



Comparison of reproductive parameters for populations of eastern North Pacific common dolphins: *Delphinus capensis* and *D. delphis*

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ABSTRACT

Reproductive parameters were estimated and compared for eastern North Pacific populations of common dolphins using specimen and photogrammetric data. Age and length data for *Delphinus capensis* and *D. delphis* specimens recovered as bycatch or strandings were used to estimate the postnatal growth rates needed to estimate age for calves measured in aerial photographs. Bayesian methods propagated uncertainty among models and revealed that the 2009 cohort of calves had birth dates centered on 6 March 2009 for *D. capensis* and 12 December 2008 for *D. delphis*. The evidence for discrete calving seasons suggests a mechanism of reproductive isolation has evolved between species. Photogrammetric data and Bayesian methods were also used to estimate the average length at which calves swim independently: 145.1 cm (\approx 11.1 mo) in *D. capensis* and 140.1 cm (\approx 14.0 mo) in *D. delphis*, and the proportion of calves (calves/dolphins counted): 0.045 in *D. capensis* and 0.069 in *D. delphis*. The latter parameter was converted to an index of calf production (calf/female dolphin) that was >50% lower than pregnancy rates suggesting few births occurred during the study year. Comparisons of regional differences in calf production suggest variability in habitat use patterns within the study area.

Key words: common dolphin, *Delphinus capensis*, *Delphinus delphis*, reproduction, calving season, birth rates, aerial photogrammetry, eastern North Pacific.

Knowledge of reproductive characteristics is essential to understanding the demography of wild animal populations. Comparing reproductive parameters among populations often reveals unique adaptations to local habitats, and quantifying interannual variability in reproduction facilitates understanding how populations respond to changing ecosystems and to anthropogenic activities. Most studies of reproduction for pelagic small cetacean populations are based on specimens collected from large-scale fishery mortalities over an extended period of time. Due to their preference for productive, upwelling-modified oceanographic habitats (Au and Perryman 1985,

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Reilly 1990, Reilly and Fiedler 1994, Becker *et al.* 2010, Pardo *et al.* 2015), common dolphins (*Delphinus* spp.) are vulnerable to being killed in commercial fisheries.

Biological data collected from individual dolphins killed in commercial fisheries have been used in life history studies for several populations of short-beaked common dolphins (*D. delphis*; Fig. 1) (Ferrero and Walker 1995, Danil and Chivers 2007, Westgate and Read 2007, Murphy *et al.* 2009). In the eastern North Pacific Ocean (ENP), such specimen-based studies have estimated growth and reproductive parameters (*e.g.* length-at-birth and calving interval) for populations affected by the purse-seine fishery in tropical waters (Danil and Chivers 2007), and the drift gill-net fishery in high latitude temperate waters (Ferrero and Walker 1995). These studies provide evidence of a latitudinal gradient in dolphin size and calving seasons that in part reflect adaptations to local ecosystems. That is, dolphins living at higher latitudes are smaller and have a relatively discrete calving season compared to dolphins living at lower latitudes that are larger and calve year round (Perrin *et al.* 1985, Ferrero and Walker 1995, Danil and Chivers 2007).

Within our ENP coastal study area (Fig. 2), knowledge about *D. delphis* is limited to a few early studies documenting their distribution, abundance and life history characteristics (Norris and Prescott 1961, Hui 1973, Evans 1975). The lack of detailed information about their life history is largely due to the limited availability and slow accumulation of specimens combined with the inherent difficulties of studying highly mobile pelagic cetacean species. *D. capensis* has long been recognized as a larger coastal morphotype distinct from *D. delphis* (Heyning and Perrin 1994), but no life history parameter estimates are currently available for *D. capensis* because samples have been rarely collected.

D. delphis and *D. capensis* live sympatrically in the ENP with the range of *D. capensis* occurring within that of *D. delphis* (Fig. 1). Species recognition for *D. capensis* was proposed in the mid-1990s on the basis of unique morphological and genetic characters (Heyning and Perrin 1994, Rosel *et al.* 1994) and has been broadly accepted. All references to *D. capensis* and *D. delphis* in this paper imply the subspecies, *D. c. capensis* and *D. d. delphis*, respectively (Perrin 2011a, b).

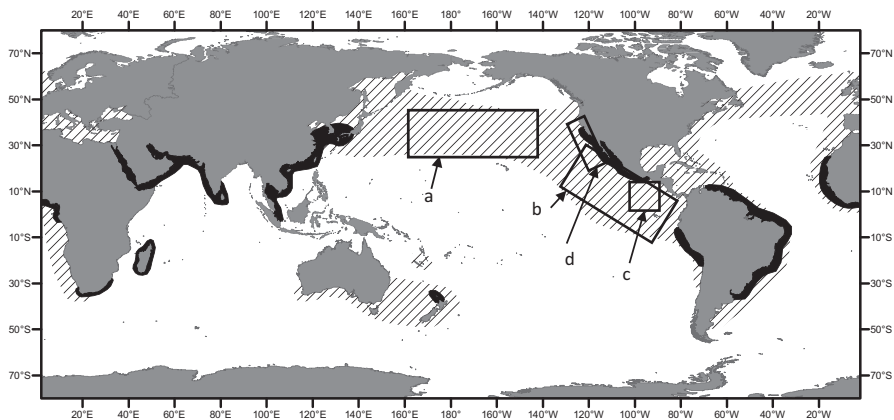


Figure 1. Distribution of *Delphinus delphis* (parallel lines) and *D. capensis* (black shaded areas) (Hammond *et al.* 2008a, b). The rectangles outline the approximate areas of published life history studies for *D. delphis* in the Pacific Ocean: (a) Ferrero and Walker (1995), (b) Perrin *et al.* (1985), (c) Danil and Chivers (2007), and (d) this study.

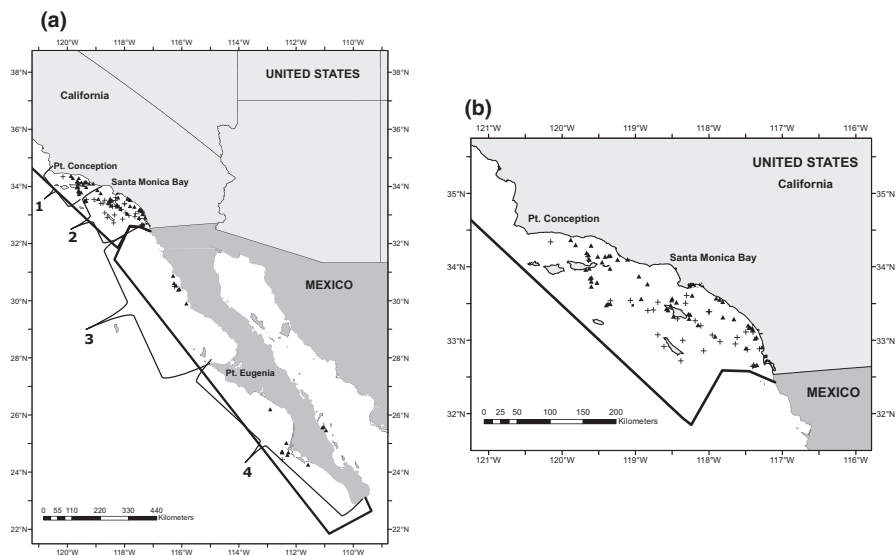


Figure 2. Locations of schools photographed during the 2009 study are shown for *D. capensis* (triangles) and *D. delphis* (crosses). (a) The study area (black boundaries) and the four biogeographical regions recognized for analyses: 1. Southern Californian, 2. Ensenadian-U.S.A., 3. Ensenadian-Mexico, and 4. Magdalenan (see Methods for description). (b) The sampling completed in the Southern California Bight north of the U.S.A./Mexico border.

Aerial photogrammetric methods can be used to collect data sets free from potential biases associated with commercial fishery sampling programs. This approach allows studies to be conducted where commercial fisheries are not the primary threat to populations or where the collection of biological samples from bycaught dolphins is not possible. While traditional photogrammetric techniques have been used to obtain measurement data, the ability to extract count data from high-resolution vertical aerial photographs has provided an additional benefit to marine mammal research (e.g., Barlow *et al.* 1998, Lowry 1999). Two studies conducted in the ENP demonstrate the utility of photogrammetric techniques for studying pelagic small delphinids. Perryman and Lynn (1993) confirmed that measurements of adult sized *D. delphis* from aerial photographs were comparable to those of bycaught specimens. The same study also found that adjacent geographic forms had different calving seasons. More recently, Cramer *et al.* (2008) used photogrammetric count and measurement data to estimate and monitor trends in the proportion of calves and length-at-dissociation (LAD) for two populations of small delphinid species whose populations have been affected by commercial fisheries: the northeastern pantropical spotted (*Stenella attenuata attenuata*) and eastern spinner (*S. longirostris longirostris*) dolphin populations (Gerrodette and Forcada 2005, Wade *et al.* 2007).

