

# The long-beaked common dolphin of the eastern Pacific Ocean: Taxonomic status and redescription of *Delphinus bairdii*

Thomas A. Jefferson<sup>1,2†</sup>  | Frederick I. Archer<sup>2†</sup>  |  
Kelly M. Robertson<sup>2</sup>

<sup>1</sup>Clymene Enterprises, California

<sup>2</sup>Southwest Fisheries Science Center, NOAA, Marine Mammal and Turtle Division, California

## Correspondence

Thomas A. Jefferson, Clymene Enterprises, 13037 Yerba Valley Way, Lakeside, CA 92040.

Email: [sclymene@aol.com](mailto:sclymene@aol.com)

## Abstract

Neritic, long-beaked common dolphins have been described as species distinct from the more oceanic and globally distributed short-beaked species, *Delphinus delphis*, although recent molecular studies have challenged this view. In the eastern North Pacific (ENP), the taxonomic status of the long-beaked (*bairdii*) form has been controversial since its original description in 1873, and has vacillated between species, subspecies, and geographic forms several times. It is currently provisionally viewed as a subspecies of *Delphinus delphis*, *D. d. bairdii*. To clarify this situation, we reviewed the literature and conducted additional analyses using both newly obtained genetic and cranial morphometric data sets. The results indicate that there are diagnostic differences in skull morphology and coloration between the eastern Pacific long- and short-beaked forms, and near-perfect diagnosability in mitochondrial DNA. These differences, along with indications of ecological distinctions, including important differences in life history parameters and reproductive timing, indicate that these forms are well on their way down separate evolutionary pathways. As such, we consider them to be distinct species in the eastern Pacific.

† Jefferson and Archer should be considered equal authors.

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The long-beaked species is referable to *Delphinus bairdii* Dall, 1873, and is redescribed as such herein.

#### KEYWORDS

California, *Delphinus capensis*, *Delphinus delphis*, long-beaked common dolphin, Mexico, nomenclature, Peru, redescription, taxonomy

## 1 | INTRODUCTION

Since first being described as a distinct species of common dolphin over 150 years ago (Dall, 1873), the taxonomic status of the long-beaked form of common dolphin from the coastal waters of the eastern North Pacific (ENP) has been controversial. It has variously been considered a distinct species in its own right, a subspecies, geographic form, or population of the wide-ranging long-beaked species *Delphinus capensis* or of the globally-distributed species *D. delphis*. Many studies have examined its status and come to very different conclusions. Heyning and Perrin (1994) seemingly had settled the controversy, by demonstrating that in southern California, the ENP long-beaked species was distinct at the species level from the partially sympatric short-beaked common dolphin (*D. delphis*). They reviewed the history of *Delphinus* taxonomy and proposed that the ENP long-beaks were the same species as *D. capensis* (originally described from the Cape of Good Hope, off southern Africa). They further considered most other long-beaked populations of the genus to be of this species as well, thereby concluding that the genus consisted of at least two species with worldwide ranges, *D. delphis*, the short-beaked common dolphin, and *D. capensis*, the long-beaked common dolphin.

Heyning and Perrin (1994) also pointed out differences in color pattern, which allowed reliable identification of the two proposed species. Most notable was the difference in the facial area, with long-beaks having a dark stripe from the lower jaw to the flipper area, giving them the appearance of a dark face mask. However, in later years, difficulties were encountered in diagnosing *D. capensis*, and several researchers found that the external and coloration differences that identified ENP long-beak common dolphins did not always apply to other areas (e.g., Amaha, 1994; Pinella et al., 2011). In the last few decades, genetic studies have shown that some populations classified as *D. capensis* were not monophyletic, and that in at least some of these cases, they grouped closely with short-beaked populations (*D. delphis*; e.g., Amaral et al., 2012; Natoli et al., 2006). This accumulated evidence indicated that the long-beaked condition had evolved recently, and more importantly, independently, in many different parts of the world's oceans, casting serious doubt on the existence of a wide-ranging long-beaked species (see Nicolosi & Loy, 2019). The Society for Marine Mammalogy's Committee on Taxonomy (2023) summarized the situation:

The long-beaked condition is apparently a convergent character state induced by regional ecology. In some regions, long-beaked common dolphins are genetically more closely related to short-beaked common dolphins than to long-beaked common dolphins in other regions (e.g., see Natoli et al. 2006). Cunha et al. (2015) summarized the relevant data and analyses, along with additional molecular data and analysis, and recommended that *Delphinus capensis* not be further used as proposed by Heyning and Perrin (1994). Their recommendation is followed here. Cunha et al. (2015) noted that because the sympatric/parapatric long-beaked and short-beaked common dolphins off California in the Eastern North Pacific (ENP) appear not to interbreed, perhaps the ENP long-beaked common dolphins might be recognized as a separate species *D. bairdii* Dall, 1873 (as advocated by Banks and Brownell (1969) based on the long-beaked condition). However, the molecular analysis for the ENP (Rosel et al., 1994) did not include common dolphins from the contiguous regions to the south in the eastern tropical and eastern South Pacific. Pending a more complete global review and revision of the common dolphins,

the long-beaked ENP form is considered here provisionally as a subspecies *D. delphis bairdii* following the usage of Hershkovitz (1966).

The current paper is intended to provide that “more complete global review and revision” for the eastern Pacific Ocean, and to clarify the uncertain taxonomic status of long-beaked common dolphins in this area.

## 2 | BACKGROUND AND HISTORY

In 1873, William H. Dall described a new species of common dolphin, *Delphinus Bairdii* (= *D. bairdii*) from two specimens collected by whaling captain and naturalist, Charles M. Scammon, off Cape Arguello, California (Santa Barbara County) (Dall, 1873, 1874). Dall (1873) did not provide any illustrations, and his description was very brief. The specimens were collected on October 29, 1872, and a more detailed description of those specimens was given in Dall (1874). The description, illustrations, and skull measurements (e.g., condylobasal length [CBL] = 477 mm, rostrum length/zygomatic width [RL/ZW] ratio = 1.71) provided in the above references make it clear that this was what is known today as the long-beaked common dolphin of the eastern North Pacific Ocean. One skeleton was apparently sent to the Smithsonian's United States National Museum [USNM], but there was no subsequent record of it having arrived there (see Heyning & Perrin, 1994). Scammon (1874), in his classic monograph on Pacific coast marine mammals, provided illustrations of the external appearance, and further added that the species had a “snout more elongated and rounded than that of the Striped or Common porpoise” (apparently referring to *Lagenorhynchus obliquidens*). However, at this time, there was little indication that this was a particularly long-beaked form of common dolphin.

Due to the paucity of information available on the species, Flower (1884) could find no evidence of specific differences between *D. delphis* (then known mostly from the Atlantic and Indian oceans) and *D. bairdii*. He cast strong doubts upon the validity of the species. True (1889) followed Flower in deciding that the limited evidence available at the time for species-level differences was not adequate, and he considered *D. bairdii* to be a synonym of *D. delphis*.

In the early twentieth century, Miller (1936), who had several more specimens available to him, pointed out for the first time the very long rostrum of *D. bairdii*, and suggested that this species could be distinguished based on a rostral length/zygomatic width (RL/ZW) ratio of 1.69 or greater. He thereby reestablished *D. bairdii* as a full species. However, later workers were still not convinced. Hershkovitz (1966), in his classic work reviewing all cetacean scientific names, considered that there was but a single species of *Delphinus* worldwide, *D. delphis*, thereby downgrading *bairdii* to a subspecies, *D. delphis bairdii*. However, Banks and Brownell (1969) conducted a thorough review of the evidence and maintained that *D. bairdii* was in fact a distinct species, a long-beaked type of common dolphin. They further suggested that a RL/ZW ratio of 1.55 or above was associated with *bairdii* and 1.53 or below with *D. delphis*.

Taking more of a global perspective, van Bree and Purves (1972) reexamined the issue, and when comparing ENP long-beaks with common dolphins from outside of the Pacific, noticed that some other common dolphins also had relatively long beaks. They concluded that beak length was not a useful taxonomic character, and therefore rejected *D. bairdii* as a distinct species. This remained the status quo for over 20 years. Evans (1975, 1982) in his extensive work on North Pacific common dolphins, did recognize the long-beaked form as an entity. However, he considered it to be a “northern neritic long-snouted” population, but still under the species *D. delphis*. Stock definition studies by the US National Marine Fisheries Service (NMFS) essentially followed this precedent, with the ENP long-beaks being defined as the “Baja neritic” stock, which was identified by reference to body length, coloration, and relative beak length for common dolphins within 100 nautical miles of Baja California, or in the Gulf of California (Dizon et al., 1994; Perrin et al., 1985). Currently, the ENP long-beaked common dolphin is treated as a separate stock in the US Stock Assessment reports (Carretta et al., 2023).

Finally, in 1994, an important advance was made. A comprehensive study of southern California common dolphins by Heyning and Perrin (1994) examined coloration, external morphology, and skeletal morphology from a large series of specimens. Later work by Rosel et al. (1994) added genetic data in the form of mitochondrial DNA



**FIGURE 1** Comparison of typical external appearance of short-beaked and long-beaked common dolphins of the eastern Pacific, as determined by Heyning and Perrin (1994): (a) short-beaked specimen showing the robust body shape, short stocky beak, and absence of dark facial markings; (b) long-beaked specimen showing slender body shape, long thin beak, and dark wide stripe in facial and thoracic area. Not all animals in a school (especially younger specimens) are as easy to distinguish. Top photo by A. Schulman-Janiger.

