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Using aerial photogrammetry and sexually dimorphic measurements to investigate seasonal differences in school composition of Delphinus spp. off Southern California

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UNIVERSITY OF SAN DIEGO

San Diego

Using aerial photogrammetry and sexually dimorphic measurements to investigate seasonal differences in school composition of *Delphinus* spp. off Southern California

A thesis submitted in partial satisfaction of the requirements for the degree of

Master of Science in Environmental and Ocean Sciences

by

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DEDICATION

To the Common Dolphins (*Delphinus* spp.), who are anything but common.

And to my friends and family, you’re pretty cool too.

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ABSTRACT

Insights into school composition can provide a means to understand basic biology and ecology, including reproductive patterns. They can also be applied to conservation assessments, allowing for better understanding of the potentially differential vulnerability of demographic groups to natural or anthropogenic disturbances that may influence their populations. However, the two subspecies of common dolphins in the waters off California (*Delphinus delphis delphis* and *D. d. bairdii*) form large, energetic groups that make characterization of school composition difficult. Remotely controlled drones now offer the opportunity for the study of school composition in *Delphinus* spp., allowing for precise morphometric measurements of individuals in large schools. This thesis is a collection of two papers aimed at: 1) improving methods we can use to determine school composition of California *Delphinus* spp. in aerial photographs, and 2) applying these methods to further understanding of school composition in *D. d. bairdii* in waters off Southern California.

In Chapter 1, I use data from stranded and fisheries bycaught common dolphins to develop sexually diagnostic measurements of *D. d. delphis* and *D. d. bairdii* that can be applied to aerial images to infer the sex of free-ranging dolphins. We chose three morphometrics based on criteria designed to ensure accurate measurability in aerial images: 1) standard total body length (hereafter "total length"); 2) an "anterior" length, from tip of the rostrum to anterior insertion of the dorsal fin; and 3) a "posterior" length, from anterior insertion of the dorsal fin to fluke notch. All three measurements exhibited interspecific

differences, but they varied in the extent of sexual dimorphism within species. For both species, posterior length showed the greatest degree of sexual dimorphism, with 58.7% and 37.3% of adult *D. d. bairdii* and *delphis* males, respectively, larger than 95% of adult females. Total length showed the next greatest degree of sexual dimorphism, due largely to the contribution from posterior length, and anterior length showed the lowest. We demonstrated the utility of these sexually dimorphic features in photogrammetry measurements of an example aerial image of *D. d. bairdii* taken by a drone at an altitude of 58m (190ft), illustrating their value for identifying likely large adult males in aerial images.

In Chapter 2, I demonstrate how drones can be used to obtain precise measurements of individual *D. d. bairdii*. Eastern North Pacific long-beaked common dolphins (*Delphinus delphis bairdii*) often form large, energetic schools that make characterization of school composition difficult. Here we demonstrate how drones can be used to obtain precise measurements of individual *D. d. bairdii.* Additionally, we apply the recently identified sexually dimorphic measurements of the subspecies (specifically "posterior" length, or the length from the anterior insertion of the dorsal fin to fluke notch) to distinguish adult males of a large size class from visually similar adult females. Using aerial images from eight schools of *D. d. baiirdi* collected during June and October (2017-2019), we obtained total length estimates of 693 dolphins and posterior length estimates of 768 dolphins in waters off Southern California. In June, measured dolphins were on average 7-8cm longer in both total and posterior length. In addition, there were proportionally fewer calves and more large adult males measured during June compared to October. In a Bayesian mixture model, two June schools were best described by a size distribution cluster with a higher proportion of large individuals than the cluster that best described all October schools and two of four June schools, which had a higher proportion of small individuals. Our results suggest that some schools sampled in June have a different composition than the other six sampled schools, and likely represent either "bachelor" groups, consisting of all males, or reproductive schools, in which adult females are also present. Insights into school composition can provide a means to understand basic biology and ecology, including reproductive patterns. They can also be applied to conservation assessments, allowing better understanding of the potentially differential vulnerability of demographic groups to natural or anthropogenic disturbances.

I analyzed data from hundreds of stranded and bycaught individuals, as well as hundreds of measurements collected from over 11,000 aerial images. This work furthers our knowledge on the basic biology and ecology of *Delphinus* spp. in the waters off California. Additionally, it shows the utility of methods that can be broadly applicable to free-ranging cetacean populations around the world, providing a non-invasive monitoring tool that can be integrated into management and conservations plans of vulnerable species.

CHAPTER 1: Sexually dimorphic measurements from stranded and bycaught specimens contribute to the characterization of group composition in free-ranging common dolphins (*Delphinus* spp.) from aerial images

Short-beaked (*Delphinus delphis delphis*) and long-beaked (*D. d. bairdii*) common dolphins are the most commonly sighted cetaceans in waters off California (Barlow, 2016; Campbell et al., 2015; Carretta and Chivers, 2005; Heyning and Perrin, 1994). Despite the frequency of sightings, little is known about the demographic structure of their schools. This information is important for understanding risks: for example, *D. d. delphis* is the most commonly entangled species in California's thresher shark and swordfish drift gillnet fishery (Carretta and Chivers, 2005; Carretta, Moore, and Forney, 2017), and vulnerability to entanglement may be related to the sex of individuals (Kerri Danil et al., 2010; Perryman and Lynn, 1993). Additionally, there is evidence that male *D. d. bairdii* are more susceptible to domoic acid toxicity, which could be attributed to sex, age, or reproductive class segregation (Kerri Danil et al., 2021; de la Riva et al., 2013).

Information on the demographic structure in free-ranging schools of these two subspecies is mostly limited to noting presence or absence of calves, which can be distinguished from other individuals by their smaller total length and close association with another dolphin presumed to be their mother (Cañadas and Hammond, 2008; Chivers et al., 2016; Perryman and Lynn, 1993). Reproductively mature male *Delphinus* spp. can be identified via the presence of a postanal hump, a keel between the anus and the flukes (Heyning and Perrin, 1994; Neumann, Russell, Orams, Baker, and Duignan, 2002). However, the postanal hump is located on the underside of the body, making identification of sex difficult from the typical vantage point of a boat-based observer. Previous studies have characterized sex composition another small delphinid, *Cephalorhynchus hectori*, through molecular analysis of biopsy samples (Oremus et al., 2013) and by using an underwater pole-mounted camera system to determine sex (Webster, Dawson, and Slooten, 2009). In *D. d. delphis* and *D. d. bairdii*, determination of sex composition using biopsies is of more limited utility, since the large group sizes typical of both subspecies render sampling an entire group impossible. Furthermore, sex-specific behaviors might affect the likelihood of an individual of a particular sex being biopsied (Kellar et al., 2013). Similar sampling considerations also apply to boat-based underwater camera systems with these subspecies.

This study suggests the potential of photogrammetric measurements from aerial images to fill key data gaps on common dolphin group composition. Aerial photogrammetry from manned aircraft has been used routinely to measure body size of cetaceans (Fearnbach, Durban, Ellifrit, and Balcomb, 2011; Fortune et al., 2012; Pitman, Perryman, LeRoi, and Eilers, 2007), including *Delphinus* spp. (Chivers et al., 2016; Perryman and Lynn, 1993). Additionally, drones now offer more opportunities for photographically sampling cetaceans from the air (J. W. Durban, Fearnbach, Barrett-Lennard, Perryman, and Leroi, 2015), with the benefit of minimizing disturbance (Christiansen, Rojano-Doñate, Madsen, and Bejder, 2016). Drones are increasingly being used to obtain precise morphometric measurements of cetaceans (Christiansen et al., 2020; Christiansen, Dujon, Sprogis, Arnould, and Bejder, 2016; Dawson, Bowman, Leunissen, and Sirguey, 2017; J. W. Durban et al., 2016; Fearnbach, Durban, Barrett-Lennard, Ellifrit, and Balcomb, 2020; Groskreutz et al., 2019), providing an opportunity to characterize demographic school composition of large dolphin schools. Here we present an example of how data from stranded and fisheries bycaught common dolphins can be used to develop sexually diagnostic measurements of *Delphinus* spp. in Southern California and demonstrate how these measurements can be applied to drone-derived aerial images of free-ranging individuals to provide information on demographic composition.