The primary objective of this study was to estimate and compare several reproductive parameters for ENP populations of *D. capensis* and *D. delphis*. To do this, we combined the more traditional specimen-based methods of cetacean life history studies (Chivers 2009) with photogrammetric techniques. Specimen data were used to estimate postnatal growth rates to provide a model for converting length to age. Count

and measurement data obtained from vertical aerial photographs of common dolphin schools taken throughout our study area (Fig. 2) were used to estimate cow (*i.e.*, an adult female with a calf) size, the proportion of calves (calf count/total dolphin count) and the average length-at-independence (LAI). We also converted measurements of calves to ages using the specimen-based model developed to estimate calf birth dates and an age equivalent of LAI. We examined each parameter for evidence of regional differences within the study area, because multiple geographic forms of *D. delphis* have been recognized (Perrin *et al.* 1985), and there is additional evidence to suggest there may be discrete populations within the study area that are not yet recognized (Farley 1995, Chivers *et al.* 2003). Our study provides new information about the life history of ENP *Delphinus* spp. populations, and the first opportunity to compare life history traits for these two closely related species in an area where they are sympatric.

METHODS

Study Area

Our study area corresponded to the known range of *D. capensis* in the ENP. This species' range extends south from central California, U.S.A., to the southern tip of Baja California, Mexico, and from the coast to a maximum of 150 km offshore (Fig. 2). These dolphins are found primarily on the continental shelf, and along the coast of Baja California, the species rarely occurs in waters more than 1,000 m deep (Gerrodette and Eguchi 2011). The eastern edge of the ENP range of *D. delphis* overlaps that of *D. capensis*, and while *D. delphis* are resident within the study area, they are likely part of a larger population that extends farther west. The ecosystem is productive largely due to coastal upwelling driven by the California Current, an eastern boundary current. The islands and bathymetry of the Southern California Bight (SCB) further modify oceanographic characteristics to define the region's ecosystem characteristics (Dailey *et al.* 1993). The influence of dominant oceanographic currents and coastal features on the ecosystem has led to the identification of three biogeographical regions within the study area: (1) the Southern Californian, from south of Point Conception to Santa Monica Bay, (2) the Ensenadian, from Santa Monica Bay to Punta Eugenia, and (3) the Magdalenan, or California Transition Zone, from Punta Eugenia to Cabo San Lucas (Hall 1964, Valentine 1966).

Data

Two types of data were used to estimate the parameters presented in this paper: specimen and aerial photogrammetric data, and we provide a schematic to show the flow of information from data to parameter estimates (Fig. 3). The specimen data were collected within our study area between 1963 and 2011 from dolphins incidentally killed in fisheries or stranded on the beach. All records were reviewed for data quality and completeness, and only specimens whose data could be verified were included in analyses. Vertical aerial photographs of dolphin schools were taken between 16 September and 17 November 2009 during a dedicated study of *Delphinus* spp. The study was primarily a line transect survey designed to estimate population abundance conducted aboard the NOAA Ship *McArthur II* (Chivers *et al.* 2010, Carretta *et al.* 2011). Photographs were taken with three Canon EOS-1 DS Mark III digital cameras mounted with Zeiss 85 mm lenses and fired simultaneously from a

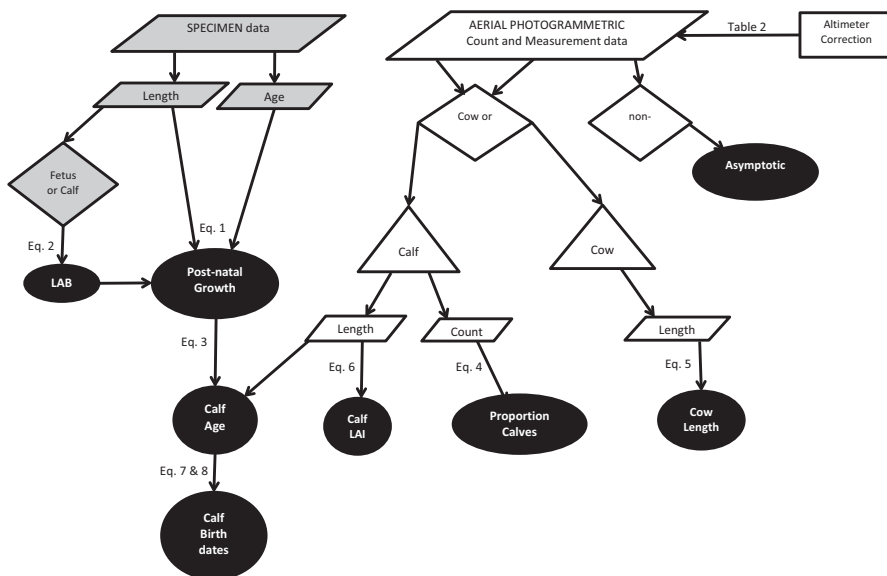


Figure 3. Schematic showing the flow of information from data source: specimen (gray) and aerial photogrammetric (white) data, to parameter estimates (black). The equation number (*i.e.*, Eq. #) identifies the model used to generate parameter estimates. Abbreviations: LAB for length-at-birth; LAI for length-at-independence.

forward-motion-compensating mount placed in the belly of the NOAA Twin Otter aircraft used for this study (http://www.aoc.noaa.gov/aircraft_otter.htm). A Honeywell RT-300 series twin antenna radar altimeter was used to measure altitude for each school photographed, and the altitudes recorded ranged from 600 to 800 ft (183 to 244 m). The aircraft photographed schools opportunistically in the vicinity of the ship's operations, occasionally sampling the same schools, in calm seas (*i.e.*, sea states < 3).

Specimen data—Two independent data sets for both species of common dolphin were compiled from specimens recovered as bycatch or strandings. One included all specimens with a standard total body length (Norris and Prescott 1961) recorded along with adequate information available to classify the specimen as a fetus or calf. We classified specimens as fetuses if they were removed from a female dolphin's uterus or presented with evidence that the dolphin had not taken a breath (*i.e.*, lungs had not been inflated). The specimens identified as calves were those that had evidence of having taken a breath (*i.e.*, lungs inflated, umbilicus healed), had rostral hair or fetal folds present, or milk present in the stomach. Inflated lungs float when placed in water, but the assessment is only valid for fresh dolphin specimens because gasses released during decomposition will cause a lung to float and result in false positives. For decomposed specimens, the other aforementioned metrics were used to distinguish fetuses and calves. The data set assembled included 19 *D. capensis* and 24 *D. delphis* fetal specimens and 69 *D. capensis* and 40 *D. delphis* calf specimens.

The other data set included specimens with standard total body length recorded and teeth collected for age determination. We determined age by counting growth layer groups (GLGs) in teeth prepared using the methods described in Myrick *et al.* (1983) and Lockyer (1995). Each GLG was equated to 1 yr, which is generally considered appropriate for small delphinids and is consistent with results of growth

layer deposition rates for spinner dolphins (Myrick *et al.* 1984) and common dolphins (Gurevich *et al.* 1980). Two readers independently aged each specimen three times without knowledge of the data available for each specimen or previous GLG counts. Each reader ages specimens <3 yr to a fraction of a year, and older specimens to the nearest whole year. The final age for a specimen is the mean of all readings rounded to the nearest 0.1 yr. The data set assembled included 120 *D. capensis* and 275 *D. delphis* specimens ranging in age from 0 to 31 yr old. The two specimen data sets are independent such that calves with age determined are only included in this data set and not the fetal-calf specimen data set.

Aerial photogrammetry data—Images of dolphin schools were taken at f5.6 in aperture priority mode with shutter speeds averaging 1/1,000th of a second. The three digital cameras were configured so that the central camera provided a vertical image and the two outboard cameras were mounted to collect shallow angle oblique images with about 10% overlap with the central camera. When a single composite image was assembled from the images taken simultaneously by all three cameras, the cross-track distance covered was comparable to that of the medium-format military reconnaissance film camera images used in earlier dolphin studies (Perryman and Lynn 1993, 1994).

After the field season, images taken simultaneously by the three cameras were merged into a single image and reviewed for quality in Adobe PhotoShop CS4 Extended. Counts were made and measurements taken using tools available in the software. The highest quality composite images were used to count dolphins, and dolphin lengths were only measured in images taken with the vertically oriented center camera. We followed the methods used in prior studies (Perryman and Lynn 1993, 1994, Cramer *et al.* 2008), and present only a summary of the methodology here.

Count data—Dolphins were counted in the composite images created for each school photographed using the images that captured all or most of the school. We recorded the number of calves, noncalves and cow-calf pairs for each school. Cow-calf pairs were identified by evaluating (1) the close proximity of two dolphins swimming together relative to others in the school, (2) the size of the smaller dolphin relative to the adult's length, and (3) the position of the smaller dolphin relative to the adult. Small dolphins swimming in calf position with an adult sized dolphin were classified as "calves." The adult sized dolphin was assumed to be the adult female that gave birth to the calf, and we refer to these dolphins as "cows." Additional "calves" were identified by their small size. All other dolphins counted were considered noncalves if they did not meet the above criteria for cows and calves.