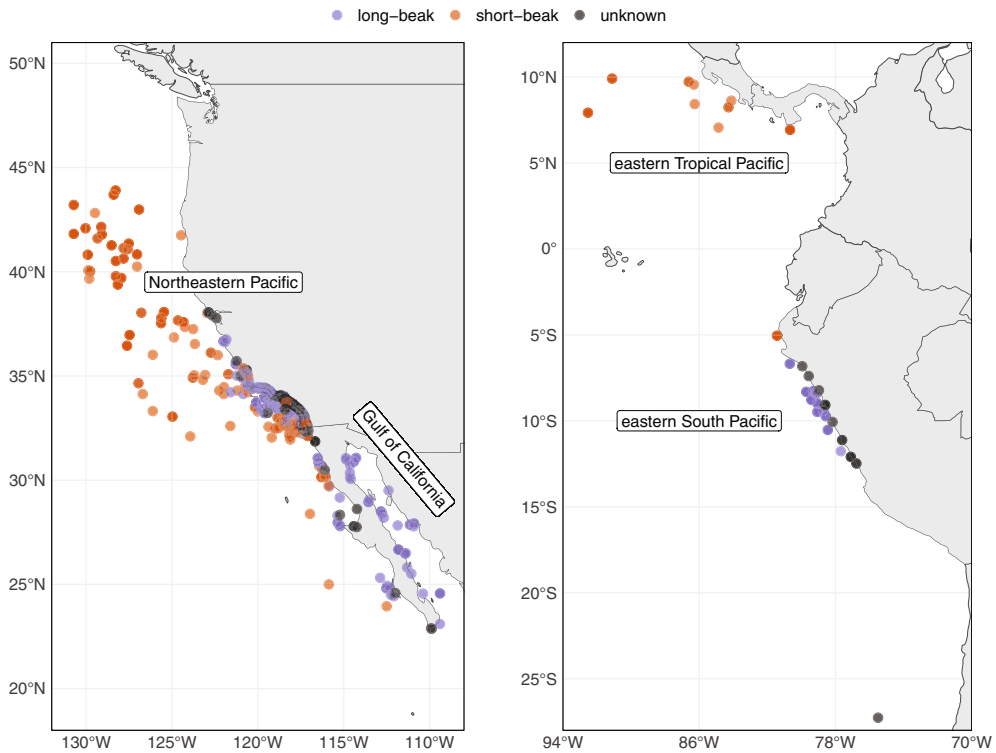
sequences for the first time. Together, these studies clearly demonstrated reliable and correlated differences between short- and long-beaked common dolphins in southern California and concluded that there were two distinct species in the area, which overlapped in distribution, but maintained separate schools and did not interbreed (Figure 1). The short-beaked species was *D. delphis*, but the long-beaked species was considered to be *D. capensis* (a species originally described from the Cape of Good Hope, South Africa, by Gray in 1828). A review of relevant information suggested to the authors that long-beaked populations of common dolphins from the western Pacific, South Pacific, Atlantic, and Indian oceans all were the same species, referable to *D. capensis*, and thus *D. bairdii* was again relegated to synonymy (though this time under *D. capensis*, rather than *D. delphis*). Later genetic work by Kingston and Rosel (2004) added amplified fragment length polymorphism (AFLP) support for the distinction of ENP long-beaks and short-beaks as two separate species.

However, based on extensive molecular sampling, especially from poorly studied areas of the Atlantic, Cunha et al. (2015) suggested that all common dolphins in the Atlantic Ocean were *D. delphis*, and further that *D. capensis* (as originally described from southern Africa, near the meeting of the Atlantic and Indian Oceans) appeared to be invalid. They did not reject the species status of the ENP long-beaks, and in fact suggested that they be recognized as *D. bairdii*. In spite of this, the Society for Marine Mammalogy's (SMM) Committee on Taxonomy in early 2016 lumped all common dolphins back under the species *D. delphis* (thereby relegating the ENP long-beaks to the subspecies, *D. d. bairdii*). The SMM noted that a thorough review was needed, thus prompting the current study, which is aimed at clarifying the taxonomic status of the ENP long-beaked common dolphin.

### 3 | MATERIALS AND METHODS

#### 3.1 | Cranial morphometrics

We collected four measurements and two tooth counts, where available, from a series of skulls of common dolphins across the eastern Pacific Ocean (Figure 2, Tables 1 and SM1). These four measurements (i.e., condylobasal length,



**FIGURE 2** Collection locations of common dolphin skull and mtDNA sequences from four regions in the eastern Pacific. Points are colored based on morphotype as validated by photographs or geography (not shown are seven samples from the Western Pacific and Northwest Pacific). Sample sizes for each data type are given in Table 1.

**TABLE 1** Summary of samples by region, type of data, and photo or geographically validated morphotype. Regions are identified in Figure 2.

Region	Data	Long-beak	Short-beak	Unknown
Eastern North Pacific	Skull	59	28	185
	CR	153	185	0
	<i>cytb</i>	0	1	0
	CR/ <i>cytb</i>	221	96	0
Gulf of California	Skull	31	0	0
	CR	5	0	0
	CR/ <i>cytb</i>	17	0	0
Eastern tropical Pacific	Skull	0	21	0
	CR	0	1	0
	CR/ <i>cytb</i>	0	9	0
Eastern South Pacific	Skull	0	0	20
	CR	40	0	0
	CR/ <i>cytb</i>	14	7	0
Northwest Pacific	CR/ <i>cytb</i>	0	4	0
West Pacific	CR	2	0	0
	CR/ <i>cytb</i>	1	0	0
Unknown	Skull	1	0	6

length of rostrum, width of rostrum at base, zygomatic width) are the ones that reflect the main differences between short- and long-beaked forms (see Heyning & Perrin, 1994). We made special attempts to obtain data from areas where the two forms are known to overlap in range, and also from areas not well represented in previous studies of the relationship of the two forms (i.e., central California, Mexico, eastern tropical Pacific (ETP), and Peru/Chile; see Heyning & Perrin, 1994). Skulls from all of these regions were measured for this study. We also computed ratios of all six unique pairs of the four measurements. Tooth counts were taken for each tooth row in both upper and lower jaws, accounting for alveoli with missing teeth. The highest complete tooth count for each upper and lower tooth row was used in analyses. All skulls were measured by TAJ, in an attempt to eliminate interobserver variability.

A skull was considered to be from an adult animal if the premaxillae were at least 75% fused to the maxillae and extensive fusion was observed around the occipital bones, primarily at the occipital crest (following Jordan et al., 2015). We noted the morphotype of the skull (long- or short-beak) as identified by the original collector (“field ID”). When available, we also examined photographs or illustrations of the external color pattern of the specimen and independently assigned skulls to morphotype based on the characteristics outlined in Heyning and Perrin (1994; “photo ID”). We used primarily the color pattern components in the facial area, but considered all elements identified by Heyning and Perrin (1994; see their fig. 1 for a diagram labeling these). Skulls collected from the central/northern Gulf of California were recorded as long-beaks and those from the ETP were recorded as short-beaks, as those were the only forms recorded from those respective regions (Hamilton et al., 2009). All analyses described below were conducted in R (R Core Team, 2022).

We examined sexual dimorphism across all skulls, as well as within each morphotype using only specimens that had been identified to form based on external color pattern. We conducted *t*-tests to examine differentiation between sexes for each measurement and tooth count independently. We also built Random Forest models (Breiman, 2001) to quantify the ability of the measurements and tooth counts to classify the skulls to sex. Each model was balanced to ensure equal sample sizes in each tree, as described in Archer et al. (2017a). The models consisted of 10,000 trees, and sampling was done without replacement. All Random Forest models were run using the “randomForest” v4.7-1.1 package for R (Liaw & Wiener, 2002) through the “rfPermute” v2.5.1 package (Archer, 2022a) in order to assess significance of the predictor importance scores. A total of 1,000 “rfPermute” replicates were conducted to compute importance *p* values. Model convergence was assessed by visual examination of the trace of out-of-bag (OOB) error rates to ensure that a sufficient number of trees were run.

We conducted *t*-tests on the four skull measurements, two tooth counts, and the six measurement ratios to examine univariate differentiation between morphotypes. We also conducted a principal components analysis (PCA) based on the original four skull measurements using the *princomp* function in R. We identified distinct clusters of skulls using the unsupervised Density Clustering algorithm (Rodríguez & Laio, 2014) as implemented in the “densityClust” v0.3.2 package for R (Pedersen et al., 2022). Pairwise Euclidean distances were computed based on the four original measurements as input for the Density Clustering. A Gaussian kernel was used to estimate the density, the distance cutoff was automatically estimated, and threshold values of *rho* and *delta* were identified after visual inspection of both the decision graph and gamma graph.

In order to evaluate the diagnosability of morphotypes, we created two Random Forest models. Both models used all four of the original measurements as well as the six pairwise ratios to classify morphotype. Only skulls that had been identified to morphotype based on external color pattern were used. The first model used all skulls for which the ten predictors were available, while the second model only used skulls identified as adults based on cranial maturity. Parameters for both models were as described above.

Finally, for predictors identified in the Random Forest model as being significantly important, we created Bayesian logistic models to estimate threshold values for those predictors to classify morphotypes. We also created Bayesian linear models to see if those predictors changed over the growth of the skull at different rates between the two morphotypes. All Bayesian models were conducted using JAGS as implemented in the “runjags” v2.2.1-7 package in R (Denwood, 2016). Model convergence and mixing were evaluated with the “coda” v0.19-4 (Plummer et al., 2006) package.

## 3.2 | Mitochondrial sequences

We compiled mitochondrial control region (CR) and cytochrome *b* (*cytb*) sequences for Pacific common dolphins that had been deposited in GenBank. To this data set, we added sequences from samples collected from free-ranging biopsies, strandings, and fisheries bycatch stored in the Southwest Fisheries Science Center's Marine Mammal and Sea Turtle Research Collection (MMaSTR), La Jolla, CA. Genomic DNA was extracted using a sodium chloride precipitation protocol (Miller et al., 1988), Qiagen DNeasy Blood and Tissue Kit (#69506, Qiagen, Germantown, MD) or a phenol-chloroform protocol (Sambrook et al., 1989). Sequences were generated using standard Sanger sequencing methods following LeDuc et al. (1999) and Chivers et al. (2007).