Measurements were taken from stranded and bycaught *D. d. delphis* and *D. d. bairdii* collected from the waters off California (32° to 42°N latitude, 126° to 117° W longitude) between 1962 and 2018 (Chivers, 2018). Three criteria were developed to identify measurements that could be identified and measured accurately in aerial photographs. To be considered, the measurement must: (1) be restricted to the dorsal side of the body, (2) have start and end points easily distinguishable in aerial photographs, and (3) reflect a part of the body that is at times flat when viewed vertically while the animal is swimming. Although error associated with photogrammetric measurements tends to be small (Dawson et al., 2017; Scott and Perryman, 1991), the smaller the measurement, the greater the influence of this measurement error. Accordingly, we avoided measurements that were typically less than 50 cm (e.g., rostrum length). As a result, three morphometric measurements were selected: standard total body length (hereafter “total length”), an “anterior” length measurement from tip of the rostrum to anterior insertion of the dorsal fin, and a “posterior” length measurement between the anterior insertion of the dorsal fin and the fluke notch (Figure 1). If field and lab measurements were available for the same specimen, preference was given to lab measurements (following Chivers, 2018; Norris, 1961). To identify sexually dimorphic measurements, adult specimens were identified by total length, as defined in Heyning & Perrin (1994, Table 1), who used physical maturity (fusion of all vertebral epiphyses to the centra) or proxies thereof (sexual and cranial maturity combined) to classify specimens as adults. Sample sizes stratified by sex and species are provided in Figure 2.

All three measurements exhibited interspecific differences (Figure 2). Specifically, *D. d. bairdii* had longer median lengths than *D. d. delphis* in all three measurements. However, the measurements varied in the extent of sexual dimorphism within subspecies. For each measurement, we quantified sexual dimorphism by calculating the percentage of adult males that were longer than 95% of the adult females. For both subspecies, posterior length showed the greatest degree of sexual dimorphism, as 58.7% and 37.3% of adult *D. d. bairdii* and *delphis* males, respectively, were longer than 95% of adult females. Total length showed the next greatest degree of sexual dimorphism (*D. d. bairdii*: 45.5%; *D. d. delphis*: 34.7%), driven largely by the component contributed by posterior length, and anterior length showed the lowest degree of sexual dimorphism (*D. d. bairdii*: 22.7%; *D. d. delphis*: 2.0%).

To demonstrate the application of these metrics, we generated photogrammetric measurements from free-ranging dolphins at sea, sampled in an aerial image collected by an octocopter drone (APO-42, Aerial Imaging Solutions, New Lyme, Connecticut) launched from a 20-meter boat that approached dolphin groups from horizontal distances of approximately 300m. The drone carried a micro 4/3 digital camera (Olympus E-PM2) and flat lens (25 mm F1.8 Olympus M. Zuiko) in a gimballed mount to collect vertical images of dolphins from an altitude of ~60 m to provide a water-level pixel resolution of <2 cm (J. W. Durban et al., 2015). Pixel measurements of dolphin morphometrics were converted to distance units using their ratio to the known size of the camera sensor (4,608 pixels = 17.3 mm wide) and were then scaled to true size (scale = altitude / focal length) using an onboard laser altimeter with typical error of ~0.1% (Dawson et al., 2017). The fluke notch is often difficult to distinguish in aerial images. Instead, the trailing edge of the fluke was marked, adding an estimated 2.5 cm to posterior length (Perryman and Lynn, 1993). For this study, this was considered too small a difference to affect interpretation of the data.

In the example image shown in Figure 3a, the anterior insertion of the dorsal fin was clearly visible, confirming the ability to measure anterior and posterior lengths in aerial photographs, as well as total length, despite a camera altitude of 58 m (190 ft). In this example image, five individuals were considered flat enough for approximately unbiased measurements. Two of the five measured individuals had a posterior length longer than 95% of the analyzed stranded and bycaught adult females (Figure 3b). As such, we concluded these individuals were likely males.

Our results will facilitate characterization of group composition in aerially photographed *Delphinus* spp. schools off Southern California. Here we demonstrated the ability of this method to identify likely large adult males in one example aerial image. This image was collected during ongoing photogrammetry sampling that collected several hundred to nearly 2000 images for each school sampled. We anticipate that, by applying the methods detailed here to all images from the same school, we will be able to measure the length composition of a large portion of individuals within the school. In addition to estimating the length distributions, we will also now be able to identify likely large adult males, providing greater insight into the demographic composition of schools.

Table 1. Range of total length (Figure 1, measurement 1) for adult male and female *Delphinus* spp. in the Southern California Bight (Heyning and Perrin, 1994).

	Male	**Female**
D. d. bairdii	202-235cm	193-224cm
D. d. delphis	172-201cm	164-193cm

Figure 1. Measurements selected for analysis, as measured in stranded and bycaught individuals: 1) *Total Length* (standard total body length, or tip of the rostrum to fluke notch), 2) *Anterior Length* (tip of the rostrum to anterior insertion of the dorsal fin), and 3) *Posterior Length* (anterior insertion of the dorsal fin to fluke notch). Revised from Chivers (2018).

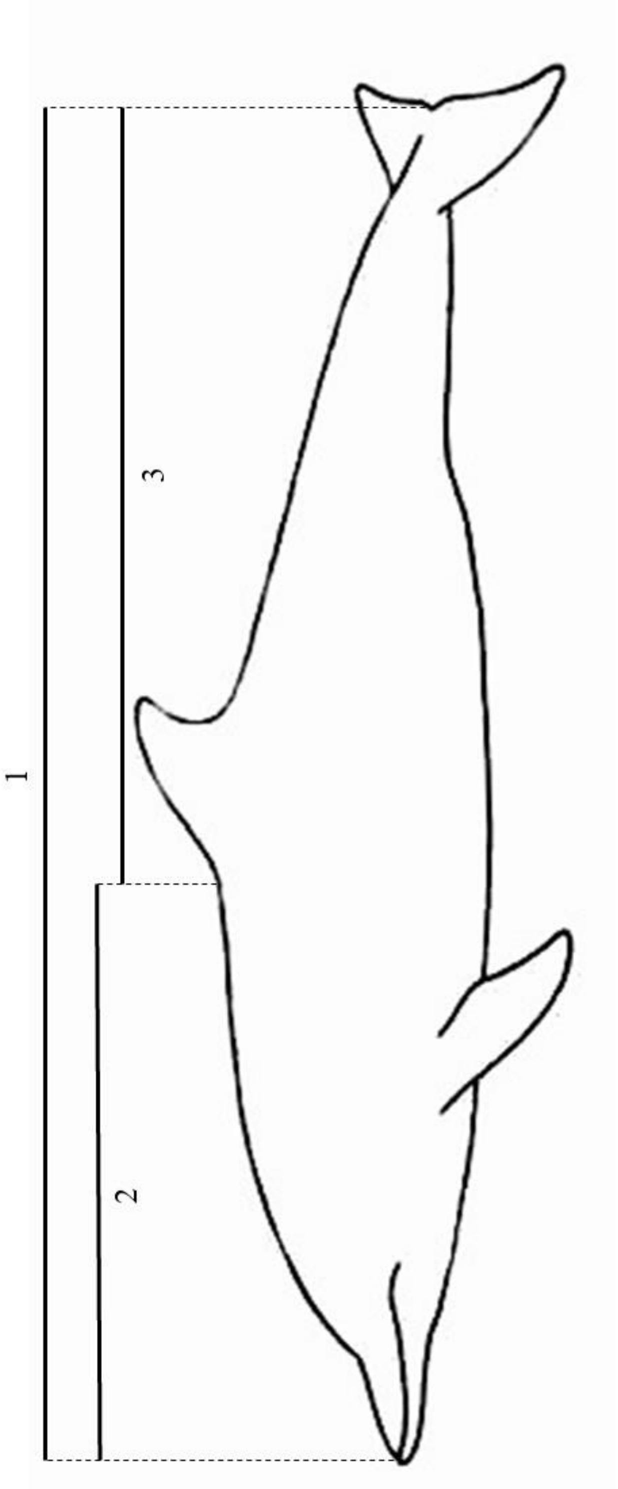

1
2
3

Figure 2. Length measurements of aerially measurable morphometrics for adult *Delphinus* spp. specimens (stranded and fisheries bycaught individuals) collected from waters off California. *Total Length* is tip of the rostrum to fluke notch, *Anterior Length* refers to the length between the tip of the rostrum and the anterior insertion of the dorsal fin, and *Posterior Length* refers to the length between the anterior insertion of the dorsal fin and the fluke notch (Figure 1). Whiskers reflect the full range of distribution, boxes mark the 25-75% quantiles of the data, and the midline represents the median.

