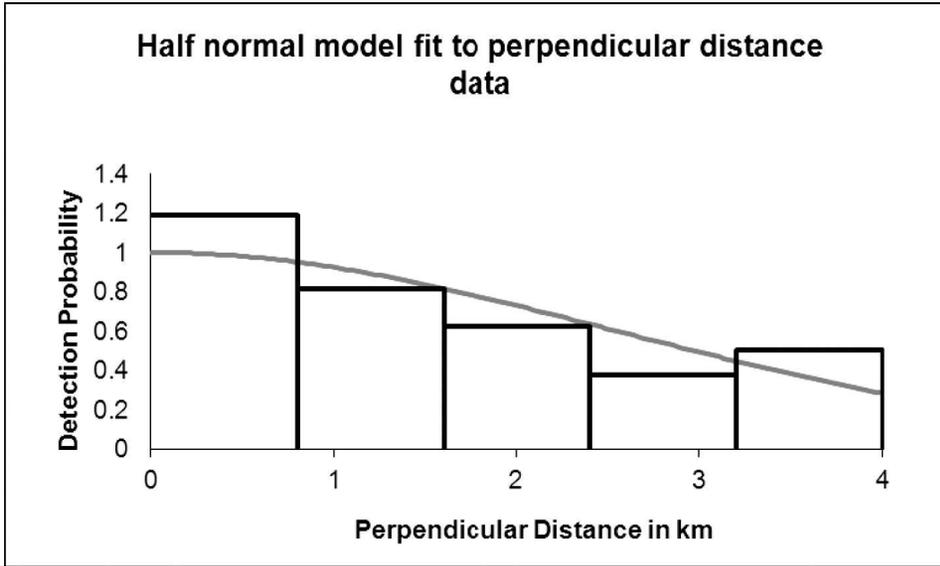


Fig. 5. Half normal model fit to *D. capensis* perpendicular sighting distances (n=56) for Beaufort sea states 0 to 4 and visibility ≥ 3.5 nmi. Model fit statistics are $f(0)=0.356 \text{ km}^{-1}$, CV=0.13, chi-square $p=0.445$, and the effective strip width (ESW) is 2.81 km. Truncation distance is 4.0 km.

The ratio of *D. capensis* to *D. delphis* strandings in southern California increased following a strong 1982–83 El Niño (Heyning and Perrin 1994). Within San Diego County, dramatic increases in the ratio of *D. capensis* to *D. delphis* strandings were observed from 2006–2008 (Danil *et al.* 2010) and these have persisted through 2010 (SWFSC unpublished stranding data). Trends in *D. capensis* abundance are not apparent from a series of six line-transect cruises conducted by SWFSC between 1991 and 2008, but it is notable that the most recent survey in the series (2008) yielded the highest estimate of abundance ($\approx 62,000$ animals, Barlow (2010), Table 1). An abundance trend analysis for *D. capensis* would be difficult to perform, as the line-transect estimates are based on few sightings and inter-annual oceanographic variability likely influences the distribution of this trans-boundary population. Discerning a trend is also confounded by the fairly recent recognition of *D. capensis* as a separate species (Heyning and Perrin 1994) and the related issue that marine mammal observers may have experienced a ‘learning curve’ in their ability differentiate *D. capensis* from *D. delphis* since that time. The relatively high estimate of *D. capensis* abundance in 2009 may be related to a

Table 5. Number of standard-effort sightings (*n*) of *D. capensis* and mean group sizes (based on 2009 photographic calibration coefficients) for three geographic strata where density and abundance were estimated. Only groups used for density and abundance estimation are included in this table. Mean group size for all strata is calculated as the weighted mean (by number of sightings in each strata) for all three strata.

Species	Central California		Southern California		Baja California		All Strata	
	<i>n</i>	Mean group size	<i>n</i>	Mean group size	<i>n</i>	Mean group size	<i>n</i>	Mean group size
<i>Delphinus capensis</i>	6	716.0	36	481.3	14	274.3	56	455

Table 6. Total number of sightings (n), estimated abundance (N), coefficients of variation (CV), lower and upper 95% confidence intervals by strata for long-beaked common dolphins. Estimates are based on group size calibration coefficients estimated from aerial photographs obtained in 2009 (see text). Stratum estimates for 'Southern CA' represent pooled estimates of Leg 1 and Leg 3 survey data. U.S. EEZ stratum values represent combined Central CA and Southern CA estimates, but do not include sightings and effort data from the 'Offshore' stratum in Figure 1. No sightings of long-beaked common dolphin were recorded in the Offshore stratum.