Measurement data—Each dolphin swimming parallel to and near the surface in the vertically oriented central camera images was measured from the tip of the rostrum to the rear edge of the flukes (Fig. 4). Measurements were recorded in pixels and converted to cm using the focal length of the camera lens and altitude of the plane. We compared the factory specified focal length of the lenses (85 mm) by measuring objects of known size from a known distance and found that no correction to the published focal length was necessary. To test the accuracy of the altimeter system, we collected a series of images of 15.24 m PVC pipes towed behind kayaks. We calculated altitude based on measurements of the pipes in each frame and compared them with the altitudes recorded by the precision output of the Honeywell RT-300 series twin antenna radar altimeter. We detected a small but consistent negative bias in recorded altitude and used the regression coefficients obtained in this comparison to correct the recorded altitude for each image from which we measured dolphin lengths



Figure 4. Dolphin lengths were measured from the tip of the rostrum to the notch of the tail flukes (black lines) in vertical aerial photographs.

(Table 1) (Perryman and Westlake 1998, Mocklin *et al.* 2010). The corrected altitude was used to convert dolphin lengths measured in pixels from photographs to true dolphin length in cm for analyses.

Analyses

All data analyses were done in R v3.0.1 (R Core Team 2013) with rjags v 3-10 running JAGS 3.3.0 (Plummer 2013). Five Markov Chain Monte Carlo (MCMC) chains were run to fit each model with a 10,000 iteration burn-in and a 200 iteration thinning interval so that 10,000 posterior MCMC samples were saved for each chain. Noninformative priors were specified for all model parameters. Any modifications to these run specifications are included with the model descriptions. Evidence of good mixing and lack of autocorrelation in the sampling of posterior distributions was evident in all model runs. Convergence was evaluated using the Coda library

Table 1. Regression coefficients used to convert dolphin length measurements made from aerial photographs in pixels to centimeters.

	Coefficients	SE	LCL ^a	UCL ^b	T-statistic	P-value	Ho: ($\alpha = 5\%$) rejected?
Intercept	7.1600	1.176	4.787	9.533	6.088	<0.0001	Yes
Altimeter (m)	0.9844	0.0046	0.975	0.994	212.580	<0.0001	Yes

^aLower value of a reliable interval.

^bUpper value of a reliable interval.

implemented in R v3.0.1 to examine heterogeneity among chains and convergence of individual chains (Plummer *et al.* 2006). Model posterior statistics are summarized in the online Supporting Information.

Analyses of the parameters estimated from the aerial photogrammetric data included a test for evidence of regional variability that would be consistent with population-level adaptations. Because several studies of coastal marine species have revealed biogeographical concordance with the bioregions recognized within our study area (*e.g.*, Dawson 2001, Horn *et al.* 2006, Blanchette *et al.* 2008), we used them as an *a priori* stratification scheme for our analyses with the following modification. We subdivided the Ensenadian region, because there is an apparent hiatus in distribution of *Delphinus* spp. (Hamilton *et al.* 2009, pp. 22–23) and a change in width of the continental shelf coincident with the U.S.A.-Mexico border. Thus, we recognized four biogeographical regions in our analyses and refer to them as (1) Southern Californian, (2) Ensenadian-U.S.A., (3) Ensenadian-Mexico, and (4) Magdalenan. Regions (1) and (2) correspond to the northern and southern parts, respectively, of the SCB in U.S.A. waters (Fig. 2).

Specimen Data

Postnatal growth—The first step in estimating growth rates is to estimate the average length-at-birth (LAB), which we estimated using the following logistic likelihood function to fit the length data for fetal and calf specimens:

$$\begin{aligned} \text{Born}_{ij} &\sim \text{Bernoulli}(\mu_{ij}) \\ \mu_{ij} &= d_0 + d_1 l_{ij}, \end{aligned} \quad (1)$$

where Born_{ij} is whether the i -th specimen for the j -th species with length l (cm) had been born (*i.e.*, 0 for fetuses, not born, and 1 for calves, born). The model parameters and their priors were d_0 : Uniform(-50, 0) and d_1 : Uniform(0, 1). LAB is estimated as the ratio of these parameters for each species and is equivalent to $P(\text{Born}) = 0.5$. The posterior mean and 95% Highest Density Interval (HDI) for LAB were used as an informative prior for L_0 in Equation 2.

Two-phase Gompertz growth models have been shown to provide the best fit to age-length data for small delphinids (Perrin *et al.* 1976, Danil and Chivers 2007, Larese and Chivers 2009, Jefferson *et al.* 2012). After verifying that this model provided the best fit to our data, we used the following normal likelihood function with data from each species:

$$\begin{aligned} x_i < c : y_i &\sim \text{Normal}(L_0 * \exp\{a_1[1 - \exp(-b_1 * x_i)], \sigma_1^2\}) \\ x_i \geq c : y_i &\sim \text{Normal}(L_c * \exp\{a_2[1 - \exp(-b_2 * x_i)], \sigma_2^2\}), \end{aligned} \quad (2)$$

where x_i is the age (yr) and y_i the total body length (cm) of the i -th sample. The model parameters and their prior distributions are:

c = age at the change point between curves: Uniform(2, 20)

L_0 = length at age 0: Normal distribution specified using the posterior distributions of the LAB model (Eq. 1),

L_c = length at the change point given parameters L_0 , a_1 and b_1 ,

a_1 and a_2 = scale parameters: Uniform(-5, 5),

b_1 and b_2 = slope parameters: Uniform(-20, 15),

σ^2_1 and $\sigma^2_2 = \text{variance: Uniform}(0, 30.0)$.

We constructed the model using all age classes to ensure proper estimation of growth rates but restrict our summary of model fits to size-at-age for ≤ 2 yr of age, because (1) data for both sexes were included in the analysis because the sex of dolphins in aerial photographs cannot be determined, and (2) they are the only ages for which growth rate estimates are of interest in this study.

Estimating age from length—In order to include uncertainty in the estimation of age from length, a posterior age distribution for each calf measured in aerial photographs was calculated using Equation 14 in Schwarz and Runge (2009), which is:

$$P(\text{age}_i | \text{length}_j) = \frac{\frac{x_{ij}}{l} \bullet z_i}{\sum_{l=1}^m \frac{x_{lj}}{l} \bullet z_l}, \quad (3)$$

$$\frac{\sum_{m=1}^m \frac{x_{im}}{l} \bullet z_i}{\sum_{l=1}^m \frac{x_{lm}}{l} \bullet z_l}$$

where x_{ij} is the number of random draws in each age class i for length j , z_i is the probability of age i , l is the number of length classes, and m is the number of age classes. We used the stable age distribution estimated for the central population of *D. delphis* in Danil and Chivers (2007) as the independent prior for z . This method uses binned data: 1 cm length classes and 0.05 yr age classes, rather than continuous data to estimate the probability that an animal of a given length is a particular age to ease computations (see p. 1778 in Schwarz and Runge 2009). The posterior distribution is obtained by estimating length 20,000 times for each age class using a random draw of age within the age class and random draws from the posterior distribution of each coefficient for the postnatal growth model described above (Eq. 2). The posterior distribution generated for age-at-length was used to generate a posterior distribution of 10,000 ages for each calf measured in the aerial photographs.

Aerial Count Data

Proportion calves—Dolphin counts made from aerial photographs were used to estimate the proportion of calves (calves/total number of dolphins counted) in each school. We compared the estimates between species with the following multifactor likelihood function using the data matrix approach of Ntzoufras (2009), which is a Bayesian equivalent for an analysis of variance:

$$Y_{ijkl} \sim \text{Binomial}(N_{ijkl}, p_{ijkl}) \quad (4)$$

$$\text{Logit}(p_{ijkl}) \sim a_0 + a_{1j} + a_{2k} + a_{3l} + a_{4jk} + a_{5jl} + a_{6kl} + a_{7jkl},$$

where y_i = the number of calves, N_i = the total number of dolphins, and p_i = the estimated proportion of calves in the i -th school. *Logit* is the sigmoidal function used to predict a binary response. Model parameters and their priors are:

α_0 = the overall mean: Normal(mean = 0, variance = 1,000),

α_{1j} = coefficient for species ($j = 1$ for *D. capensis*, 2 for *D. delphis*): Normal(0, 1,000),

α_{2k} = coefficient for area ($k = 1-4$ for the biogeographical regions: Southern Californian, Ensenadian-U.S.A., Ensenadian-Mexico, and Magdalenan): Normal(0, 1,000),

α_{3l} = coefficient for sample type ($l = 1$ for partially and 2 for completely sampled schools): Normal(0, 1,000),

α_{4jk} = coefficient for the species, area interaction: Normal(0, 1,000),

α_{5jl} = coefficient for the species, sample type interaction: Normal(0, 1,000),

α_{6kl} = coefficient for the area, sample type interaction: Normal(0, 1,000),

α_{7jkl} = coefficient for the species, area, sample type interaction: Normal(0, 1,000).