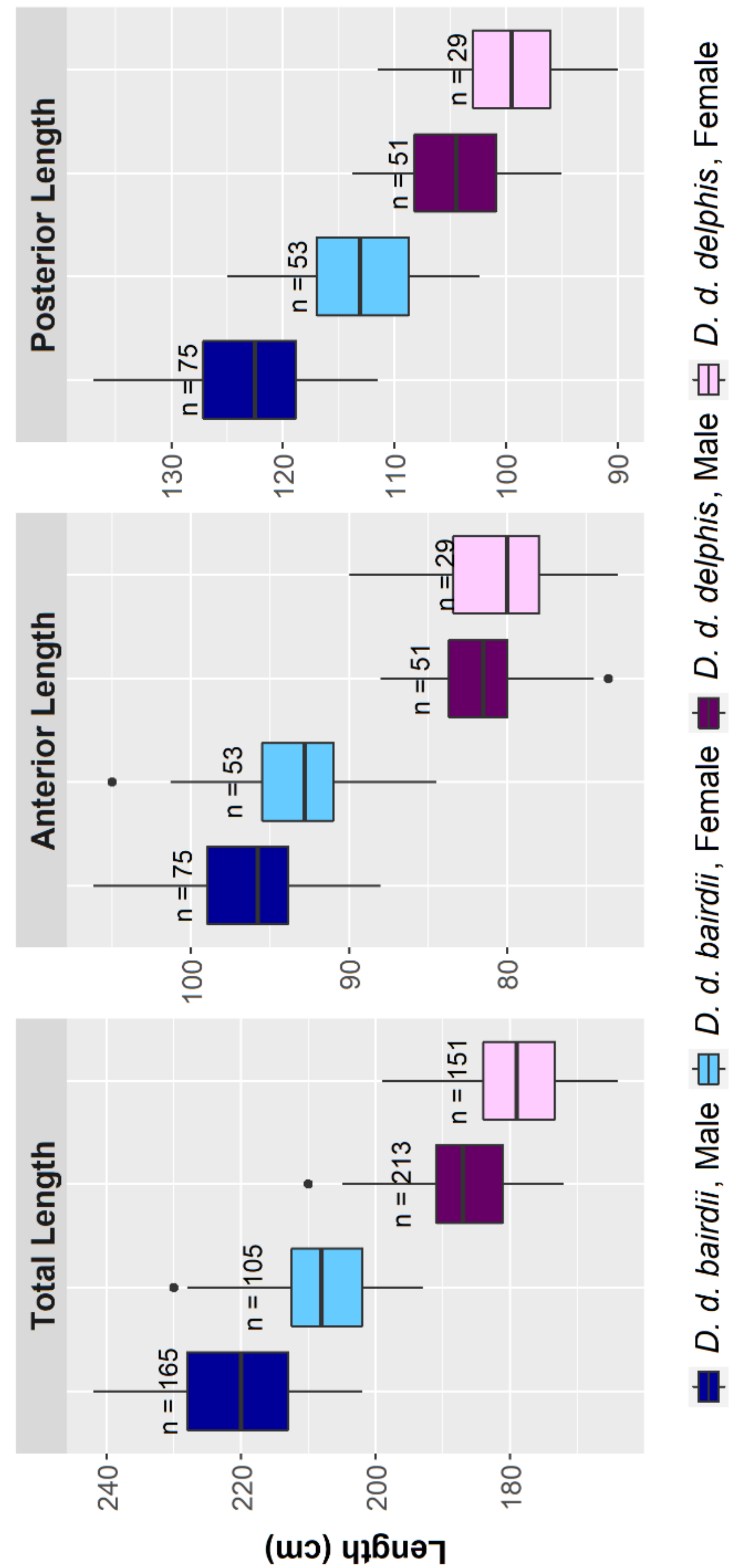
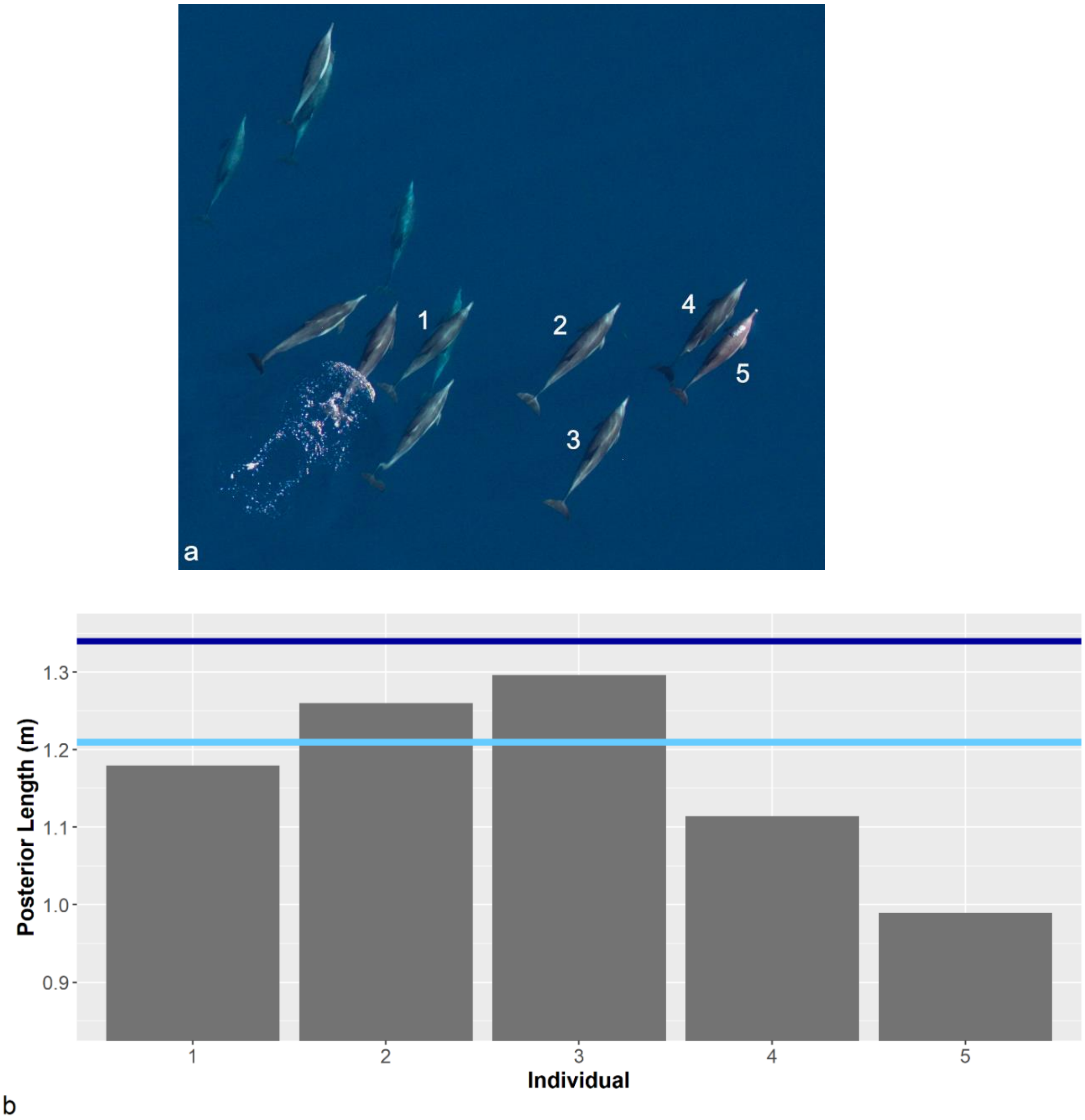

Length (cm)
Total Length
240
220
200
180
n = 165
n = 105
n = 213
n = 151
Anterior Length
100
90
80
n = 75
n = 53
n = 51
n = 29
Posterior Length
130
120
110
100
90
n = 75
n = 53
n = 51
n = 29
D. d. bairdii, Male
D. d. bairdii, Female
D. d. delphis, Male
D. d. delphis, Female

Figure 3a. Aerially photographed *D. d. bairdii* group, taken at an altitude of 58m (190ft). Individuals considered to be in approximately flat surfacing orientation are numbered corresponding to measurements in panel b.

Figure 3b. Posterior length (anterior insertion of dorsal fin to fluke) measured from the image. The light blue line marks the 95th percentile (1.21m) of analyzed stranded and bycaught females and the dark blue line marks the 95th percentile (1.34m) of analyzed stranded and bycaught males. Individuals 2 and 3 are most likely males, since their posterior length is larger than 95% of the analyzed stranded and bycaught females.