We validated the form (long- or short-beak) of GenBank sequences based on information contained in the publications, reported location of the samples, and our evaluation of experience of the authors with both forms. For the new samples, as well as GenBank samples that originally came from the MMaSTR collection, form validation was based on reviews of stranding and bycatch observer records and photos, or sighting photos and notes for free-ranging biopsies when available. Long-beak sequences were stratified as coming from the ENP, Gulf of California, eastern South Pacific, and west Pacific. Short-beak sequences were from the ENP, ETP, eastern South Pacific, and western North Pacific (Figure 2).

All sequences were aligned with MAFFT (Katoh et al., 2002) with gap opening penalty of 3, gap extensional penalty of 0.123 and all other parameters left by default. Resulting alignments were refined by eye. Because the CR and *cytb* sequences varied in length among studies, we identified sequence windows (range of consecutive sites) for each region that maximized the number of individuals of each form and variable sites. Alignments for these windows were used for all analyses below. Additionally, as several individuals had sequences for both mitochondrial regions, a concatenated CR and *cytb* alignment (CR/*cytb*) was created and its optimal window identified.

Haplotypic diversity (Nei, 1978) was computed using the “strataG” package in R (Archer et al., 2017b). The effective number of haplotypes (the Hill number of order 1) was computed using the “sprex” package (Archer, 2022b) following Jost (2007). Clusters of haplotypes for each mitochondrial region were identified with the Density Clustering algorithm using the “densityClust” package in R as described above. Pairwise distances between haplotypes were computed with the *dist.dna* function in the “ape” (Paradis & Schliep, 2019) package using pairwise deletion, and the Tamura-Nei 1993 substitution model (TN93), which was identified as the closest appropriate substitution model available in “ape” by *jModelTest* (Posada, 2008). Percent Diagnosability (PD) between forms was assessed using Random Forest as implemented in the “randomForest” package (Liaw & Weiner, 2002) with balanced models following Archer et al. (2017a). Nei's net nucleotide divergence ( $d_A$ ) between forms was calculated using *strataG* with the TN93 substitution model and pairwise deletion as for the Density Clustering analysis.

## 4 | RESULTS

### 4.1 | Cranial morphometrics

Skull measurements and tooth counts were collected from a total of 351 *Delphinus* spp. skulls from the ENP (Figure 2, Table 1). Of those, the morphotype (long- or short-beak) of 126 skulls could be confirmed with photos or illustrations of the external color pattern or geographic location. Of these morphotype-confirmed specimens, 74 long-beaks (24 from Gulf of California and 50 from the ENP) and 43 short-beaks (24 from the ENP and 19 from the eastern tropical Pacific) were considered to be adults based on fusion of the premaxillae and cranium. Of these morphotype-confirmed adults, 58 long-beaks and 41 short-beaks had all four measurements collected, and 46 long-beaks and 39 short-beaks had all four measurements and both tooth counts collected. An additional 126 skulls (113 from the ENP, 8 from Peru, and 5 from unknown locations) were considered to be adults and had all four measurements collected but could not be independently assigned to morphotype. A total of 15 specimens (11 long-beak

and 4 short-beak) had all four measurements and both tooth counts collected but were either determined not to be adults or adult status could not be evaluated. A summary of the measurements for both forms and sexes for the photo-confirmed specimens is provided in Table 2.

Within both long- and short-beaks, condylobasal length of adult male skulls was significantly greater than that of adult female skulls by approximately 15 mm and 16 mm, respectively ( $t$ -test  $p < .05$ ). The zygomatic width of males was approximately 9 mm greater than of females for long-beaks and 7 mm greater for short-beaks. However, a Random Forest analysis of adult skulls could only correctly classify 80% of the long-beak skulls and 72% of the short-beak skulls to sex (Table 3). In both of these models, zygomatic width was the most significant important predictor variable. Because these differences represented less than 5% of the absolute value of the measurements and were not strongly diagnostic of sex, we analyzed both sexes and skulls of unknown sex for both forms together in the analyses that follow.

Univariate tests of differentiation between the morphotypes indicated that adult long-beak skulls had significantly greater condylobasal length (CBL), length of the rostrum (L.ROST), zygomatic width (ZYG.W), and lower and upper tooth counts (LTC and UTC) than adult short-beak skulls ( $t$ -test  $p < .05$ ). Notably, only two specimens with adult skulls and photo verified color pattern overlap in the length of the rostrum, both measuring 274 mm (Table 2). However, if specimens with only a validated morphotype identification are considered as well, the shortest rostrum in the long-beak form is 272 mm, while the longest rostrum in the short-beak form remained at 274 mm. Additionally, all measurement ratios showed significant differentiation between the morphotypes.

In the PCA of the four skull measurements on all adult skulls, the first component accounted for 96% of the variance (Figure 3). This first component had high loadings of the two length measurements (CBL and L.ROST) indicating that it described overall skull length. The second component accounted for 3% of the variance and was a contrast between length of the rostrum and the two width measurements (ZYG.W and W.ROST.BS) with zygomatic width having much higher loading.

The unsupervised Density Clustering algorithm identified three clusters in the same data used in the PCA using a pairwise distance matrix derived from the four measurements (Figure 3). The first cluster contained 39 skulls of confirmed short-beaks, while the second cluster contained 37 of the 58 confirmed long-beaks and 2 short-beaks, and the third cluster contained the remaining 21 confirmed long-beak skulls (Figure 3a, Table 4). Clusters 2 and 3 are mainly differentiated along the first axis, thus indicating that these two clusters primarily represent skulls of different length groups.

With the exception of two short-beaks, which were from the ETP, both clusters 2 and 3 were composed of long-beaks from the ENP, Gulf of California, and eastern South Pacific (Figure 3b, Table 4). In Figure 3b, it is apparent that, although skulls from the eastern South Pacific overlap with the other two regions, they tend to have a higher loading on the second axis, indicating that they are wider on average.  $T$ -tests on ZYG.W and W.ROST.BS indicate that these values are significantly ( $p < .001$ ) greater in the eastern South Pacific than the ENP and Gulf of California combined, by approximately 11 mm and 7 mm, respectively.

Random Forest models built on the four measurements, tooth counts, and six pairwise ratios with all morphotype-validated skulls ( $n = 100$ ), as well as just the adult morphotype-validated skulls ( $n = 85$ ), classified 100% of the skulls to morphotype (Figure 4a). The most important predictor in both models was the ratio of the length of the rostrum to the zygomatic width (L.ROST\_ZYG.W; Figure 4b). Other ratios that described similar length of skull vs. width of skull features (e.g., CBL\_W.ROST.BS or CBL\_ZYG.W) were also significantly important predictors in these models, as were the absolute length of the rostrum and condylobasal length. The median assignment probability was between .98 and .99, with a lower 95-percentile greater than .66 for all morphotypes across both models (Table 5). In both models, and for both morphotypes, approximately two-thirds (68%) of the skulls had correct assignment probabilities greater than 95%.

Given that the Random Forest models identified the ratio of the length of the rostrum to the width of the zygomatic process (hereafter, "RL/ZW ratio") as the most significant predictor of the morphotypes, we further examined the distribution of this value between the two morphotypes. As seen in Figure 5, this RL/ZW ratio is larger in

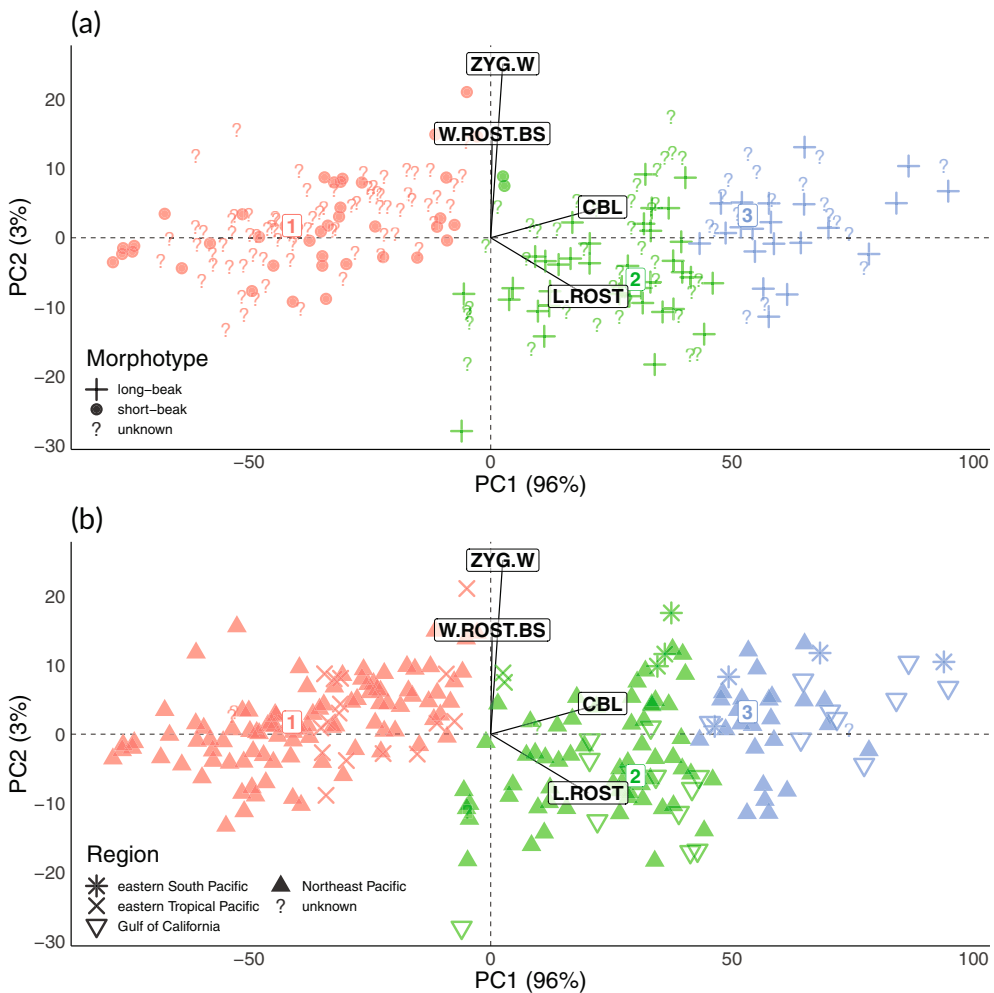


**TABLE 2** Summary of measurements and tooth counts for adult skulls by form and sex. Summary values for each measurement are, top: number of skulls without missing data, middle: mean and (standard deviation), and bottom: median and (range).