The estimated proportion of calves provides an index of calf production (calf/female), or birth rate, when adjusted for the sex ratio of the population. We assumed a sex ratio of 1:1 males:females, which is generally expected for populations of unexploited small delphinids, and doubled the estimated proportion of calves for each species to convert them to per capita female birth rates (Perrin and Reilly 1984). The birth rate estimates were compared to pregnancy rates estimated from hormone concentrations in the blubber of female dolphins sampled during this study and reported by Kellar *et al.* (2014) to provide insight about fetal and neonatal mortality.

Aerial Measurement Data

Dolphin length—For each species, we estimated asymptotic length and mean cow length for dolphins measured in aerial photographs. The asymptotic length we report is the 99th percentile of the length distribution (Barlow and Boveng 1991), which we consider an estimate of asymptotic length appropriate for males because of the magnitude of sexual dimorphism in these species (Heyning and Perrin 1994).

Cow size—The mean length of cows provides an equivalent estimate of the mean length of mature females that is typically estimated for cetaceans using specimen-based data (Perrin and Reilly 1984). Using the measurement data for cows photographed, we examine variability in size between species among biogeographical regions with the following multifactor likelihood using the data matrix approach of Ntzoufras (2009):

$$Y_{ijk} \sim \text{Normal}(\mu_{ijk}, \sigma^2) \quad (5)$$

$$\mu_{ijk} = \beta_0 + \beta_{1j} + \beta_{2k} + \beta_{3jk},$$

where y_{ijk} is cow length (cm) of the i -th dolphin measured. Model parameters and their priors are:

β_0 = the overall mean: Normal(0, 1,000),

β_{1j} = coefficient for species ($j = 1$ for *D. capensis*, 2 for *D. delphis*): Normal(0, 1,000),

β_{2k} = coefficient for area ($k = 1-4$ for the biogeographical regions: Southern Californian, Ensenadian-U.S.A., Ensenadian-Mexico, and Magdalenan): Normal(0, 1,000),

β_{3jk} = coefficient for the species, area interaction: Normal(0, 1,000)

σ^2 = model precision: Uniform(0, 10).

Length-at-independence—Average length-at-independence (LAI) is the length at which the probability of a calf swimming alone is 0.5 and was estimated using the following multi-factor likelihood function:

$$\begin{aligned} \text{Alone}_{ijk} &\sim \text{Bernoulli}(p_{ijk}) \\ \text{Logit}(p_{ijk}) &\sim \delta_0 + \delta_{1i} + \delta_{2ij} + \delta_{3ik} + \delta_{4ijk}, \end{aligned} \quad (6)$$

where Alone is whether the i -th dolphin sampled from the j -th species in the k -th area was observed alone (*i.e.*, 0 for calves and 1 for noncalves). LAI is estimated as the ratio of the model parameters: $-(\delta_0/\delta_1)$. A 100 iteration thinning interval was used for each chain of this model. Model parameters and their priors are:

- δ_0 = the overall mean: Normal(0, 1,000),
- δ_{1i} = coefficient for length (cm): Normal(0, 1,000),
- δ_{2j} = coefficient for species ($j = 1$ for *D. capensis*, 2 for *D. delphis*): Normal(0, 1,000),
- δ_{3k} = coefficient for area ($k = 1-4$ for the biogeographical regions: Southern Californian, Ensenadian-U.S.A., Ensenadian-Mexico, and Magdalenan): Normal(0, 1,000),
- δ_{4ijk} = coefficient for the species, area interaction: Normal(0, 1,000).

We converted the LAI estimates to age using Equation 3 and report the average age-at-independence (AAI) equivalent for this parameter with the uncertainty associated with converting length to age.

Calving seasons—To characterize calving seasons, we generated a distribution of birth dates for each species by back-calculating when the calves sampled in 2009 were born:

$$\text{BirthDay}_i = \text{SamplingDay}_i - \text{Age}_i \quad (7)$$

where SamplingDay is the ordinal day an aerial photograph was taken and Age, in days, is estimated from Equation 3 for the i -th calf measured. We then compared the distributions of birth dates between species among biogeographical areas and schools using the following multilevel Bayesian model:

$$Y_{ijkl} \sim \text{Normal}(\gamma_0 + \gamma_{1ij} + \gamma_{2ik} + \gamma_{3il}, \sigma^2), \quad (8)$$

where y_{ijkl} is the estimated BirthDay for the i -th calf in the photogrammetric data set sampled from the j -th species in the k -th area from the l -th school. Model parameters and their priors are:

- γ_0 = overall mean: Normal(0, 1,000),
- γ_{1ij} = coefficient for species ($j = 1$ for *D. capensis* and 2 for *D. delphis*): Normal(0, 1,000),
- γ_{2ik} = coefficient for area ($k = 1-4$ for the biogeographical regions: Southern Californian, Ensenadian-U.S.A., Ensenadian-Mexico, and Magdalenan): Normal(0, 1,000),
- γ_{3il} = coefficient for school ($l = 1-56$ for *D. capensis* and 1-29 for *D. delphis*): Normal(0, 1,000),
- σ^2 = variance: Uniform(0, 150).

RESULTS

Specimen Data

Postnatal growth—The posterior mean estimates of LAB (Eq. 1) were 88.7 cm (95% HDI: 81.9–94.8 cm) for *D. capensis* and 72.2 cm (95% HDI: 61.0–81.2 cm) for *D. delphis* (Table S1a, Fig. S1, Fig. 5).

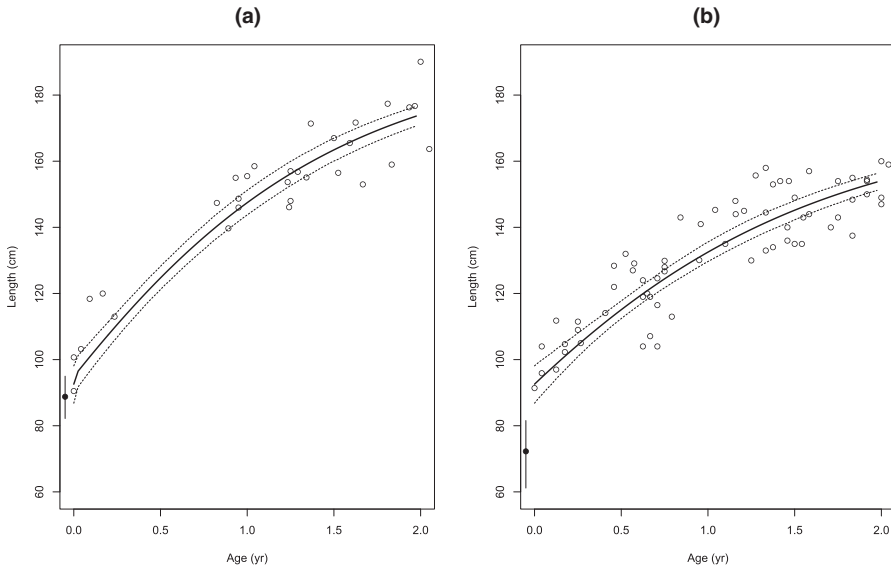


Figure 5. The posterior mean (solid line) and 95% HDIs (dashed line) of the postnatal growth model is shown along with the specimen data (o) for calves aged 0–2 yr for (a) *D. capensis* and (b) *D. delphis*. The posterior mean and 95% HDIs for the length-at-birth (LAB) estimate generated by the logistic model is shown (solid dot and vertical bars) slightly offset from age 0 for visibility.

The Gompertz growth model (Eq. 2) estimated size at age 0 yr was 94.8 cm (95% HDI: 89.9–99.6 cm), at age 1 yr was 147.8 cm (95% HDI: 144.2–151.6 cm), and at age 2 yr was 174.0 cm (95% HDI: 171.1–176.7 cm) for *D. capensis*. Similarly, the estimated size at 0 yr was 89.2 cm (95% HDI: 83.6–95.3 cm), at age 1 yr was 134.7 cm (95% HDI: 131.4–137.9 cm) and at age 2 yr was 153.3 cm (95% HDI: 150.6–156.0 cm) for *D. delphis* (Table S1b, Fig. 5). The length estimates for age 0 yr are longer than LAB, because they were estimated from the model fit to postnatal specimen data with LAB used as an informative prior for L_0 , the starting value, for the model.

Aerial photogrammetric data—We photographed 75 *D. capensis* and 34 *D. delphis* schools that were representative of the sighting distributions for both species throughout the study area (Table 2, Fig. 2; also see fig. 2, 3, and 18 in Chivers *et al.* 2010). Individual dolphins were counted and measured from all of these schools (Table 3, Fig. 6). The three *D. capensis* schools sampled opportunistically in the Gulf of California were included because the size data were comparable to those of other *D. capensis* sampled in the study area.

Aerial Count Data

Proportion calves—The full model was used to estimate the proportion of calves for each species in each biogeographical region, because the multifactor Bayesian model revealed strong support for the main effects: species, area and sample type, and most of the interaction coefficients (Table S2a). The proportion of calves (count of calves/dolphins) in *D. capensis* was 0.045 (95% HDI: 0.017–0.085) compared to

Table 2. Summary of the number and size (dolphin counts) of *Delphinus* spp. schools with aerial photographs taken during 2009.