1
2
3
4
5
a
Posterior Length (m)
1.3
1.2
1.1
1.0
0.9
1
2
3
4
5
Individual
b

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CHAPTER 2: Seasonal differences in school composition of long beaked common dolphins (*D. d. bairdii*) off Southern California

2.1 Abstract

Eastern North Pacific long-beaked common dolphins (*Delphinus delphis bairdii*) often form large, energetic schools that make characterization of school composition difficult. Here we demonstrate how drones can be used to obtain precise measurements of individual *D. d. bairdii.* Additionally, we apply the recently identified sexually dimorphic measurements of the subspecies (specifically “posterior” length, or the length from the anterior insertion of the dorsal fin to fluke notch) to distinguish adult males of a large size class from visually similar adult females. Using aerial images from eight schools of *D. d. baiirdi* collected during June and October (2017-2019), we obtained total length estimates of 693 dolphins and posterior length estimates of 768 dolphins in waters off Southern California. In June, measured dolphins were on average 7-8cm longer in both total and posterior length. In addition, there were proportionally fewer calves and more large adult males measured during June compared to October. In a Bayesian mixture model, two June schools were best described by a size distribution cluster with a higher proportion of large individuals than the cluster that best described all October schools and two of four June schools, which had a higher proportion of small individuals. Our results suggest that some schools sampled in June have a different composition than the other six sampled schools, and likely represent either “bachelor” groups, consisting of all males, or reproductive schools, in which adult females are also present. Insights into school

composition can provide a means to understand basic biology and ecology, including reproductive patterns. They can also be applied to conservation assessments, allowing better understanding of the potentially differential vulnerability of demographic groups to natural or anthropogenic disturbances.

2.2 Introduction

The Eastern North Pacific long-beaked common dolphin (*Delphinus delphis bairdii*, formerly *D. capensis*) is one of the most commonly sighted cetaceans in waters off Southern California, often forming large groups, called schools, containing several hundred individuals (Heyning and Perrin 1994; Barlow 2016). Although reproduction occurs year-round, recent data suggest *D. d. bairdii* show a calving peak around March, which is thought to coincide with periods of high upwelling and productivity (Chivers et al. 2016). Calves swim alongside their mothers for approximately eleven months, becoming independent at a length of about 1.45m (Chivers et al. 2016). Other life history parameters for the subspecies are unknown, partially due to their similarity to the short beaked common dolphin (*D. d. delphis*), from which they were only recently distinguished taxonomically (Heyning and Perrin 1994; Barlow 2016).

Proportions of calves in each school, total sex ratios, and pregnancy rates vary throughout the geographic range of *D. d. bairdii* (Kellar et al. 2013, 2014; Chivers et al. 2016), suggesting potential sex, age, and/or reproductive class segregation. This could potentially lead to different demographic groups being exposed to different levels of natural and anthropogenic stressors. For example, data suggest that male *D. d. bairdii* are more susceptible to domoic acid toxicity compared to females, for reasons not related to differences in diet (de la Riva et al. 2013; Danil et al. 2021). Additionally, the subspecies is exposed throughout much of their Southern California range to anthropogenic activity, including mid-frequency active sonar on U.S. Navy test ranges (Carretta et al. 2019; Rice et al. 2019), making it important to understand the details of how demographic segregation may affect exposure to these stressors.

New research tools now offer the potential to fill key data gaps through an increased understanding of school composition in free-ranging delphinid schools. Previously, manned aircraft have been used to measure body size of cetaceans (Fearnbach et al. 2011; Fortune et al. 2012), including *Delphinus* spp. (Perryman and Lynn 1993; Chivers et al. 2016). The recent advent of remotely controlled drones has enabled cost effective and lower-altitude sampling, allowing more precise morphometric measurements of individuals (Christiansen et al. 2016b, 2020; Durban et al. 2016; Dawson et al. 2017; Groskreutz et al. 2019; Fearnbach et al. 2020), while still maintaining the benefit of limited disturbance (Christiansen et al. 2016a). Additionally, recent research has shown that male *D. d. bairdii* have a longer posterior body segment (as measured from anterior insertion of the dorsal fin to fluke notch), allowing for the detection of large adult male individuals in aerially photographed schools (Leander et al. 2021). Here we use aerial photogrammetry to: 1) estimate school size distribution, 2) identify calves and large adult males within schools, and 3) compare school composition of schools sampled between two months.

2.3 Methods

2.3.1 Image Collection

Images were collected from aerial platforms in waters off Southern California during June and October in 2017, 2018, and 2019 (Figure 1). They were collected as a part of two projects: the first aimed at quantifying behavioral and physiological response of dolphins to mid-frequency active sonar around Catalina Island and the second aimed at surveying coastal cetaceans. Both projects followed the same protocols for aerial photogrammetry and used similar drone configurations.

Two remotely controlled drones were used to collect images: 1) octocopter drone (APO-42, Aerial Imaging Solutions), and 2) hexacopter drone (APH-22, Aerial Imaging Solutions). Both drones carried a micro 4/3 digital camera (Olympus E-PM2) and flat lens (25mm F1.8 Olympus M. Zuiko) mounted to a gimbal that constantly adjusted the camera angle to maintain a nadir orientation. Drones were launched from boats that approached dolphin schools to horizontal distances between 100 and 500m. Images were collected from altitudes of 30-60m (Figure 2a), which was high enough to cover a large image footprint on the water (approximately 21 x 16m = 336m^2 at 30m and 42 x 31m = 1300m^2 at 60m), while also providing a water-level pixel resolution of 1-2cm (J. W. Durban, Fearnbach, Barrett-Lennard, Perryman, and Leroi, 2015).

Flights, the term used to describe the time between the drone leaving and returning to the boat, were only conducted during optimal environmental conditions (e.g., flat water, Beaufort sea state of 1 or less; bright skies) to achieve good surface light penetration for photogrammetry. Flight time was a function of school behavior and battery endurance, with a median of 24.5 min (range = 5-30 min). Eight schools were sampled over ten flights (Table 1), with two of these schools opportunistically sampled with a second flight over the same school. During flights, the pilot was guided by a live video transmission that was monitored on a portable ground unit in real-time by a co-pilot to facilitate targeting of the same focal dolphins in the frame for as long as possible during each flight. Once contact with the school had been established, the pilot remotely triggered the camera to record 16MP still photographs at one-second intervals for entire time the dolphins were visible in the camera's footprint. A laser altimeter (Dawson et al. 2017) mounted directly on the camera recorded precise (<0.1% error) altitude, which was linked to each image through a timestamp to enable subsequent photogrammetric measurements.

2.3.2 Image Processing

Images were processed using a custom workflow developed in the open source image analysis program ImageJ (Abràmoff et al. 2004). Starting with the first image within each flight that contained dolphins, the locations and orientations of individuals were recorded in pixel coordinates by drawing a 2-part segmented line connecting: 1) tip of rostrum to anterior insertion of dorsal fin (referred to subsequently as "anterior" length), and 2) anterior insertion of dorsal fin to fluke notch (referred to subsequently as "posterior" length, Figure 2b). In some images, it was not possible to discern fluke notch. In these images, the line was drawn to trailing edge rather than fluke notch, and 2.5cm was subtracted from posterior length (following Perryman and Lynn, 1993).

Each dolphin was labeled with a unique identification code and tracked from frame to frame, when possible. The same dolphin was identified in sequential frames based on position and orientation relative to other dolphins within the frame, as well as body size and markings. If there was any question as to whether a dolphin represented the same individual in sequential frames, it was assigned a new unique identification code, starting a new sequence of measurements associated with the new code. Although this approach enabled dolphins to be tracked through frames with confidence, it undoubtedly resulted in some individuals being sampled more than once in the resulting dataset. Here, our sample sizes (n) and the number of "individuals" in a school to refer to measurements known to be from the same dolphin in the dataset, although it is likely that true number of dolphins sampled was lower.

Measurements were first made in pixel coordinates recorded in ImageJ. Dolphins were measured if they were considered "flat," an orientation in which the dolphin was close to the surface and one or both body segments were fully elongated (Figure 2c). Only measurements of flat segments were analyzed. A custom R script was then used to combine pixel measurements with telemetry sensor information to estimate absolute lengths by multiplying the pixel dimensions by Ground Sampling Distance (GSD), which denotes the length in meters at ground level represented by a single pixel (Baker 1960). GSD was calculated using the following formula with parameters of camera altitude measured by laser altimetry, lens focal length (0.025 m), and sensor width in pixels (4608 pixels) and in meters (0.0173 m):

$$GSD = \frac{Altitude\ (m)}{Focal\ Length\ (m)} * \frac{Sensor\ Width\ (m)}{Sensor\ Width\ (pixels)}$$

Photogrammetric measurements can underestimate lengths if the dolphin is positioned at an angle to the surface of the water or is not fully elongated at the time the photograph is taken (Durban et al., 2016; Fearnbach et al., 2011). Accordingly, if the same individual was measured more than once, the maximum measurement for each line segment was taken to represent the best estimate of that segment length. Total length was calculated as the sum of the maximum values of anterior and posterior lengths (Groskreutz et al. 2019). Individuals were classified as adult males if their maximum posterior length exceeded 1.21m (Leander et al. 2021) and were classified as calves if their maximum total length was less than 1.45m (Chivers et al. 2016). Calves often surface steeply to breathe from their echelon travel position next to the mother. Therefore, to account for potential under-representation of calves in the measurements, the presence of calves in a school was noted whenever possible, even if they were not flat for measurements. Calves were identified in images from their shorter total length and close association with another dolphin, presumed to be their mother (Perryman and Lynn 1993; Chivers et al. 2016).