Morphotype	Sex	n	Condylobasal length (CBL)	Length of rostrum (L.ROST)	Width of rostrum at base (W.ROST.BS)	Zygomatic width (ZYG.W)	Upper tooth count (UTC)	Lower tooth count (LTC)
Long-beak	F	21	21	21	21	21	17	17
		459 (15)	294 (12)	84 (3)	179 (4)	54 (3)	52 (2)	
	460 (434–486)	293 (274–314)	85 (78–91)	178 (171–189)	54 (50–61)	52 (48–55)		
M	27	27	27	27	27	24	24	24
		474 (13)	302 (11)	89 (4)	188 (5)	54 (2)	51 (2)	
	474 (446–502)	304 (283–323)	89 (83–99)	188 (178–203)	54 (51–59)	51 (48–57)		
All	74	72	72	72	73	63	54	54
		471 (18)	301 (13)	87 (5)	184 (8)	54 (3)	52 (3)	
	470 (430–514)	300 (274–333)	87 (77–106)	184 (161–203)	54 (47–62)	52 (44–57)		
Short-beak	F	19	17	17	17	17	17	19
		407 (18)	245 (15)	89 (5)	178 (5)	49 (2)	48 (2)	
	414 (381–433)	248 (223–266)	88 (80–100)	178 (171–194)	49 (46–52)	47 (44–52)		
M	21	21	21	21	21	19	19	19
		423 (13)	255 (11)	91 (5)	185 (6)	50 (3)	48 (2)	
	420 (396–444)	251 (237–274)	92 (84–101)	186 (175–199)	50 (45–57)	48 (45–52)		
All	43	41415 (18)	41250 (14)	4190 (5)	41182 (7)	3950 (3)	4148 (2)	4148 (2)
		418 (381–447)	251 (223–274)	90 (80–101)	180 (171–199)	50 (42–57)	48 (44–52)	

**TABLE 3** Confusion matrices from Random Forest models classifying sexes for each morphotype.

Morphotype	Original	Predicted		% Correct	95% CI
		F	M		
Long-beak	F	14	3	82.35	56.57, 96.2
	M	5	19	79.17	57.85, 92.87
	Overall			80.49	65.13, 91.18
Short-beak	F	12	5	70.59	44.04, 89.69
	M	5	14	73.68	48.8, 90.85
	Overall			72.22	54.81, 85.8

**FIGURE 3** Principal Components Analysis of common dolphin skulls. Points are color-coded based on cluster from Density Clustering analysis. In (a) shapes indicate morphotype of validated long-beaks (pluses) or short-beaks (circles). Samples with no photo or geographical validation are indicated by "?". In (b) shapes indicate region of collection. Points are color coded by cluster designated in Density Clustering analysis (red = 1, green = 2, blue = 3).

**TABLE 4** Number of adult samples with complete data for all four skull measurements by density cluster, region, and morphotype.

Cluster	Region	Long-beak	Short-beak	Unknown
1	Eastern North Pacific	0	22	77
	Eastern tropical Pacific	0	17	0
	Unknown	0	0	2
2	Eastern North Pacific	33	0	28
	Gulf of California	4	0	8
	Eastern tropical Pacific	0	2	0
	Eastern South Pacific	0	0	3
	Unknown	0	0	2
3	Eastern North Pacific	17	0	8
	Gulf of California	4	0	5
	Eastern South Pacific	0	0	5
	Unknown	0	0	1

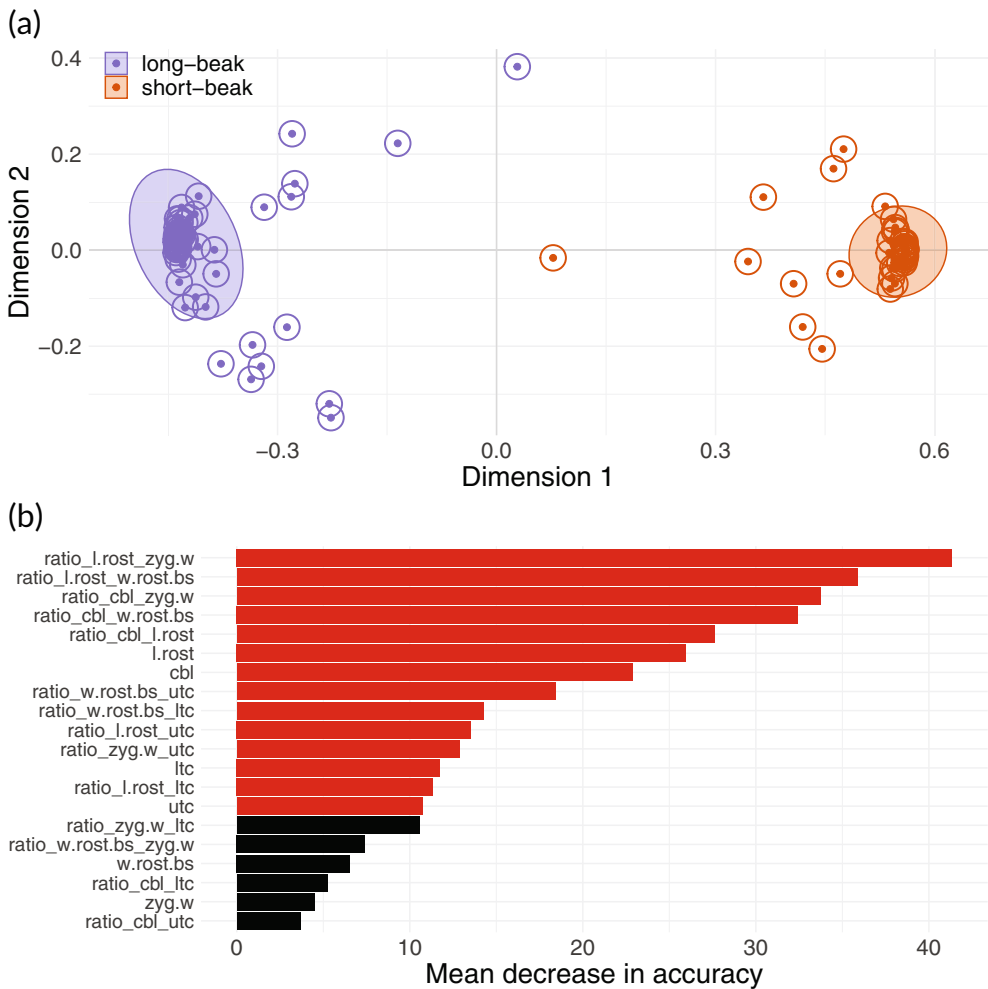
long-beaks, with clear separation between the two forms. With a Bayesian logistic model (see Supplemental Materials for methods), we estimated the RL/ZW ratio breakpoint between the morphotypes to be approximately 1.476 (95% HDI = 1.449–1.506). All morphotype-validated skulls with lower values were short-beaks, while all greater than this were long-beaks (Figure 5).

We also estimated the parameters of a linear regression of RL/ZW ratio and condylobasal length (CBL) for each morphotype separately to examine how this ratio changed with skull growth (Figure 5c, Table 6). The intercept for long-beaks was approximately 0.66 units greater than that for short-beaks (95% HDI = 0.287–1.067), and 99% of the posterior difference was greater than zero. The difference between the slopes was small (approximately 0.001), but 96% of the posterior difference was greater than zero.

Using the Random Forest models and the estimated RL/ZW ratio threshold from the Bayesian logistic model trained on the morphotype-validated skulls, we estimated the morphotype of the skulls for which we had no independent morphotype identification (Figure 5c). Based on the Random Forest model, almost two-thirds (62%) of these skulls were assigned with probabilities greater than 95%, and 83% were assigned with probabilities greater than 80% (Figure SM1, Table SM2). Only three skulls did not have the same morphotype assignment using the Random Forest model and the RL/ZW ratio threshold. All three of these skulls (all cranially mature) had RL/ZW ratios very close to the median threshold and had been identified in the field as short-beaks. One (SDNHM 21205), collected off Catalina Island, California, was assigned as a long-beak with the Random Forest model ( $p = .60$ ), but a short-beak given the RL/ZW ratio (1.4751). The other two (LACM 72307, 72137) were collected from the ETP and assigned as short-beaks with the Random Forest model (assignment probabilities = .52 and .73, respectively), but as long-beaks given the RL/ZW ratio (1.49 and 1.48, respectively). Five of the six samples with unknown locality were strongly assigned ( $p > .95$ ), two to short-beaked and three to long-beaked (Table SM2). The sixth (LACM 47147) was weakly assigned to long-beak ( $p = .6$ ).