<i>Delphinus capensis</i>	Stratum	n	N (CV)	Lower 95% CI	Upper 95% CI	Density per 1000 km ²
	Central CA	6	71,658 (0.79)	14,650	224,313	3,080
	Southern CA	36	111,738 (0.44)	44,618	229,417	2,643
	Baja CA	14	95,786 (0.47)	36,150	205,078	545
	U.S. Strata	42	183,396 (0.41)	78,149	379,325	2,798
	All strata	56	279,182 (0.31)	148,753	487,323	1,158

moderate El Niño event that began in mid-2009 (NOAA Climate Prediction Center), which may have shifted *D. capensis* distribution northward into U.S. waters. Differences in abundance estimates between this and previous surveys may also be due to analytical differences. We did not use Beaufort 5 data in our analysis, which has been necessary to include in previous survey analyses that suffered from poor weather. Nor did we use covariate modeling in our line-transect approach (Marques and Buckland 2003, Barlow and Forney 2007), but instead utilized simple stratification to select good weather conditions for inclusion (which was only possible because of the inshore nature of our transect coverage).

Our estimates are also influenced by the group size correction factors derived from the aerial photographs, though it should be noted that even our uncorrected estimates of abundance are higher than any previous estimates in this region (Table 1, Figure 6).

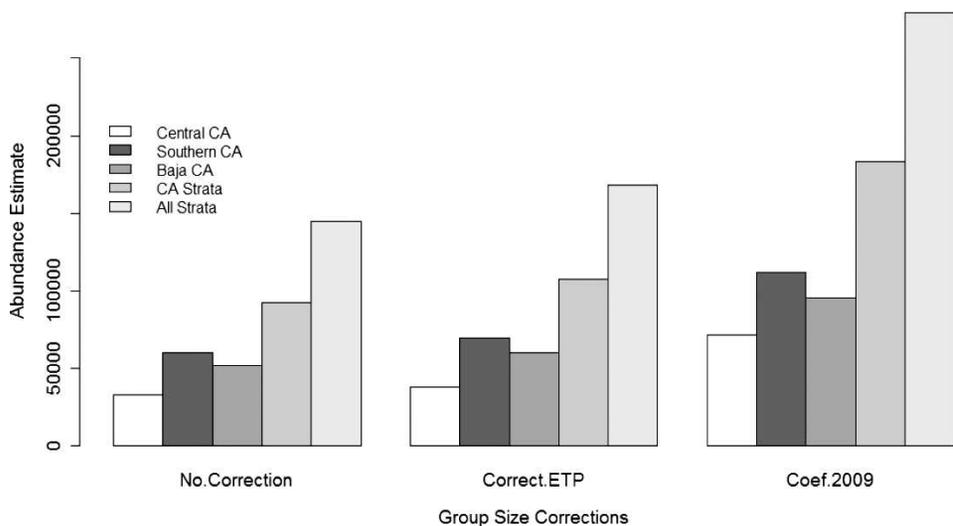


Fig. 6. Estimates of abundance by stratum for long-beaked common dolphin (*Delphinus capensis*). Estimates shown are based on uncorrected group sizes, group size corrections based on coefficients developed from 2009 aerial photographs, and a global correction factor for 52 observers, based on the ratio of observer best estimates to photo counts in the Eastern Tropical Pacific (Gerrodette *et al.* 2002).

Abundance estimates obtained with group size calibration coefficients based on 2009 aerial photographs were nearly double that of abundance estimates obtained with uncorrected group sizes (Figure 6). This is similar to the ratio of mean photo counts divided by mean observer counts (1.87) for the 12 calibration groups in Table 2. This highlights the challenges of accurately estimating dolphin numbers from a research vessel. The 2009 coefficients also provided estimates that are considerably higher than estimates that would be obtained if one applied the inverse of the mean ratio of observer best estimates to aerial photo counts ($=0.860$) for 52 calibrated observers in the ETP (Gerrodette *et al.* 2002) (Figure 6). The ETP correction factor is based primarily on spotted (*Stenella attenuata*) and spinner (*Stenella longirostris*) dolphin schools, where the mean number of dolphins per school was approximately 230 (based on photo counts). In contrast, our calibration coefficients are derived from 10 schools of long-beaked common dolphin and 2 schools of short-beaked common, with a mean of 539 animals per school (Table 2). Long-beaked common dolphin schools are typically characterized by the largest group sizes of any cetacean encountered in the California Current (Barlow and Forney 2007). Barlow and Forney (2007) noted that in their calibration of observers' estimates of group size, it was apparent that proportionately larger corrections were applied to larger groups. Thus, the large increases in group size (and abundance) resulting from our calibrations are not extraordinary, considering the relatively large mean group sizes observed in 2009.

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