2.3.3 Bayesian Mixture Model

To test for similarities and differences between the length distributions of each school while accounting for uncertainty due to sample size differences, we adopted a Bayesian mixture model for identifying clusters of histograms with similar underlying distributional models for proportions across size bins (Durban et al. 2010). We used the distributions of posterior lengths in our mixture model, because they exhibited the greatest separation between adults of different sexes (Leander et al. 2021). Based on the standard deviation of measurements obtained from the same individual (see Results), we set the bin size for these distributions at 10cm.

Data for each school were the number of flat individuals m_i in each of the $i = 1, \ldots 10$ size bins, which was modelled as a multinomial sample from an overall sample size n, or the total number of flat individuals measured. The multinomial bin probabilities were then derived from a mixture model for the underlying distributions, with the number of clusters (C) unknown. The component cluster distributions were defined by allowing different parameters for the mean and variance of bin proportions on the logit scale, and these values were estimated from non-informative uniform prior distributions. Different clusters were identified as those with differences in the pattern of proportions across the ten size bins, and schools with a high probability of deriving from the same distribution were identified as drawn from the same component of the mixture. The probabilistic approach to Bayesian inference offers intuitive advantages in interpretation (Ellison 1996), in this case providing estimates of the probability that a given histogram conformed to one or more general patterns. Cluster fitting was accomplished using Markov Chain Monte Carlo (MCMC) implemented in the WinBugs software (Lunn et al. 2000). Inference was based on 10,000 iterations after discarding 20,000 as burn-in and thinning a subsequent 100,000 chain to minimize effects of autocorrelation.

2.4 Results

2.4.1 Data

A total of 11,019 images and 212 minutes of flight time were processed from ten flights flown over eight schools, four in June and four in October (Table 1). The number of images and flight time was nearly equal between months, with 5,667 images (average 1,417) and 114 (average 28.5) minutes for each school in June, and 5,352 (average 1,338) images and 98 (average 24.5) minutes for each school in October. A total of 1,149 "flat" measurements were obtained, 592 in June and 557 in October. Individuals were usually measured once, though individuals were measured up to 9 times in June and up to 8 times in October. Accounting for individuals with multiple measurements, we obtained total length measurements from 693 individuals and posterior length measurements from 768 individuals.

2.4.2 Total Length

Photogrammetric estimates of total length ranged from 1.03m to 2.46m in June (n = 401, median = 2.07m, 25% quantile = 1.94m, 75% quantile = 2.17m), and 1.10m to 2.36m in October (n = 292, median = 1.99m, 25% quantile = 1.89m, 75% quantile = 2.09m, Figures 3 and 4). For individuals known to be measured more than once, the average standard deviation in total length was 0.09m (n = 175), with higher variation in June (SD = 0.11m, n = 80) than October (SD = 0.07m, n = 95). Although the lower limit of the range of total lengths in June was smaller than October, only 3 individuals (0.8%) were classified as calves. In contrast, 18 individuals (6.2%) in October were classified as calves. At least one calf was observed in all but two schools (1 and 3). Although calves were noted in the images, none presented in measurement orientation in schools 4 and 5.

2.4.3 Posterior Length

Photogrammetric posterior length estimates ranged from 0.56m to 1.41m in June (n = 440, median = 1.15, 25% quantile = 1.05m, 75% quantile = 1.23m), and 0.60m to 1.32m in October (n = 328, median = 1.08, 25% quantile = 1.01m, 75% quantile = 1.15m, Figures 5 and 6). For individuals known to be measured more than once, the average standard deviation was 0.04m (n = 203) for posterior length (June SD = 0.05m, n = 91; October SD = 0.03m, n = 112). Inferred adult males comprised 30.7% of the measurements in June, and 13.4% of the measurements in October. None of the individuals measured in October had a posterior length greater than 1.32m, while there was at least one individual greater than 1.32m measured in every June school. In total, 23 individuals (5.2%) measured in June had a posterior length of 1.32m, compared to none in October.

To investigate similarities and differences in posterior length distributions between schools, we allowed as many clusters as there were different schools.

However, only two distributional clusters were selected to describe schools (Figure 7). The probability of assignment to a single mixture component cluster was high, ranging from 0.93 to 1 for each of the 10 flights (Table 2).

Cluster 1 was characterized by relatively higher proportions of larger individuals than cluster 2, which was characterized by relatively higher proportions of smaller individuals (Figure 7). Two of four June schools were best fit by cluster 1. Compared to these schools, the other two June schools had lower proportions of larger individuals, and one had individuals in the smallest bin classes, as typical with the October schools. These two June schools, along with all four October schools, were best fit by cluster 2.

2.5 Discussion

This study demonstrates that drones can be used to fill key gaps in our knowledge of small dolphin species such as *D. d. bairdii*. We were able to use precise photogrammetric measurements to identify clear differences in school composition between the two months of sampling. In June, individuals were typically larger in both total and posterior length. Additionally, there were proportionally more inferred males and fewer calves in June compared to October, a relationship further supported by a Bayesian mixture model. Based on these results, sampled schools can be separated into 1) schools with calves and 2) schools without calves.

Schools with calves: All October schools and half of June schools were best fit by cluster 1, described by greater proportions of smaller individuals. Calves were observed in all cluster 1 schools, but not all had calves represented in the measurements, potentially a result of their tendency to surface at a steep angle. Still, all were fit to the same cluster based on the distribution of measurements, indicating there were more similarities in school composition than simply the presence or absence of calves. Specifically, there was a larger proportion of smaller adults and juveniles, likely due to the presence of the mothers of observed calves. Additionally, all schools contained at least one inferred large adult male, although fewer proportionately than schools best fit by cluster 2.

Schools without calves: Half of June schools were best fit by cluster 2, described by greater proportions of larger individuals. These groups had more inferred large adult males than schools best fit by cluster 1 and no measured or observed calves. Large adult males occurred with smaller individuals of an unidentified demographic group. These schools potentially represent either: 1) a "bachelor" group, composed of entirely males, or 2) a reproductive school, including adult females without calves. The gestation period of tropical *D. d. delphis* has been estimated to be 11.4 months (Danil and Chivers 2007). However, *D. d. bairdii* might have a different gestation period, as other life history parameters (e.g., length at independence) have been shown to differ between the subspecies (Chivers et al. 2016). If we assume this gestation period also applies to *D. d. bairdii,* and that the calving peak projected to March applies to years sampled here (Chivers et al. 2016), then the majority of reproduction occurred in April. If the schools we have measured in June are indeed reproductive schools, we suggest one or a combination of the following: 1) these groups are more common in April, 2) the calving peak is different than previous data suggest, 3) the gestation period of *D. d. bairdii* is different than that of *D. d. delphis*, or 4) the formation of these groups in June does not result in as many pregnancies as during other times of the year.

Considerations include spatial scale of separation between schools, sampling protocol, and potential resampling. Each June school best fit by cluster 1 was sampled within a week of a school best fit by cluster 2, within the same geographic area. There might be a small distance between different types of schools, and schools may mix or exchange individuals. All schools were sampled with a protocol of staying over the same individuals, so images may have missed individuals of a different age or sex that occurred in a different section of the same school. Additionally, to further reduce disturbance on potentially vulnerable groups, schools with neonates were not sampled as a part of protocol. Since schools with neonates are not represented in these data, it is not clear if those schools would follow similar compositional patterns as sampled schools with calves. While the resampling of individuals within schools likely occurs, the observed seasonal differences are not a product of resampling. The chance of resampling is the same between June and October, since flights were only conducted in good weather conditions and the duration of flights was similar in both months. Additionally, there are some patterns within the data that cannot be explained entirely by resampling. For example, all four June schools contained at least one individual with a posterior length greater than the maximum observed in all October schools. Although possible that some of these measurements were due to error, as they were all within 10cm of the maximum posterior length observed in October, it is unlikely, as these measurements were recorded 23 times in June and 0 times in October.