## 4.2 | Mitochondrial DNA

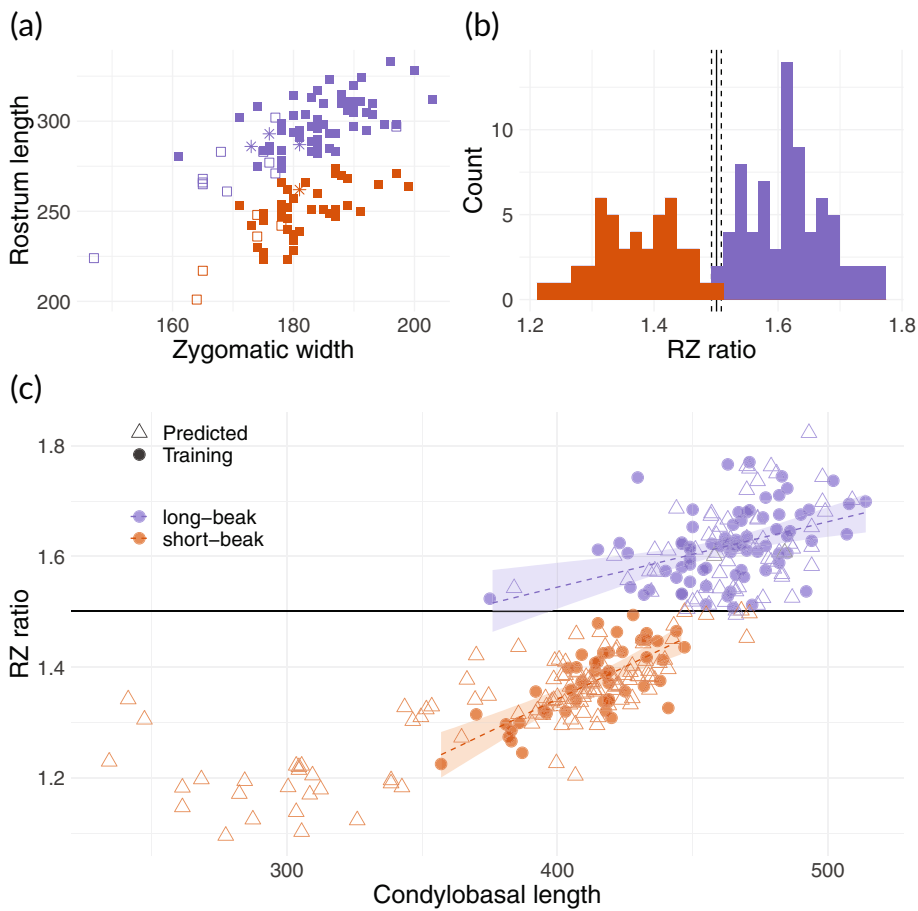
The optimal window for the control region (CR) alignment was 405 bp long, which contained 755 sequences and 277 haplotypes. The optimal cytochrome *b* (*cytb*) alignment was 360 bp long and contained 370 sequences and 51 haplotypes. A total of 369 individuals had both CR and *cytb* sequences, which were represented by



**FIGURE 4** (a) Proximity plot from Random Forest analysis of skull measurements. Color of inner circle indicates original photo-ID form designation, while color of outer ring indicates Random Forest form prediction. (b) Distribution of predictor importance from Random Forest analysis based on mean decrease in accuracy. Red bars indicate predictors with permutation  $p$  values  $\leq .05$ . Abbreviations for variables on y-axis are from Figure 2 and Table 1 for raw measurements, and “ratio\_a\_b” for the ratio of measurements “a” and “b” (a/b).

**TABLE 5** Summary of assignment probabilities (percent of votes) for Random Forest models classifying morphotypes using all and only adult skulls. Last column is the percent of assignment probabilities that are greater than 0.95.

Data	Morphotype	$n$	Median	95% CI	Percent > 0.95
All	long-beak	57	0.988	0.734, 1	0.737
	short-beak	43	0.98	0.756, 1	0.791
Adult	long-beak	46	0.992	0.677, 1	0.761
	short-beak	39	0.988	0.777, 1	0.795



**FIGURE 5** (a) Distribution of rostrum length to zygomatic width (RL/ZW) ratio for short and long-beak common dolphin skulls. Closed squares are adult skulls, while open squares are juveniles. Skulls with unknown maturity are denoted with asterisks. (b) Histogram of RL/ZW ratio for short-beak and long-beak common dolphins. Solid and dashed lines are the median and 95% HPD of the estimated threshold RL/ZW ratio from the Bayesian model. (c) Fit of the Bayesian linear models of RL/ZW ratio relative to condylbasal length for each form. Closed circles represent skulls used in the Random Forest model for which photo identification of form was available. Open triangles are skulls that were predicted to form by the Random Forest model.

**TABLE 6** Summary of posterior distribution of intercept and slope from Bayesian linear regression of RL/ZW ratio on condylbasal length for each morphotype and difference between posteriors (delta). Last column is the percent of the delta posterior distribution that is greater than 0.

Model	Parameter	Median	95% HDI	Percent > 0
Long-beak	intercept	1.071	0.791–1.363	
	slope	0.001	0.001–0.002	
Short-beak	intercept	0.41	0.122–0.693	
	slope	0.002	0.002–0.003	
Delta	intercept	−0.666	−1.067–−0.287	0.001
	slope	0.001	0–0.002	0.995

137 concatenated haplotypes. GenBank accession numbers, field morphotype designations, and collection information for all sequences in these windows are provided in Table SM3.

Three haplotypes were shared between the forms in the CR and *cytb* alignments. One individual, MMaSTR 23174, sampled from a gill net offshore of California, was identified in the field as a short-beak, but shared both CR and *cytb* haplotypes with 73 and 179 long-beaks, respectively. A second individual, MMaSTR 90803, a biopsy taken from a school offshore of California, was identified from photos of the school as a long-beak but shared both CR and *cytb* haplotypes with 17 and 14 short-beaks, respectively. Finally, one short-beak (MMaSTR 9564) and one long-beak (GenBank EU557094, Xiong et al., 2009), both strandings from China, shared CR and *cytb* haplotypes. These individuals were all sequenced a second time to verify the original sequence.

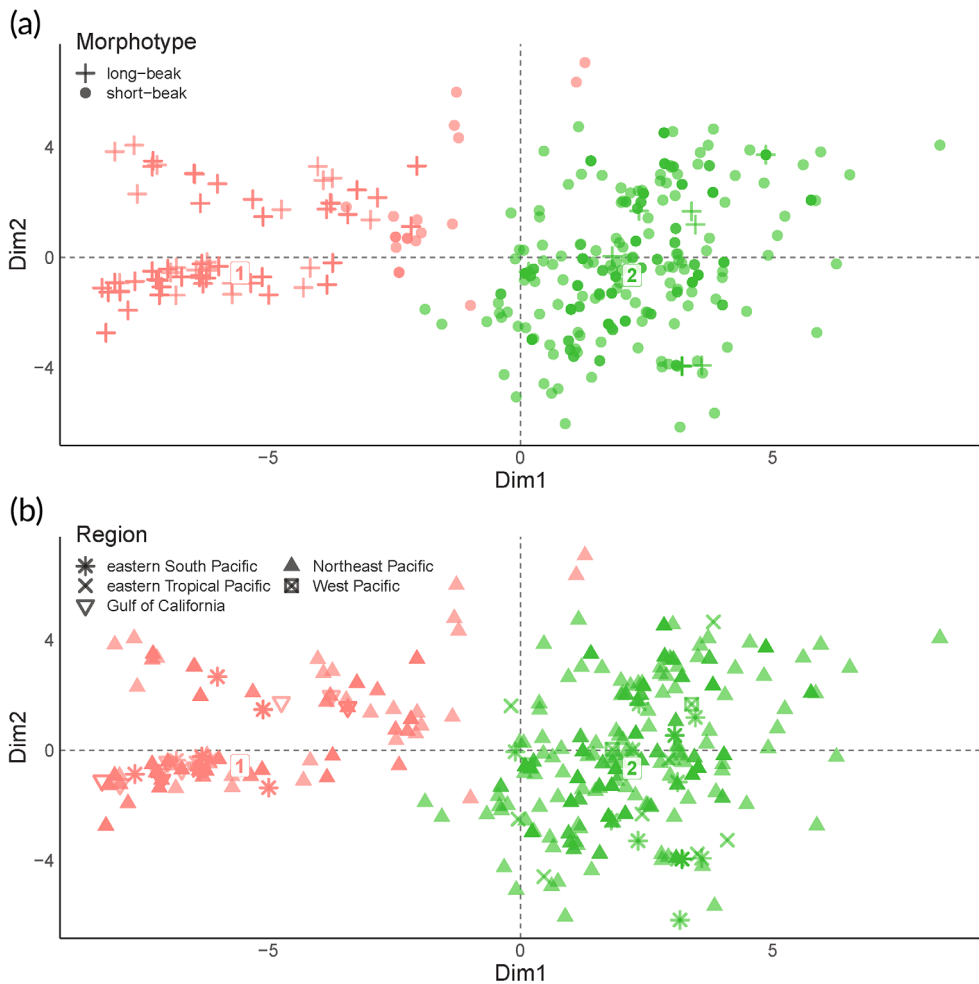
As measured by the effective number of haplotypes, diversity was three to ten times greater in short-beaks than long-beaks, with the greatest absolute difference being in the ENP CR data set (142 vs. 27; Table 7). Haplotypic diversity in the ENP was relatively high in CR for both short-beaks and long-beaks (0.99 and 0.94, respectively), and *cytb* for short-beaks (0.9), but low in *cytb* for long-beaks (0.48) (Table 7). Complete haplotype frequency distributions for the CR, *cytb* and CR/*cytb* data sets are provided in Table SM4.

The Density Clustering analysis identified two clusters of CR sequences (Figure 6), only a single *cytb* cluster, and three CR/*cytb* clusters (Figure 7). Of a total of 453, 439 (97%) long-beaks were in CR cluster 1, while 282 of the 302 (93%) short-beaks were in CR cluster 2 (Table 8). CR/*cytb* cluster 1 had all long-beaks from the eastern South Pacific ( $n = 14$ ), 13 of the 17 long-beaks from the Gulf of California, 156 of the 221 long-beaks from the ENP, and 1 short-beak from the ENP (Table 9). CR/*cytb* cluster 2 had the remaining four long-beaks from the Gulf of California and 64 long-beaks from the ENP. Both clusters 1 and 2 had 99% of the long-beaks, while CR/*cytb* cluster 3 had 115 of the 116 short-beak sequences (99%).