Species	Schools photographed	Schools completely photographed	School size		
			Mean	Median	Range
<i>D. capensis</i>	75	43	438	309	13–1,529
<i>D. delphis</i>	34	13	551	439	48–2,334

Table 3. Sample sizes for the count and measurement data obtained from vertical aerial photographs taken during 2009.

Species	Counts		Measurements		
	Calves	All dolphins	Calves	Cows	All dolphins
<i>D. capensis</i>	1,484	32,832	411	407	7,774
<i>D. delphis</i>	1,258	18,724	348	378	3,354

0.069 (95% HDI: 0.031–0.138) for *D. delphis* (Table 4). In addition to the strong support for a between species difference in the proportion of calves in the study area (α_1 in Table S2a), there was support for differences between species within each biogeographical region and between regions within species (Table 4, S2b, c, Fig. 7). Additionally, the posterior mean estimates were more variable among regions for *D. capensis* than *D. delphis*. For *D. capensis*, the proportion of calves was highest in the Southern Californian region and lowest in the Ensenadian-Mexico region. For *D. delphis*, the proportion of calves was highest for the Magdalenan region, but with broad HDIs reflecting the influence of small sample sizes resulting in limited support for a difference. The next highest proportion of calves estimate for *D. delphis* was for the Southern Californian region for which there was also limited support for a difference.

The mean proportion of calves equate to a mean birth rate (calf/female) of 0.090, or 9.0%, for *D. capensis* and 0.138, or 13.8%, for *D. delphis*, when a 1:1 sex ratio is assumed. This rate incorporates calf mortality through to ages of calves sampled. In our study, the mean ages characterize the age distributions of calves sampled (Fig. 6), which were 6 and 9 mo for *D. capensis* and *D. delphis*, respectively, with ages ranging from <1 mo to 19 mo.

Aerial Length Data

Dolphin length—Estimated asymptotic length (*i.e.*, the mean length of the 99th percentile of the length distribution) was 241.0 cm (SD = 0.028, $n = 78$) and 208.0 cm (SD = 0.010, $n = 34$) for *D. capensis* and *D. delphis*, respectively.

Cow size—The full Bayesian model was used to estimate and compare cow size by species and biogeographical region (Table 4) even though there was not strong support for the species-region interaction term (Table S3a). *D. capensis* cows were 204.2 cm (95% HDI: 203.0–205.4; $n = 407$), or 21.4 cm larger (95% HDI: 18.7–24.3), than *D. delphis* cows: 182.7 cm (95% HDI: 180.2–185.2; $n = 378$).

Among biogeographical regions, there was support for differences in *D. capensis* cow size for three comparisons: Southern Californian to Magdalenan, Ensenadian-

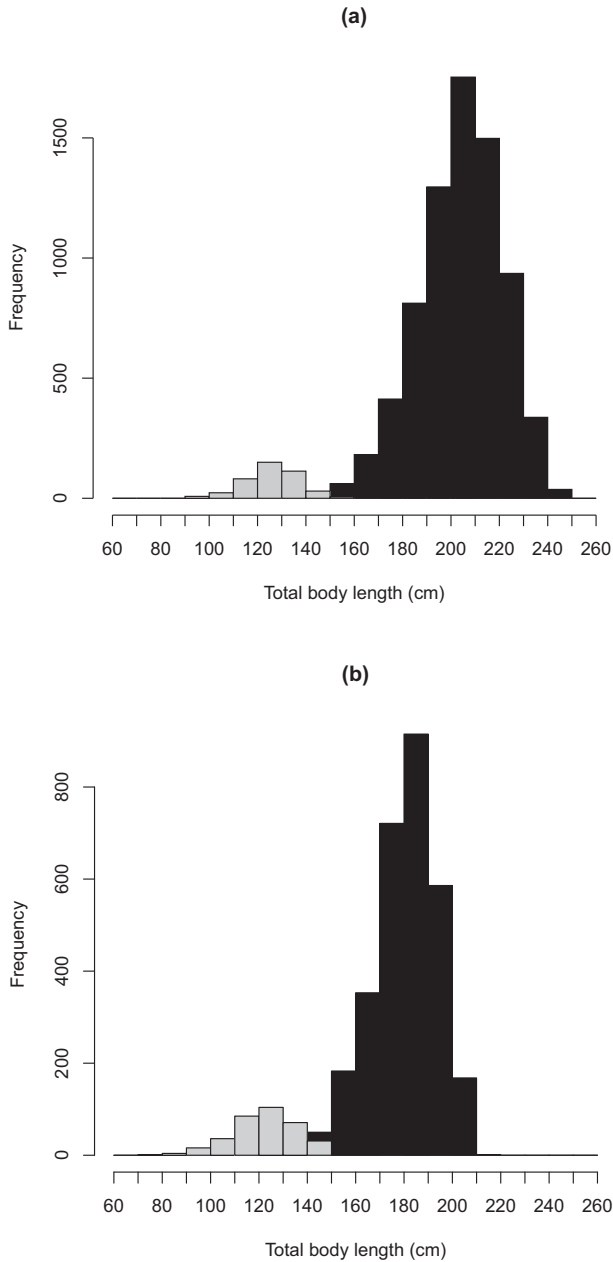


Figure 6. The frequency distribution of calf (gray) and noncalf (black) dolphins measured in aerial photographs for (a) *Delphinus capensis* and (b) *D. delphis*.

U.S.A. to Ensenadian-Mexico and Ensenadian-Mexico to Magdalenan (Table 4, S3b, c). Two of these comparisons were to the southernmost bioregion, the Magdalenan, suggesting cows in this region are approximately 5 cm smaller. However, results of

Table 4. The posterior distributions: means and 95% highest density intervals (HDIs), are summarized for each analyses by species and biogeographical region (see Methods for descriptions). The sample sizes: individual dolphins counted or measured, and number of schools photographed for each analyses and stratum are also presented.

Analysis	Species	Parameter	Study area	Southern			Magdalenan
				Ensenadnian-U.S.A.	Ensenadnian-Mexico	Californian	
Proportion of calves (calf/total dolphin count)	<i>D. capensis</i>	Mean	0.045	0.034	0.081	0.020	0.043
		95% HDI <i>n</i> (individuals, schools)	(0.017–0.085) (1,403, 63)	(0.030–0.038) (495, 31)	(0.075–0.088) (632, 18)	(0.016–0.024) (88, 6)	(0.037–0.049) (188, 8)
	<i>D. delphis</i>	Mean	0.069	0.053	0.066	0.042	0.114
		95% HDI <i>n</i> (individuals, schools)	(0.030–0.137) (1,258, 33)	(0.046–0.060) (1012, 26)	(0.056–0.076) (154, 4)	(0.032–0.053) (84, 2)	(0.056–0.189) (8, 1)
Cow size (cm)	Difference	Mean	-0.024	-0.018	0.016	-0.022	-0.071
		95% HDI	(-0.095–0.028)	(-0.027–0.009)	(0.004–0.027)	(-0.034–0.011)	(-0.146–0.012)
	<i>D. capensis</i>	Mean	204.2	203.4	205.3	207.5	200.5
		95% HDI <i>n</i> (individuals)	(203.0–205.4) (407)	(202.0–204.9) (149)	(204.0–206.6) (187)	(203.8–211.3) (24)	(197.8–203.1) (47)
<i>D. delphis</i>	Mean	182.7	180.7	181.1	183.1	185.9	
	95% HDI <i>n</i> (individuals)	(180.2–185.2) (378)	(179.6–181.7) (302)	(177.8–184.5) (29)	(180.4–185.9) (43)	(176.9–194.9) (4)	
LAI (cm)	Difference	Mean	21.5	22.7	24.2	24.4	14.6
		95% HDI	(18.7–24.2)	(20.9–24.5)	(20.6–27.7)	(19.8–29.0)	(5.2–23.9)
	<i>D. capensis</i>	Mean	145.1	145.3	145.9	144.8	144.3
		95% HDI <i>n</i> (individuals)	(142.4–147.5) (7,772)	(143.6–146.7) (3,537)	(143.5–148.1) (1,792)	(142.9–146.6) (1,341)	(141.5–146.9) (1,102)
<i>D. delphis</i>	Mean	140.1	140.4	140.9	139.9	139.3	
	95% HDI <i>n</i> (individuals)	(137.5–142.5) (3,353)	(138.9–141.8) (2,663)	(139.0–142.8) (392)	(137.8–141.7) (265)	(136.3–142.2) (33)	
Difference	Mean	4.9					
	95% HDI	(2.7–7.1)					

(Continued)

Table 4. (Continued)