Delphinus delphis bairdii is one of the most common cetaceans in Southern California, an area where anthropogenic disturbances, including mid-frequency active sonar, are common. Understanding the demographic composition of exposed groups, including presence of individuals that may be particularly vulnerable (e.g., calves), is critically needed to parameterize demographic-based models of population consequences of disturbance (Pirotta et al. 2018). Consequently, direct measurements of demographic composition of common dolphins and other large population species (which are exposed to disturbance in large numbers) provide baseline natural history insights and may be important to inform conservation measures and management decisions for protected marine species.

Table 2. Date, starting latitude and longitude, flight duration, number of images, and number of individual posterior length measurements for each of the schools analyzed. Schools will hereafter be referred to by their number, listed in column 1.

School #	Date	Latitude (N)	Longitude (W)	Flight Duration (minutes)	# Images	# Individuals Measured
1	2017-06-25	33.42	118.39	19	896	28
2	2017-06-29	33.49	118.47	44	2077	95
3	2018-06-19	33.47	118.48	27	1482	203
4	2018-06-21	33.57	118.48	24	1212	114
5	2017-10-23	33.10	117.4	9	504	48
6	2019-10-22	33.48	118.47	54	2835	149
7	2019-10-24	33.28	118.2	30	1750	105
8	2019-10-26	33.39	118.51	5	263	26

Table 3. Bayesian mixture model summaries for each school. Schools 1-4 were sampled in June, and schools 5-8 were sampled in October.

School #	**Cluster with maximum probability**	**Probability of cluster assignment**
1	1	0.93
2	2	0.97
3	1	1
4	2	0.97
5	2	0.97
6	2	1
7	2	0.97
8	2	0.97

Figure 2. Map of Southern California, with the locations of sampled *D. d. bairdii* schools marked. Schools were sampled using drones between 2017 and 2019.

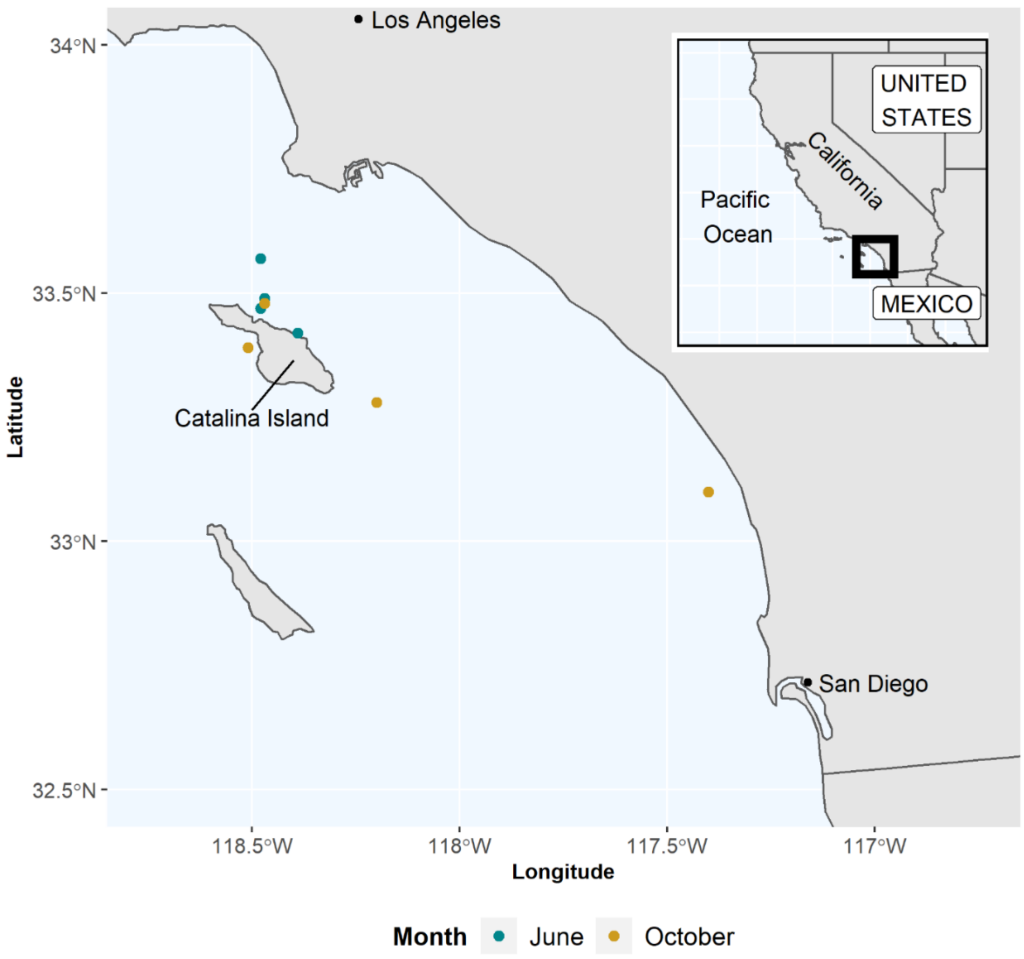
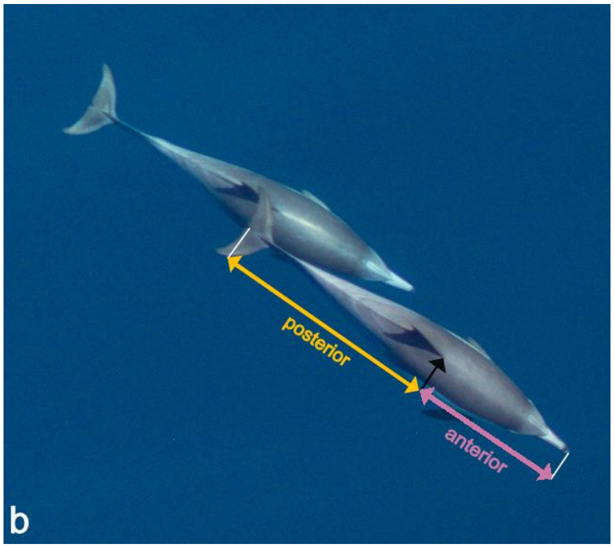

Los Angeles
UNITED STATES
California
Pacific Ocean
MEXICO
Catalina Island
San Diego
34°N
33.5°N
33°N
32.5°N
Latitude
118.5°W
118°W
117.5°W
117°W
Longitude
Month
June
October

Figure 2a. Aerial image showing a school of *D. d. bairdii*, taken with the drone from an altitude of 60m.


a

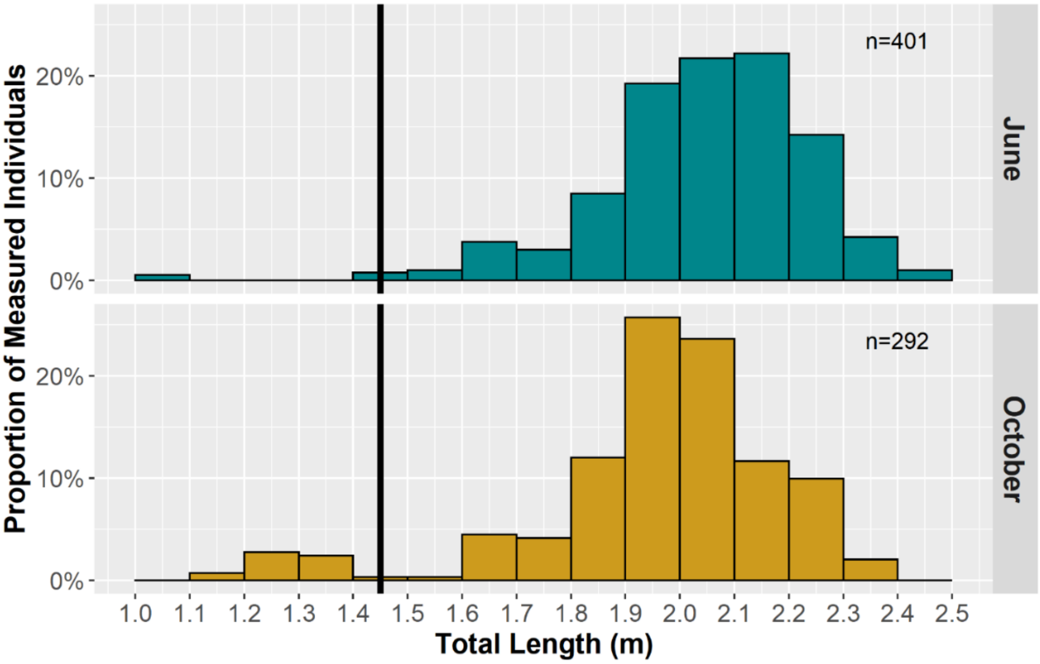
Figure 2b. Aerial image showing the 2-part segmented lines drawn on dolphins in aerial images: anterior (pink) connects the tip of the rostrum to the anterior insertion of the dorsal fin and posterior (orange) connects the anterior insertion of the dorsal to fluke notch (black arrow). Total length is the sum of these segments.