There were 50 specimens for which we had mtDNA control region sequences and a measurement of the RL/ZW ratio. Of these, 38 had RL/ZW ratios greater than 1.476 and all were in CR cluster 1 with the other field-identified long-beaks. Eleven of the remaining 12 specimens that had RL/ZW ratios less than 1.476 were in CR cluster 2 with

**TABLE 7** Number of individuals, haplotypes, heterozygosity, and effective number of haplotypes for mtDNA control region (CR), cytochrome *b* (*cytb*) and concatenated sequences (CR/*cytb*) by region and Delphinus form. Metrics are number of sequences (N), number of haplotypes (H), haplotypic diversity (HD), and effective number of haplotypes (He).

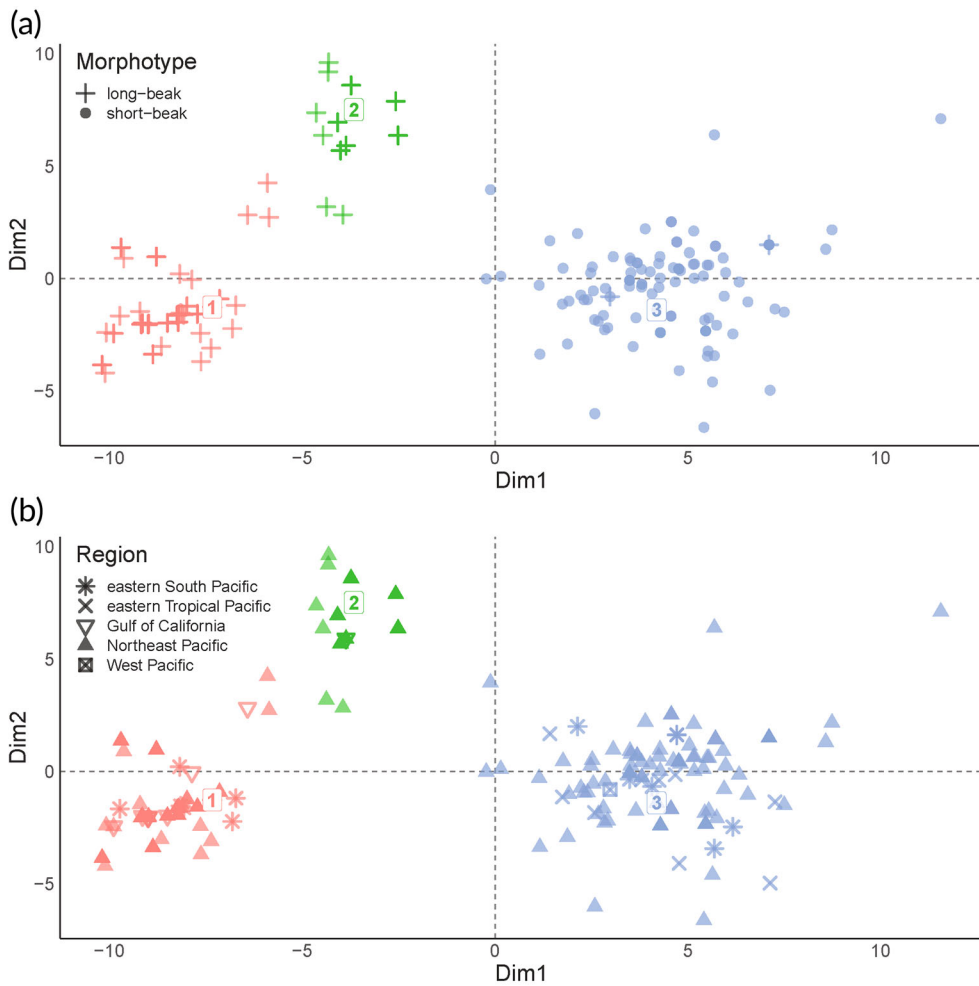
Locus	Metric	Long-beak				Short-beak			
		Eastern South Pacific	Gulf of California	Eastern North Pacific	West Pacific	Eastern South Pacific	Eastern tropical Pacific	Eastern North Pacific	Northwest Pacific
CR	N	54	22	374	3	7	10	281	4
	H	15	11	58	3	6	10	183	4
	HD	0.8121	0.8512	0.9424	0.6667	0.8163	0.9	0.9889	0.75
	He	8.413	8.478	26.85	3	5.742	10	141.9	4
<i>cytb</i>	N	14	17	221	1	7	9	97	4
	H	1	3	10	1	5	7	31	4
	HD	0	0.4429	0.4754	0	0.7755	0.8148	0.9036	0.75
	He	1	2.123	2.634	1	4.711	6.24	16.5	4
CR/ <i>cytb</i>	N	14	17	221	1	7	9	96	4
	H	7	9	44	1	6	9	68	4
	HD	0.6429	0.8374	0.9458	0	0.8163	0.8889	0.9668	0.75
	He	4.267	7.293	25.45	1	5.742	9	51.14	4



**FIGURE 6** First two axes of Principal Coordinates Analysis of mtDNA control region haplotypes. Points are color coded by cluster designated in Density Clustering analysis. Point shapes correspond to (a) validated morphotypes, and (b) region of collection.

the short-beaks. The sole specimen with a RL/ZW ratio less than 1.476, yet was in CR cluster 1 (MMaSTR 8415/LACM 92081), was identified in the field as a long-beak, had an RL/ZW ratio = 1.42, and did not have cranial fusion, indicating it was not yet adult.

Nei's net nucleotide diversity ( $d_A$ ) between long- and short-beaks was 0.009 for the control region data set, 0.006 for *cytb*, and 0.008 for the concatenated CR/*cytb* data set. The Random Forest models showed high diagnosability for both forms with a PD greater than 99% for all three data sets (Table 10). In the CR data set, three short-beaks and six long-beaks were misclassified. The *cytb* and CR/*cytb* models had very similar performance, where one short-beak and two long-beaks were misclassified, which were also misclassified in the CR model and were the same three with shared haplotypes described above (MMaSTR 23174, 90803, and GenBank EU557094). Of the other six misclassified in the CR model, two were long-beaks from Peru, two were long-beaks from Japan, and two were short-beaks from Mexico and Peru. Classification accuracy was relatively high, with over 95% of both forms being correctly classified with probabilities greater than 80% in all models (Figure SM2). All misclassifications



**FIGURE 7** First two axes of Principal Coordinates Analysis of concatenated mtDNA control region and cytochrome *b* haplotypes. Points are color coded by cluster designated in Density Clustering analysis. Point shapes correspond to (a) validated morphotypes, and (b) region of collection.

**TABLE 8** Number of mtDNA control region sequences by cluster (Figure 7), region, and morphotype.

Cluster	Region	Long-beak	Short-beak
1	Eastern North Pacific	373	20
	Gulf of California	22	0
	Eastern South Pacific	44	0
2	Eastern North Pacific	1	261
	Eastern tropical Pacific	0	10
	Eastern South Pacific	10	7
	Northwest Pacific	0	4
	West Pacific	3	0



**TABLE 9** Number of concatenated mtDNA control region / cytochrome *b* sequences by cluster (Figure 8), region, and morphotype.

Cluster	Region	Long-beak	Short-beak
1	Eastern North Pacific	156	1
	Gulf of California	13	0
	Eastern South Pacific	14	0
2	Eastern North Pacific	64	0
	Gulf of California	4	0
3	Eastern North Pacific	1	95
	Eastern tropical Pacific	0	9
	Eastern South Pacific	0	7
	Northwest Pacific	0	4
	West Pacific	1	0

**TABLE 10** Confusion matrices from mtDNA Random Forest models.

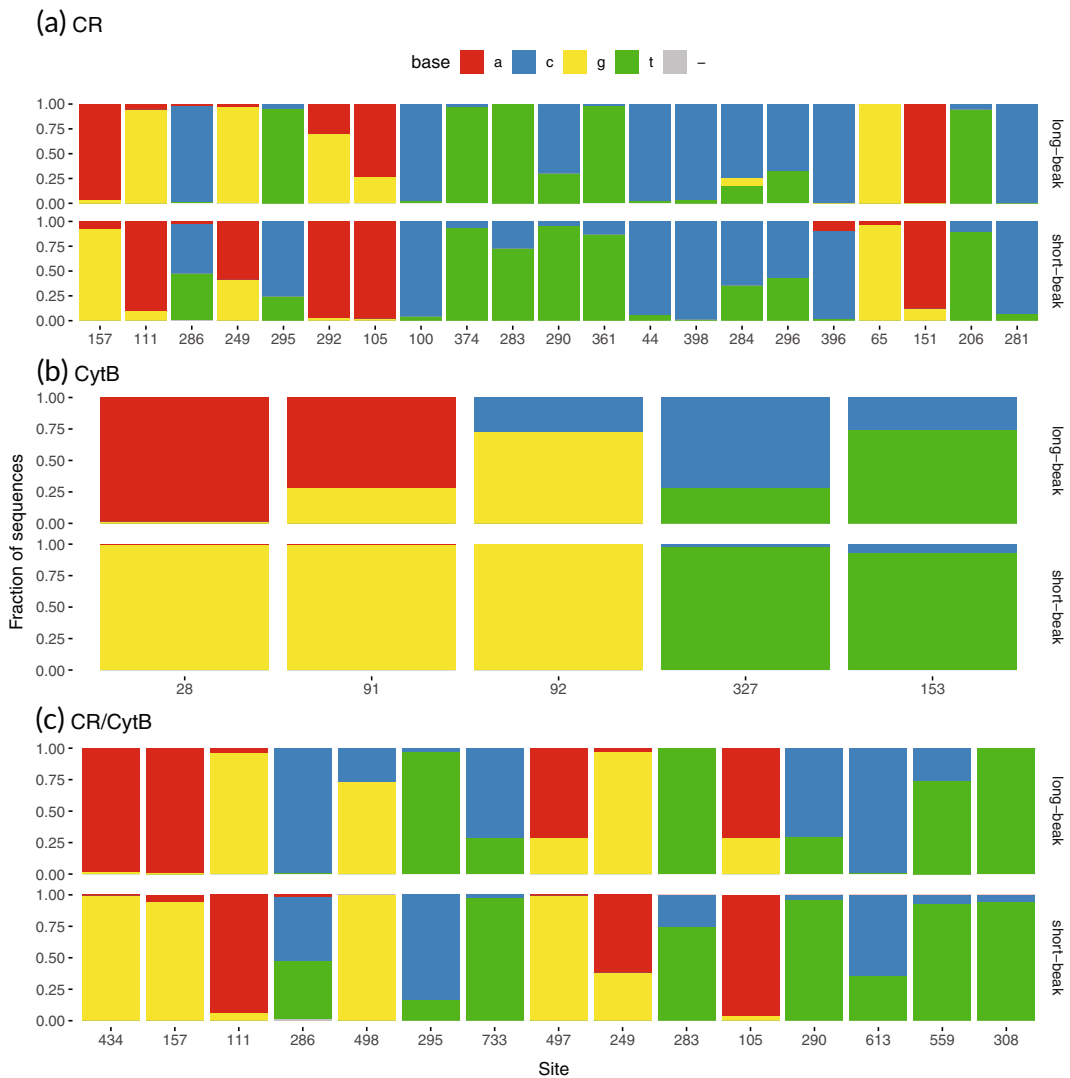
Locus	Original	Predicted		% Correct	95% CI
		Long-beak	Short-beak		
CR	Long-beak	447	6	98.68	97.14, 99.51
	Short-beak	3	299	99.01	97.12, 99.79
	Overall			98.81	97.75, 99.45
cytb	Long-beak	251	2	99.21	97.17, 99.9
	Short-beak	1	116	99.15	95.33, 99.98
	Overall			99.19	97.65, 99.83
CR/cytb	Long-beak	251	2	99.21	97.17, 99.9
	Short-beak	1	115	99.14	95.29, 99.98
	Overall			99.19	97.64, 99.83