Analysis	Species	Parameter	Study area	Southern			Magdalenan
				Californian	Ensenadian-U.S.A.	Ensenadian-Mexico	
Calving season (ordinal day [month day])	<i>D. capensis</i>	Mean	64.3 [Mar 6]	63.1 [Mar 5]	92.2 [Apr 3]	60.4 [Mar 2]	41.5 [Feb 11]
		95% HDI n (individuals)	(57.9-70.5) (411)	(50.6-76.3) (202)	(82.4-101.7) (138)	(39.3-80.3) (22)	(25.3-58.1) (49)
	<i>D. delphis</i>	Mean	-19.3 [Dec 12]	-20.5 [Dec 11]	8.5 [Jan 9]	-23.3 [Dec 8]	-42.1 [Nov 19]
		95% HDI n (individuals)	(-31.6-7.2) (346)	(-37.6-3.3) (29)	(-1.3-18.8) (279)	(-46.3-0.2) (34)	(-63.7-21.1) (4)
Difference		Mean	83.6				
		95% HDI	(69.0-98.8)				

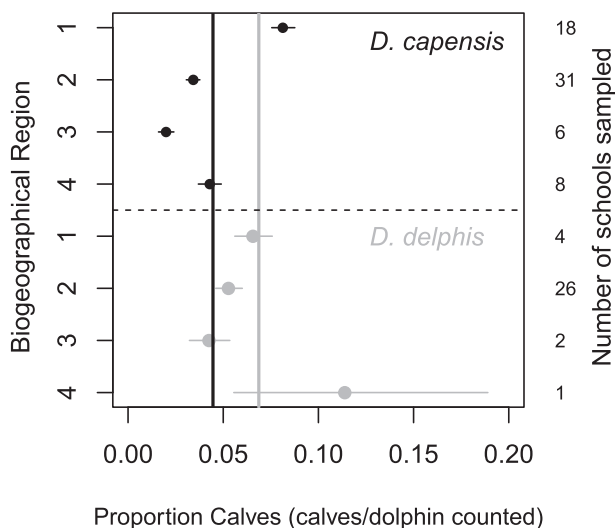


Figure 7. Posterior mean (dots) and 95% HDIs (horizontal solid lines) for the estimated proportion calves in each biogeographical region: (1) Southern Californian, (2) Ensenadian-U.S.A., (3) Ensenadian-Mexico, and (4) Magdalenan for *D. capensis* (black), and *D. delphis* (gray). Vertical lines are the posterior mean proportion calves for each species throughout the study area. See Table 4 for the number of individuals counted.

the regional comparisons are inconsistent, and there is not strong support for a latitudinal gradient in cow size (Fig. 8). No evidence for a difference in cow size among bioregions was detected for *D. delphis*.

Length-at-independence—LAI differed by species but not biogeographical region (Table 4, S4, Fig. 9). LAI estimates were 145.1 cm (95% HDI: 142.4–147.5 cm; $n = 7,772$) and 140.1 (95% HDI: 137.5–142.5 cm; $n = 3,353$) for *D. capensis* and *D. delphis*, respectively.

Using Equation 3, the AAI equivalents for LAI were 11.1 mo (95% HDI: 10.2–12.0 mo) for *D. capensis* and 14.0 mo (95% HDI: 13.6–14.2 mo) for *D. delphis*.

Calving seasons—Calving seasons differed by species, biogeographical region and school, and the full model was used for this analysis (Table 4, S5a). On average, *D. capensis* calves were born 83.7 d (95% HDI: 69.1–88.6) later than *D. delphis* calves with the birth date distributions centered on 6 March 2009 in *D. capensis* and 12 December 2008 in *D. delphis*. Although there was strong support for the species having discrete calving seasons, there was little support for regional differences in the birth date distributions within a species suggesting calving is relatively synchronous within the study area for both species (Table 4, S5b, c). However, estimated birth dates varied considerably among the individual calves sampled with estimates spanning much of the year. Posterior mean estimated birth dates also varied considerably within and among schools (Fig. 10).

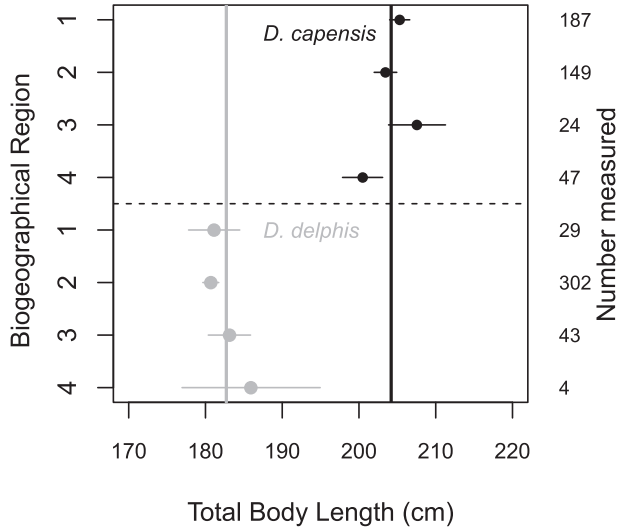


Figure 8. Posterior mean (dots) and 95% HDIs (horizontal solid lines) of cow size by biogeographical region: (1) Southern Californian, (2) Ensenadian-U.S.A., (3) Ensenadian-Mexico, and (4) Magdalenan for *D. capensis* (black) and *D. delphis* (gray). The vertical lines are the posterior mean cow size for each species throughout the study area.

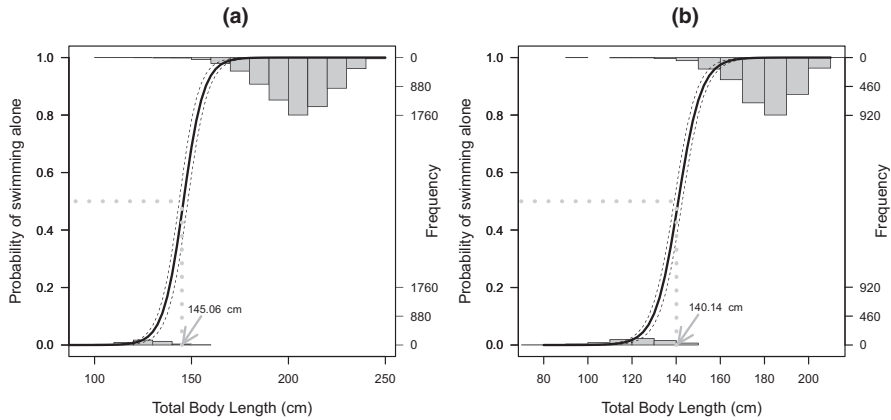


Figure 9. Posterior mean (solid black line) and 95% HDIs (dashed black lines) of the logistic regression fit estimate the average length at 50% of calves are swimming independently (LAI) for (a) *D. capensis* and (b) *D. delphis*. The length frequency data are summarized by 10 cm intervals. The posterior mean estimate of LAI is shown (dashed gray lines and arrow); the 95% HDIs are in Table 4.

DISCUSSION

This study combined specimen and photogrammetric data to estimate reproductive parameters for ENP populations of *D. capensis* and *D. delphis*. The combined data sets were essential to generating birth date distributions, and the Bayesian models propagated uncertainty in calf growth rates to estimated birth dates for calves mea-

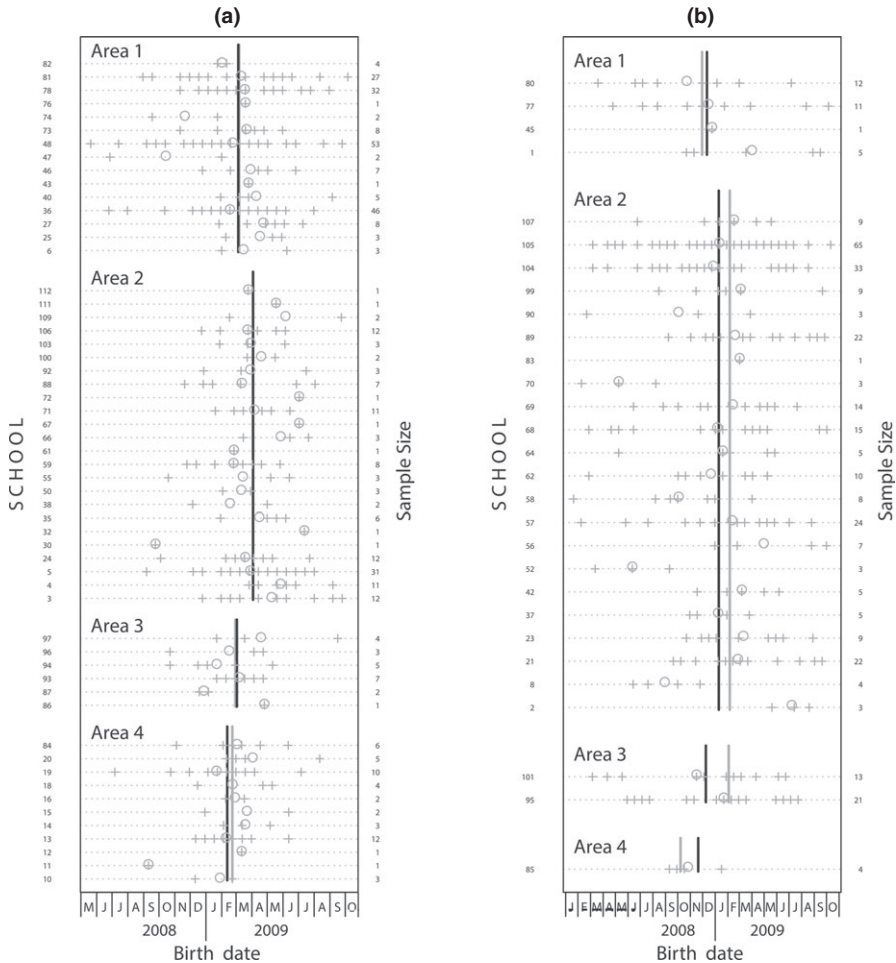


Figure 10. Posterior mean distributions of calf birth dates for (a) *D. capensis* and (b) *D. delphis* by biogeographical region: (1) Southern Californian, (2) Ensenadian-U.S.A., (3) Ensenadian-Mexico, and (4) Magdalenan. The vertical bars indicate the posterior means (black) for each biogeographical region estimated by the model (Eq. 8) and the average (gray) of the posterior mean estimates for each school (o). The posterior mean estimate for each calf sampled (+) is also presented.