Figure 2c. flatness selection: dolphins marked with a number are “flat”, that is, close to the surface with one or both segments fully elongated (reproduced from Leander et al. 2021).


posterior
anterior
b

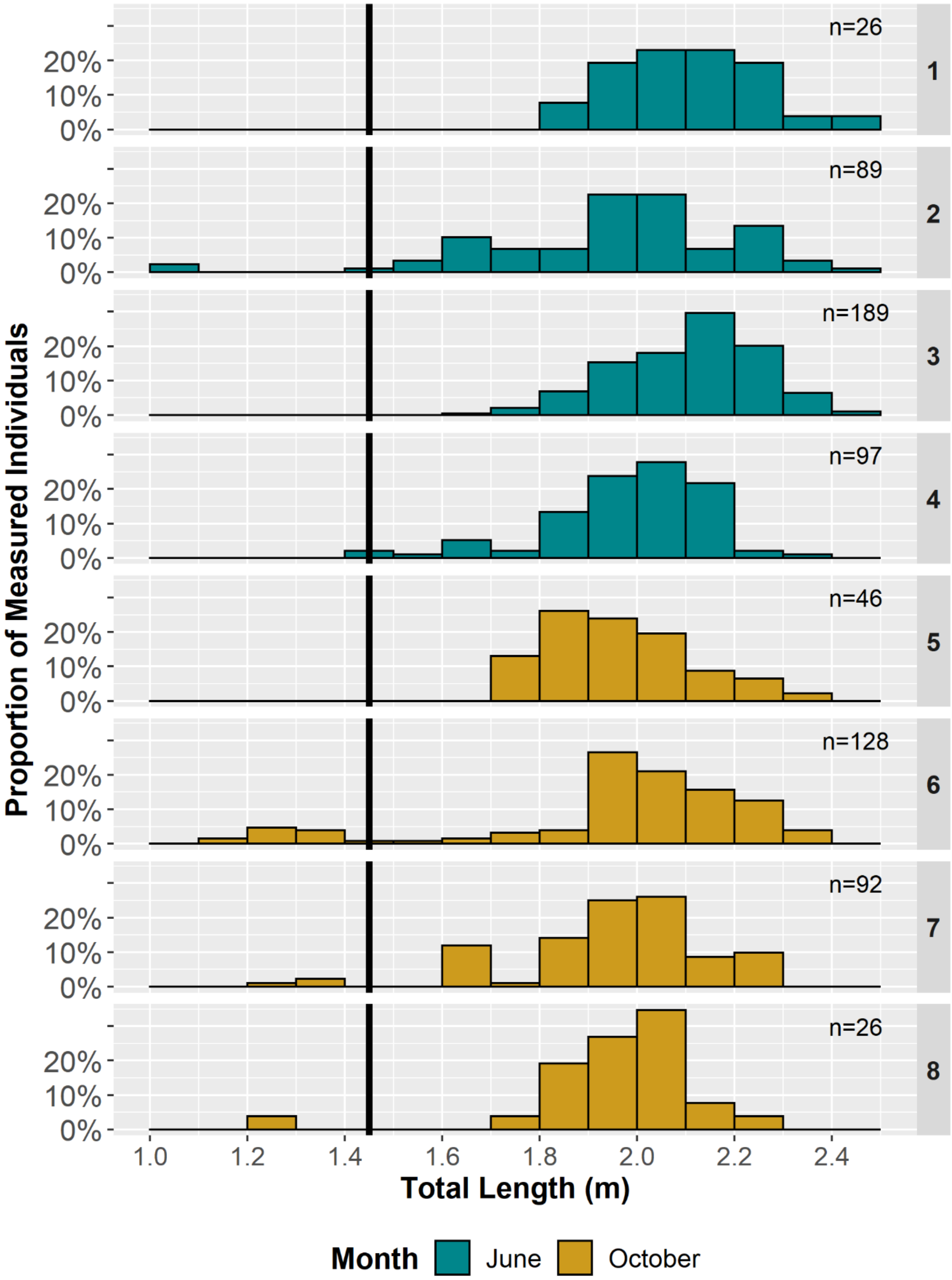

1
2
3
4
5
c

Figure 3. Total length estimates for individuals in flat measurement orientation in four schools in June and four schools in October. Individuals with measurements less than 1.45m (shown by the thick black line) are classified as calves (Chivers et al. 2016).



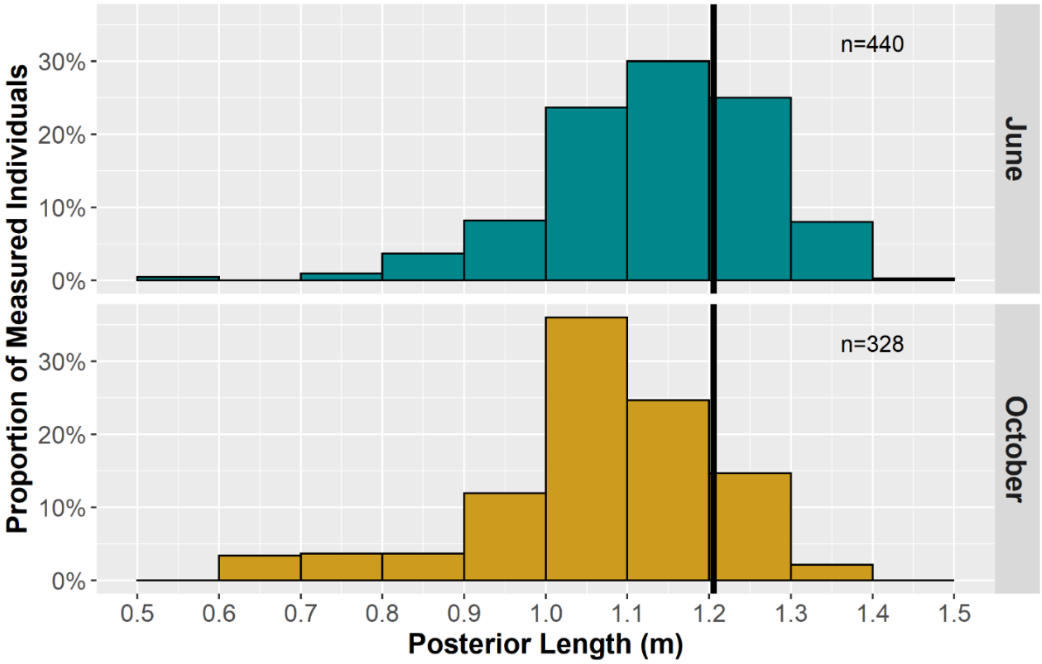
n=401
June
n=292
October
Proportion of Measured Individuals
0%
10%
20%
1.0
1.1
1.2
1.3
1.4
1.5
1.6
1.7
1.8
1.9
2.0
2.1
2.2
2.3
2.4
2.5
Total Length (m)

Figure 4. Total length estimates of individuals in each school, numbered on the right of the graph following Table 1. Individuals with measurements less than 1.45m (shown by the thick black line) are classified as calves (Chivers et al. 2016).



Proportion of Measured Individuals
20%
10%
0%
n=26
1
n=89
2
n=189
3
n=97
4
n=46
5
n=128
6
n=92
7
n=26
8
1.0
1.2
1.4
1.6
1.8
2.0
2.2
2.4
Total Length (m)
Month
June
October

Figure 5. Posterior length estimates from individuals in flat surfacing orientation in four schools in June and four schools in October. Individuals with measurements greater than 1.21m (shown by the thick black line) are classified as adult males (Leander et al. 2021).



n=440
June
n=328
October
Proportion of Measured Individuals
0%
10%
20%
30%
0.5
0.6
0.7
0.8
0.9
1.0
1.1
1.2
1.3
1.4
1.5
Posterior Length (m)

Figure 6. Posterior length estimates for individuals in each school, numbered on the right of the graph following Table 1. Individuals with measurements greater than 1.21m (shown by the thick black line) are classified as adult males (Leander et al. 2021).