had high assignment probabilities to the incorrect form (>95%), except the two short-beaks from Mexico and Peru, which were classified as long-beaks with probabilities of approximately 53%.

Although the *cytb* and CR/*cytb* Random Forest models had fewer overall misclassifications and a higher correct classification rate than the CR model, only five sites were found to be significant predictors in the *cytb* model, as compared to 21 significant predictor sites in the CR model (Figure 8). In the concatenated CR/*cytb* model, there were 15 significant predictor sites. Given that two haplotypes were shared between the morphotypes as described above, there were no diagnostic sites.

## 5 | DISCUSSION

The analyses in this study show that long- and short-beaked common dolphins in the ENP are 100% diagnosable to form with cranial characteristics and greater than 99% diagnosable with mtDNA sequences. Both morphology and genetics have long been regarded as strong lines of evidence for delineating taxa (e.g., Perrin et al., 1994, 2009; Taylor et al., 2017). Given that this study shows that both data sets are congruent with external coloration, there is strong evidence that long- and short-beaked common dolphins in the eastern Pacific are not currently experiencing



**FIGURE 8** Base-frequency distribution of sites identified as significantly important in predicting forms from Random Forest analysis on (a) control region, (b) cytochrome *b*, and (c) concatenated control region and cytochrome *b* sequences. Sites are sorted from most important on the left to least important on the right. Each bar shows the relative frequency of the base pairs (colors) within the sequences for that form.

significant gene flow (despite being partially sympatric) and should be considered as distinct species. Below we detail and discuss the combined evidence for species status, including both information from the literature and the results from the current study.

## 5.1 | Color pattern

We have no new quantitative data on coloration; the following discussion is based on information in the literature, and observations by the authors of schools of long- and short-beaked common dolphins in southern California, and off Baja California. We use the terminology of Heyning and Perrin (1994; see their fig. 1 for a diagram showing

and labeling the color pattern components). In relation to the parapatric short-beaked common dolphin, long-beaked specimens have several unique color pattern features. However, on some postmortem darkened specimens these may not always be obvious, and some young specimens may not show the full diagnostic color pattern characteristics.

Compared to short-beaks, the thoracic patch in long-beaks is generally darker, showing less contrast with the dark spinal field (cape). There is less contrast of the eye patch with the adjacent thoracic patch. The white belly (abdominal field) rarely extends above the flipper stripe. Light patches on the flippers and dorsal fin are rare, and when present, tend to be weakly developed (Heyning & Perrin, 1994). However, the light patches are variable by age and possibly geographic area, and so this difference is not absolute. The flipper stripe narrows somewhat anterior to the eye. Evans (1975, 1982) stated that the flipper stripe is more strongly developed and wider in the long-beaked form, often being so wide as to contact the gape. However, as can be seen from Figure 9, this is not actually the case. The flipper stripe starts out as distinct stripe extending from the flipper to the lower jaw/chin, as in the short-beaked form, though it may be somewhat wider in the long-beaked form.

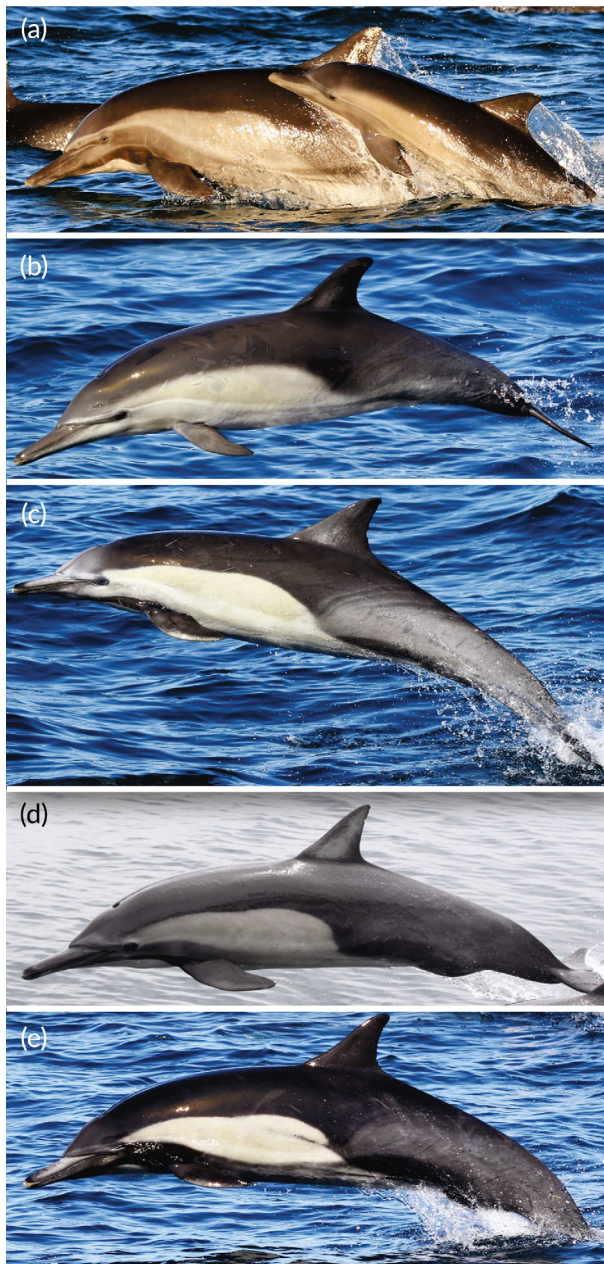
The primary difference between the two forms is that in the long-beaked form, there is a stripe that runs from gape to-anus (encompassing both the eye and the flipper, and present in all ages classes; Figure 9), which is adjacent to and usually somewhat lighter than the flipper stripe. The posterior part of this stripe is called the flipper-to-anus stripe by Heyning and Perrin (1994). In long-beaks these two stripes merge and darken to form a dark “face mask” in larger adults (especially adult males). This complex of merged and darkened stripes gives adults of the long-beaked form their distinctive dark face (Figure 9). In contrast, the facial area of short-beaks, in which the white of the abdominal field extends above the flipper stripe, appears much lighter and makes the eye stripe and eye patch appear very distinct (Figure 1). When a gape-to-anus or flipper-to-anus stripe is present in the short-beaked form, it is much narrower and only exists as a dark stripe in the posterior area near the urogenital region.

## 5.2 | External morphology

We have no new data on external morphology, and the following discussion is based largely on information in the literature. Eastern North Pacific long-beaked common dolphins grow to larger sizes than the parapatric short-beaked form. In specimens collected as strandings or captures from California, sexually mature long-beaked males ranged from 202 to 235 cm, and sexually mature females were 193–224 cm; short-beaked males ranged from 172 to 201 cm, and females were 164–193 cm (Heyning & Perrin, 1994). Similar results were found from a larger sample of specimens from California measured from aerial photographs at sea: adult long-beaked males ranged from 202 to 243 cm, and sexually mature females were 193–228 cm; short-beaked adult males ranged from 172 to 205 cm, and females were 174–199 cm (Leander et al., 2021). Not surprisingly, the beak is also longer (both absolutely and relatively) in the long-beaked form, though there is overlap. Beak length in eastern Pacific long-beak adults is 133–175 mm, and in short-beaks it is 105–140 mm (Heyning & Perrin, 1994). In eastern Pacific long-beaks, the body has a more slender appearance overall, and the head is longer, but relatively narrower. The melon rises from the beak at a shallower angle, giving the melon a slightly flatter appearance (Heyning & Perrin, 1994).