sured in aerial photographs. Additional parameters were estimated from the aerial photogrammetric data: cow size, the proportion of calves, and LAI using Bayesian models to quantify uncertainty associated with estimating these parameters from the data collected during our 2009 study. Comparisons of the estimated parameters revealed differences between species as well as some within species variability among biogeographical regions. Each parameter estimate is discussed in turn below.

Proportion calves—There was strong support for differences in the proportion of calves between species within each region and some support for differences among regions. *D. delphis* had higher posterior means than *D. capensis* in all biogeographical

regions except the Southern Californian, but the estimates for *D. capensis* were more variable. There was strong support for *D. capensis* having highest calf production in the Southern Californian bioregion (Table 4), which is an inherently productive area within the SCB (Dailey *et al.* 1993, Clark *et al.* 2005). This regional variability is generally consistent with the spatial variability observed in pregnancy rates during 2009 (Kellar *et al.* 2014). Additional research is needed to determine whether this regional variability is consistent in future years.

The coefficient for sample type (*i.e.*, whether the entire school was sampled or not) was revealed to have an important influence on the estimated proportion calves. The model coefficient was negative indicating a lower sampling rate for calves in partially sampled schools (α_5 in Table S2a). The influence of this source of sampling variability in analyses of aerial data has not been previously reported, but the result is consistent with field observations made from the aircraft that calves tend to be clustered together and that the clusters are randomly placed within schools. While this aspect of structuring within schools of small dolphins has not been quantified from photographs, our results and field observations are consistent with those reported in the literature about the tendency for calves to be clustered in schools of other small dolphin species (Norris and Dohl 1980, Weir *et al.* 2010). This aspect of school structure also means that when schools are scattered over a wide area, they can only be partially photographed, and thus, the sampling of calves may be biased.

We also found that the sampling rates of partially and completely sampled schools differed by species. That is, our data set included fewer partially sampled *D. capensis* schools ($n = 32$ or 43% of schools were partially photographed) than *D. delphis* ($n = 21$ or 62% of schools were partially photographed). We think this suggests behavioral differences (*e.g.*, dolphin swimming depth, sensitivity to the aircraft and school formation) between the species that influences how effectively schools can be sampled from the air, and thus highlights the importance of characterizing this aspect of sampling during aerial missions.

The regional variability detected in the proportion of calves and the influence of sample type on those estimates also raises the question of whether there is age and sex segregation in these populations that may influence estimates of population parameters. There is currently no evidence of segregation in the ENP populations of *Delphinus* spp. In our study, calves were present in 100 of the 109 schools sampled suggesting that segregation may be limited in these populations even though calves tend to be clustered together in schools and the proportion of calves varied regionally. Additionally, the large school sizes observed (Table 2) (Carretta *et al.* 2011) suggests school structure and dynamics within the ENP populations may differ from those of the northeast Atlantic populations of *D. delphis* in which age and sex segregation has been well documented (Murphy 2004, Murphy *et al.* 2013).

The estimated birth rates: 9.0% and 13.8% for *D. capensis* and *D. delphis*, respectively, were converted from the estimated proportion calves assuming a 1:1 male:female sex ratio in the population. The pregnancy rates for *D. capensis* and *D. delphis* estimated from steroid hormones quantified for females sampled during the 2009 study were 22.1% and 28.1%, respectively (Kellar *et al.* 2006, Kellar *et al.* 2014). Assuming a similar proportion of females are pregnant and give birth each year, the discrepancy corresponds to birth rates that were 59.3% and 50.9% lower than pregnancy rates in *D. capensis* and *D. delphis*, respectively. If no fetal loss occurs during pregnancy, pregnancy rates would equate to birth rates and discrepancies between the rates would increase with calf age due to calf mortality. The mean age of calves sampled was <1 yr, and thus we expected birth rates would be $\leq 20\%$ lower than preg-

nancy rates depending on the age distribution of calves sampled given a first year mortality rate of 18.9% for common bottlenose dolphins (*Tursiops truncatus*), which we consider a reasonable model species for small delphinids (Wells and Scott 1990). The apparently large discrepancy in rates we observed suggests few calves were born, or that fetal or calf mortality was high for the 2009 cohort. However, interpreting the apparently large discrepancy between rates is complicated because our reproductive rate estimates are out-of-phase. That is, the pregnant females sampled in 2009 are expected to produce a calf during the next (2010) calving season and no pregnancy rate estimates are available for females who produced calves in 2009.

Interannual variability in birth rates would be expected because of the multiyear calving cycles for adult females (*i.e.*, tropical *D. delphis* have a 2 yr calving interval Danil and Chivers 2007) and the influence of environmental variability on the availability of prey quality and quantity that likely influences the body condition of breeding females. There are no data yet to quantify interannual variability in reproduction for either common dolphin species, but oceanographically, 2009 was anomalous. In the spring, there was insufficient wind to generate upwelling that typically occurs in this region, and in the fall, a moderately strong El Niño was influencing the oceanography of the region (NOAA 2013). The lack of spring upwelling severely limited prey availability and was considered the cause of a large die-off in newly weaned and yearling California sea lions (*Zalophus californianus*; Melin 2010). This event may also have impacted the ability of adult female dolphins to forage and feed a calf, especially the youngest, nutritionally dependent calves that were born in the spring of 2009, and may have contributed to the observed discrepancy between pregnancy and birth rates. Similarly, the fall El Niño may have negatively impacted reproductive success as these oceanographic conditions have been correlated with reduced calf production in ETP *Stenella* spp. populations (Cramer *et al.* 2008). Future work to quantify inter-annual variability in pregnancy and birth rates will help refine our understanding about how variable these rates are and how to interpret discrepancies between them.

Dolphin length and cow size—Examining the size of all dolphins, and the subset identified as cows measured in aerial photographs allowed us to verify that the photographic measurements were comparable to those published from specimen data for these species in the ENP.

Our results for asymptotic length are only slightly longer than those previously published for males by Heyning and Perrin (1994): 235 cm for *D. capensis* ($n = 15$) and 201 cm for *D. delphis* ($n = 28$) and likely reflect differences in sample sizes between studies. Similarly, the adult female sizes reported here are similar to those previously reported for sexually mature females from specimens collected in our study area: 207.7 cm in *D. capensis* ($n = 37$) and 180.1 cm in *D. delphis* ($n = 10$) (Heyning and Perrin 1994).

The 2009 aerial data set also provided an opportunity to examine variability of cow size within the study area. Dolphin size may differ if dolphins become uniquely adapted to different habitats as is evident in the markedly different sizes of central and northern stocks of ETP *D. delphis* (Perrin *et al.* 1985). Our analyses did not reveal strong evidence for differences in cow size among the biogeographical regions for either species, but the results for *D. capensis* suggest that cows may be 5 cm shorter in the southernmost bioregion, the Magdalenan. That is, two of the three comparisons to the Magdalenan region were significant for *D. capensis* suggesting that re-examining this question of morphological variability may be appropriate when larger sample sizes are available. No evidence for a difference in size among bioregions was detected

for *D. delphis*. While our results may be due in part to having relatively few samples collected off Baja, there is no published information to suggest a size gradient occurs in our study area.

Length-at-independence—LAI provides an estimate of the size at which a calf transitions from swimming in cow-calf formation to swimming independently. In the literature, the term has been used interchangeably with weaning although there is little evidence to link the two (Clapham *et al.* 1999). Age is likely a better metric for this transition and one that will facilitate comparisons among species.

Analyses of our data set estimated LAI to be 145.1 cm (\approx 11.1 mo) and 140.5 cm (\approx 14.0 mo) for *D. capensis* and *D. delphis*, respectively. Our expectation is that LAI will be longer than average length-at-weaning, which is the size at which calves begin eating solid food (see Archer and Robertson 2004), because we expect this parameter characterizes when calves begin spending more time foraging alone. Similarly, we would expect AAI to be older than average age-at-weaning. Unfortunately, estimates of age-at-weaning and length of the lactation period are not currently known for ENP *Delphinus* spp. populations.