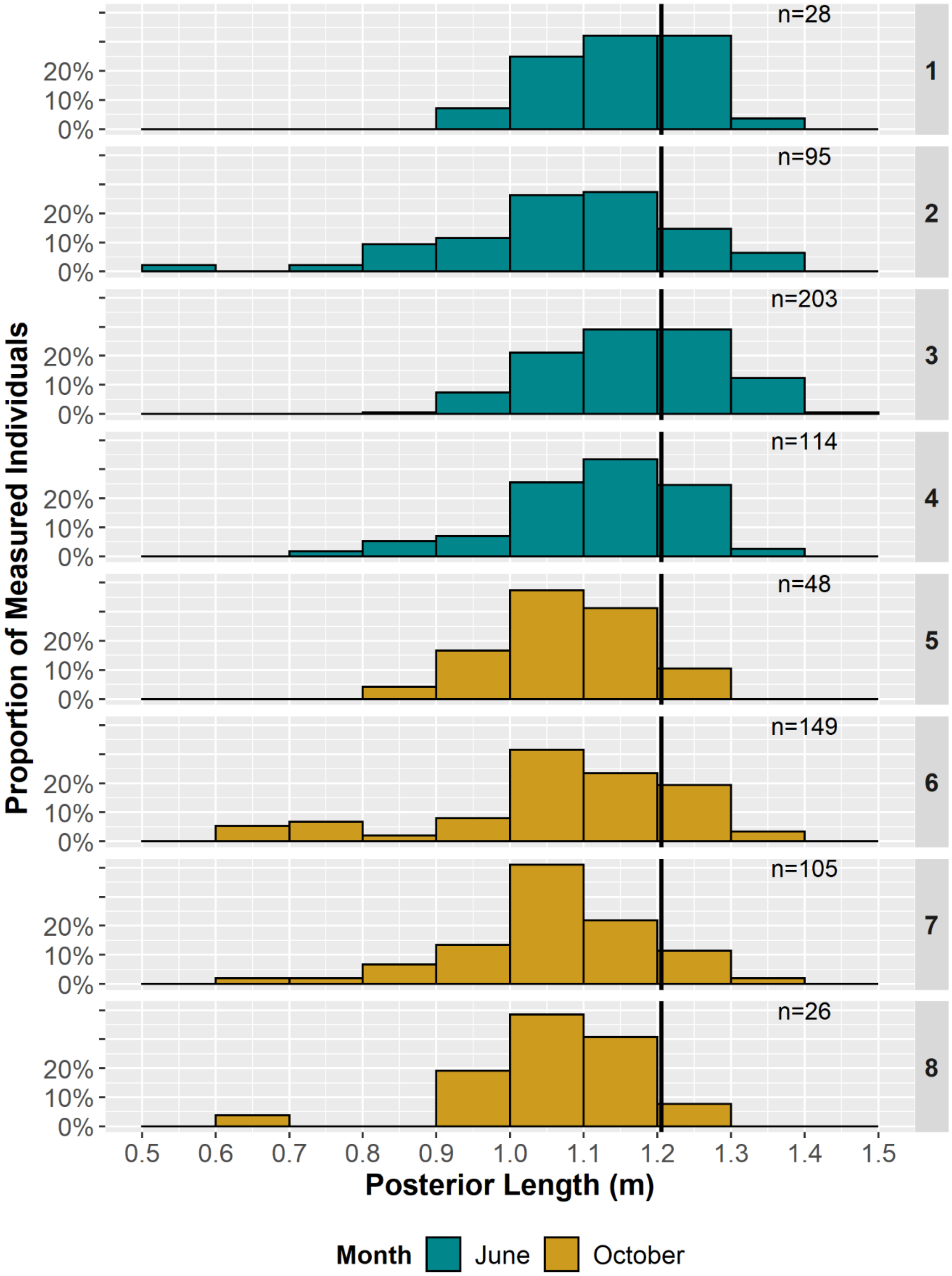
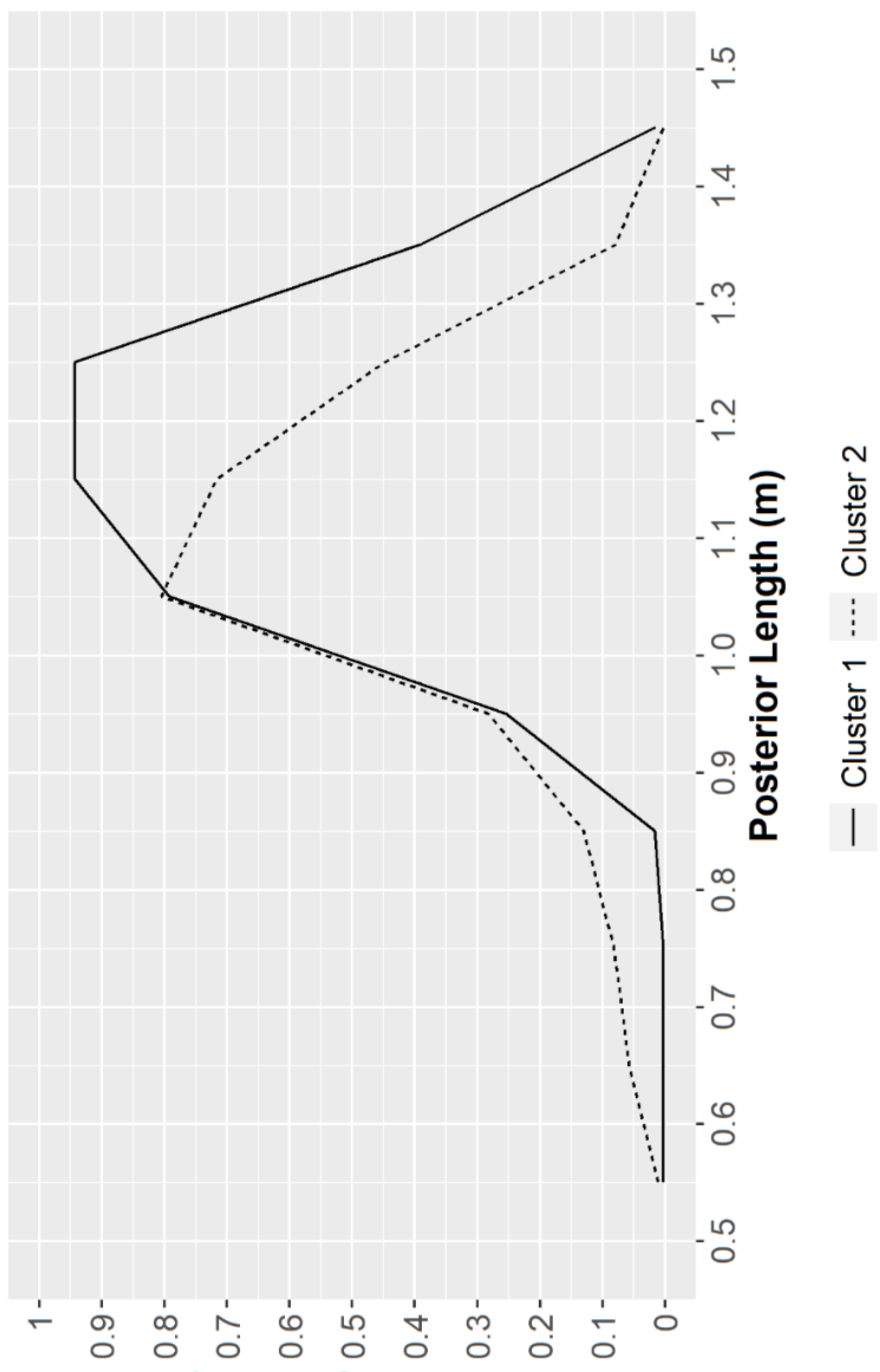

n=28
n=95
n=203
n=114
n=48
n=149
n=105
n=26
1
2
3
4
5
6
7
8
20%
10%
0%
Proportion of Measured Individuals
0.5
0.6
0.7
0.8
0.9
1.0
1.1
1.2
1.3
1.4
1.5
Posterior Length (m)
Month
June
October

Figure 7. Posterior length distributions for the two distributional clusters that were estimated to best represent sampled schools. Lines are medians of MCMC values during cluster fitting.


Probability Density
0
0.1
0.2
0.3
0.4
0.5
0.6
0.7
0.8
0.9
1
Posterior Length (m)
0.5
0.6
0.7
0.8
0.9
1.0
1.1
1.2
1.3
1.4
1.5
Cluster 1
Cluster 2

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