The only other estimates of LAI available for small delphinids are those published by Cramer *et al.* (2008) for *Stenella* spp. in the eastern tropical Pacific Ocean (ETP). Their study provides evidence that LAI, which is equivalent to their LAD, likely occurs after weaning and may reflect condition of the pantropical spotted dolphin population. For example, the average age-at-weaning estimates for pantropical spotted dolphin calves is 9 mo (Archer and Robertson 2004), and the LAI estimates presented by Cramer *et al.* (2008) equate to ages ≥ 3 yr. These results suggest that cow-calf associations extend more than two years beyond the start of weaning. Additionally, the temporal change in LAI estimates reported by Cramer *et al.* (2008) suggests the parameter is flexible and may be linked to other processes, including, but not limited to, an individual female's condition, which may be influenced by habitat quality or exploitation history where the dolphins live.

Like ETP pantropical spotted dolphin, the LAI for ETP eastern spinner dolphins equates to an older age at independence than we estimated for ENP common dolphin populations. The LAI differences between ETP and ENP dolphin species may in part be explained by differences in the exploitation histories of their populations. Both ETP dolphin populations were well below carrying capacity and were continuing to experience fishery mortality when studied (Gerrodette and Forcada 2005, Wade *et al.* 2007, Cramer *et al.* 2008). On the otherhand, the available information for the ENP common dolphin populations we studied indicates they have been insignificantly impacted by fishery, or any other human caused, mortality (Barlow *et al.* 1994, Carretta *et al.* 2014) such that their life history parameters likely reflect those of unexploited dolphin populations. Life history studies to further our understanding of LAI, and more generally, how changes in habitat quality or population density influence reproductive parameters are essential to identify appropriate parameters for monitoring population condition. The available evidence suggests LAI may be a valuable parameter to monitor.

Calving seasons—This particular analysis highlights the value of using (1) Bayesian methods and (2) aerial photogrammetric techniques. The use of Bayesian methods allowed uncertainty to be propagated among models. Thus, the uncertainty evident in the posterior distribution of birth dates for calves measured in aerial photographs (Fig. 10) incorporates the uncertainty in converting length to age, which incorporates the uncertainty in individual size at birth and early postnatal growth rates estimated from specimen data (Fig. 5). Additionally, the large sample of calves measured in the

aerial photographs taken during 2009, contributed to characterizing the uncertainty in calf birth dates used to quantify the calving seasons for populations of ENP common dolphins.

The calving season of ENP *D. capensis* has been unknown until this study and uncertain for ENP *D. delphis*. The available literature provides evidence of fall, winter, spring, and early summer calving in *D. delphis* off California and Baja California, Mexico (Hui 1973, Evans 1975, Perryman and Lynn 1993, Ferrero and Walker 1995). While this apparent uncertainty suggests a protracted calving season, the variability in estimated birth dates observed in our 2009 study (Fig. 10) indicates that these studies had too few samples to adequately characterize the breeding season. For example, the study by Evans (1975) included only 8 fetuses and 26 calves, and the Perryman and Lynn (1993) study included only 75 calves. Similarly, differences among studies may also be due to the use of different LAB and early postnatal growth rate estimates used to back calculate birth dates. For example, the LAB estimates for *D. delphis* were previously inferred from one sample collected in the CNP: 82 cm (Ferrero and Walker 1995) and one sample collected off California: 82.9 cm (Hui 1973). Given these caveats, our results are not inconsistent with those of earlier studies conducted within our study area.

From our analyses, we conclude that calving peaks in winter for *D. delphis* and in early spring for *D. capensis*. This timing coincides with early spring upwelling in the SCB for *D. capensis* and the winter extension of the Davidson Current into the SCB for *D. delphis* (Hickey 1998). Thus calving appears to occur during periods of high productivity in the SCB. However, calving seasons would be expected to correspond to the season of highest productivity as measured by prey biomass. Again, the calving seasons coincide with seasonal peaks in anchovy biomass, which occur in the winter and spring quarters, as primary production is increasing (Smith and Eppley 1982), an example of the “match-mismatch” hypothesis first proposed by Cushing (1969). While prey composition is poorly known for these small delphinid species, we expect anchovy to provide a reasonable index of SCB ecosystem productivity for them.

One additional study, presented evidence for a summer (*i.e.*, June, July, and August) breeding season for *D. delphis* off southern California (Kellar *et al.* 2009). This apparent discrepancy between calving and breeding seasons needs further investigation. We expect the two seasons to overlap because gestation time is approximately 11 mo (Danil and Chivers 2007) and that there will be as much variability in estimated breeding dates as we observed in individual birth dates (Fig. 10). Thus, delineating the breeding seasons for common dolphins will require a large sample size of individual dolphins collected over a large portion of the habitat occupied by these species. We think that the sample size in the Kellar *et al.* (2009) study (*i.e.*, $n = 114$) was too small and limited geographically to accurately characterize the breeding season of *D. delphis*.

Conclusions

In addition to providing valuable knowledge about the life history of *D. capensis* and *D. delphis* off the west coast of California, U.S.A., and Baja California, Mexico, this study demonstrates the value of aerial photography to effectively sample cetacean populations for life history studies. The life history parameters presented are primarily associated with reproduction. Predominantly winter-spring calving peaks were revealed for both species of common dolphin with an offset in peak calving of approximately 12 wk between species. This is the first evidence suggestive of a biological

mechanism of reproductive isolation being in place for these two species. *D. capensis* calves swim independently approximately 3 mo earlier than *D. delphis*, which may indicate *D. capensis* have slightly different life history characteristics that may include a shorter interbirth interval than *D. delphis*. While this result has the potential to result in higher reproductive rates, the proportion of calves in *D. capensis* was generally lower and more variable than in *D. delphis*. Until additional data are available, we will not know how to interpret LAI or whether 2009 was an anomalous year for calf production for these species. Regardless, the parameter estimates presented provide a reference point for future monitoring of reproductive variability in the ENP populations of these species.

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SUPPORTING INFORMATION

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Figure S1. The posterior mean (solid line) and 95% HDIs (dashed black line) of the logistic regression fit to fetal and calf specimen length data for estimating mean length-at-birth (LAB) for (a) *D. capensis* and (b) *D. delphis* are shown. The posterior mean estimate of LAB is indicated by the dashed gray line with the value printed and indicated with an arrow on the *x*-axis.

Table S1. The posterior mean and 95% highest density intervals (HDIs) for each coefficient of the length-at-birth (Eq. 2) and postnatal growth (Eq. 1) models fit to data for (a) *D. capensis* and (b) *D. delphis*.

Table S2a. Posterior mean and 95% highest density intervals (HDIs) for coefficients of the multi-factor Bayesian likelihood model for estimating the proportion calves (Eq. 4). The baseline case for the model was for complete schools of *D. capensis*

sampled in Area 1: Southern Californian.

Table S2b. The posterior mean and 95% highest density intervals (HDIs) for differences in proportion calves between pairs of biogeographical regions for *D. capensis* are presented. Sample sizes are given in Table 4 of the main paper. Bold type indicates comparisons with strong support for differences (*i.e.*, the posterior distribution does not contain 0).

Table S2c. The posterior mean and 95% highest density intervals (HDIs) for differences in proportion calves between pairs of biogeographical regions for *D. delphis* are presented. Sample sizes are given in Table 4 of the main paper. Bold type indicates comparisons with strong support for differences.

Table S3a. Posterior mean and 95% highest density intervals (HDIs) for coefficients of the multifactor Bayesian likelihood model for the cow size analysis (Eq. 5). The baseline case for the model was for complete schools of *D. capensis* sampled in Area 1: Southern Californian.

Table S3b. The posterior mean and 95% highest density interval (HDI) for differences in *D. capensis* mean cow size among bioregions are presented. Sample sizes are given in Table 4 of the main paper. Bold type indicates comparisons with strong support for differences (*i.e.*, the posterior distribution does not contain 0).

Table S3c. The posterior mean and 95% highest density intervals (HDIs) for differences in *D. delphis* mean cow size among bioregions are presented. There was no statistical support for any of the comparisons. Sample sizes are given in Table 4 of the main paper. There was not strong support for differences in any of the comparisons.

Table S4. Posterior mean and 95% highest density intervals (HDIs) for coefficients of the multifactor Bayesian likelihood model for length-at-independence (LAI) analysis (Eq. 6). The baseline case for the model was for complete schools of *D. capensis* sampled in Area 1: Southern Californian.

Table S5a. Posterior mean and 95% highest density intervals (HDIs) for coefficients of the multifactor Bayesian likelihood model for the calving season analysis (Eq. 8).

Table S5b. The posterior mean and 95% highest density intervals (HDIs) for the comparison of calving seasons among bioregions are presented in the lower diagonal for *D. capensis*. Differences between species are essentially the same because the variance specification in the model results in shrinkage to the same mean difference between species in each area.

Table S5c. The posterior mean and 95% highest density intervals (HDIs) for the comparison of calving seasons among bioregions are presented in the lower diagonal for *D. delphis*.