## 5.3 | Skeletal morphology

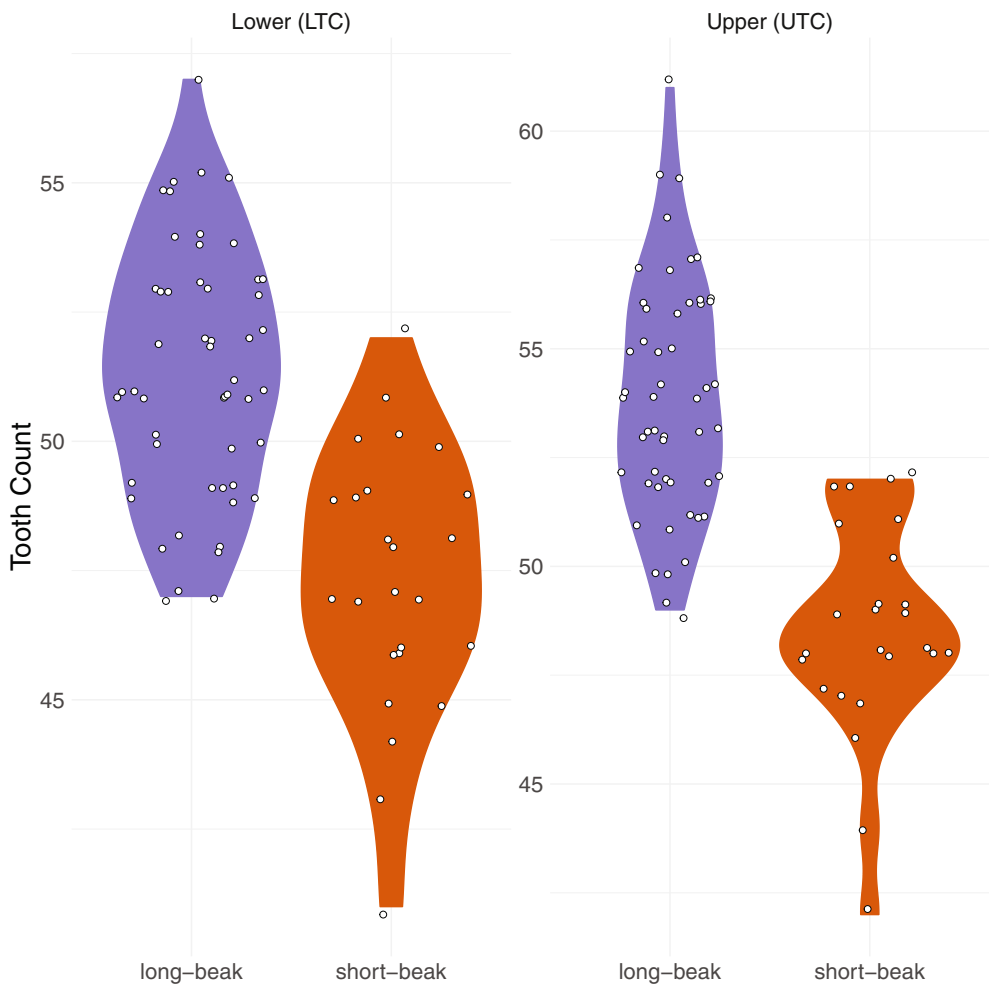
Eastern Pacific long-beaked common dolphins have longer and relatively more slender skulls than those of short-beaks from this ocean basin. In this study, we found a range of 415–514 mm for the condylobasal length of skulls from adult-size eastern Pacific long-beaked common dolphins. The equivalent range for eastern Pacific short-beaks was 386–447 mm. The most informative metric for distinguishing skulls of the two species is the rostral length to zygomatic width ratio (RL/ZW ratio). From this study, common dolphins in the ENP with an RL/ZW ratio greater



**FIGURE 9** Age and sex related variation in the color pattern of *D. bairdii*: (a) calf with its mother, (b) juvenile, (c) subadult or young adult, (d) adult male, (e) adult male.

than 1.476 should be diagnosed as long-beaked common dolphins, while those with an RL/ZW ratio less than this can be identified as short-beaked common dolphins. This relationship holds for both immature and mature skulls. While there are modal differences in tooth counts between the two species, there is a large area of overlap, and therefore tooth counts have limited utility in distinguishing the species (Figure 10).

The morphological analysis was limited by several factors. First, most of photo-identified specimens were from California. This limited geographic coverage of independently validated skulls restricted the scope of the analyses



**FIGURE 10** Distribution of lower (LTC) and upper (UTC) tooth counts for long- and short-beaked common dolphins for specimens with photo identifications, showing extensive overlap between the species.

that could be done, especially with respect to a priori stratified tests including samples from the eastern South Pacific, primarily Peru. However, the Density Cluster analysis suggested that the eight adult skulls in this analysis from the eastern South Pacific were long-beaks and that those skulls tended to be significantly, but not diagnostically, wider than those in the ENP and the Gulf of California. This suggests further differentiation within long-beaks in the eastern Pacific, most likely at the level of subspecies.

Secondly, although it is known that short-beaks occur off Peru (Llapasca et al., 2018), we had no measurements of short-beaked specimens from this region. Future studies should strive to better sample both forms of common dolphins in the eastern South Pacific, as it would be useful to understand how short-beaks in this region compare to the Peruvian long-beaks and ENP short-beaks, which we included in this study.

Finally, the number of skull measurements taken was limited. Since previous studies had indicated that only a few measurements were likely to be useful in discriminating the two forms, this was an a priori decision to prioritize obtaining data from many different specimens vs. collecting a large number of measurements from a smaller number of specimens. However, more measurements may provide greater resolution of differentiation at a greater geographical scale.

## 5.4 | Molecular genetics

The genus *Delphinus* is estimated to have diverged approximately 2 MYA within the Pleistocene (Amaral et al., 2012; McGowen et al., 2009; Urrutia Osorio et al.<sup>1</sup>). Within the genus, short-beaked common dolphins are considered to be the ancestral type, with long-beaked forms diverging independently in each ocean basin (Amaral et al., 2012; Cunha et al., 2015). Using a coalescent approach (Ima) with mitochondrial control region sequences, Segura-Garcia et al. (2016) estimated a divergence time between long and short-beak forms in the Pacific at a relatively recent 12 KYA. However, fossil-calibrated divergence time estimates are all relatively consistently longer, at approximately 1 MYA (Amaral et al., 2012; McGowen et al., 2009; see Footnote 1).

There are a number of extant cetacean sister species that are believed to have diverged within the last 2 million years (McGowen et al., 2009, 2020). For example, the two recently resurrected species of southeast Asian river dolphins (*Platanista gangetica* and *P. minor*) are estimated to have diverged around 550 KYA (Braulik et al., 2015, 2021a). Speciation within the finless porpoise (genus *Neophocoena*) was estimated to have occurred more recently, around 100 KYA (Zhou et al., 2018) or even around 18 KYA (Jefferson & Wang, 2011), though mating behavior and timing may differ among these three genera. Perhaps more comparable to the case of *Delphinus*, Louis et al. (2021) estimated that western North Atlantic coastal (Tamanend's) bottlenose dolphins (*Tursiops erebennus*) diverged from the offshore form (*Tursiops truncatus*) approximately 80 KYA (see Costa et al., 2022 for further review of differentiation within the genus *Tursiops*).

The relatively recent divergence of short- and long-beaked common dolphins in the Pacific is evidenced by the small degree of consistent differences among mitochondrial sequences. In a study using sequences from 14 short-beaks from California and the ETP and 11 long-beaks from California, Rosel et al. (1994) found no shared haplotypes between the two forms. The forms were also distinguished by one fixed difference in the control region and another in *cytb*. Although long-beaks were monophyletic, there were short-beak haplotypes that were more closely related to the long-beaks than they were to other short-beaks. Similarly, in their study of the molecular relationships of common dolphins from Senegal, West Africa, Becker et al.<sup>2</sup> found support for a monophyletic clade of long-beaked common dolphins from California, Peru, and possibly China (the latter based on only a single sample), but no support for a worldwide long-beaked clade.

Although we found strong differentiation in this study with a much larger sample size and geographic coverage than Rosel et al. (1994), and near-perfect diagnosability, we did observe three shared haplotypes between the two forms. Two of these were shared in the ENP, and one was shared in the western Pacific. For the two ENP haplotypes, only one short-beak or long-beak individual was found with the haplotype that was relatively common in the other form. In both of these cases, our best efforts to validate the two odd individuals through review of the biopsy and survey metadata did not change their original form identification. Since the same haplotypes were produced after resequencing, we can largely rule out errors in labeling or in-lab tube mix-ups as a concern.

Thus, we are left with either the possibility that these shared haplotypes result from ancestral polymorphism or from extremely low levels of gene flow. It is difficult, if not impossible, to distinguish between these two scenarios with this data set. As described above, the extent of mtDNA differentiation between the forms is not inconsistent with that of other recently diverged species. Additionally, the short and long beak sequences in this study very closely correspond to two natural clusters, making it clear that these two forms are far along the process of lineage sorting, but it may not be fully complete.

Given that long-beaked and short-beaked common dolphin populations within the California Current are estimated at around 83,000 and 1 million individuals, respectively (Becker et al., 2020), it is expected that genetic

<sup>1</sup>Urrutia-Osorio, M. F., Archer, F. I., Morin, P. A., Hancock-Hanser, B. L., & Jefferson, T. A. (In revision). Phylogenetic relationships among eastern Pacific common dolphins (*Delphinus* spp.). *Aquatic Mammals*.

<sup>2</sup>Becker, M. A., Murphy, K. R., Archer, F. I., Jefferson, T. A., Keith-Diagne, L. W., Potter, C. W., Urrutia-Osorio, M. F., Ndong, I., & McGowen, M. R. (In revision). Common dolphin (*Delphinus delphis*) mitochondrial genomes from Senegal reveal geographic structure across the North Atlantic, but provide no support for global long-beaked clade. *Marine Mammal Science*.

variation would remain high throughout the lineage sorting process. Observing a few shared haplotypes, even in the absence of mating between the forms should not be surprising. This is similar to the more recently diverged *Neophocoena phocoenoides* and *N. asiaorientalis*, in which one of seven identified haplotypes was shared (Wang et al., 2008). However, coalescent-based analyses of combined mitochondrial sequences and microsatellite loci indicated that there was no contemporary gene flow between the two *Neophocoena* species (Wang et al., 2008). Thus, given that finless porpoises are estimated to have diverged considerably more recently than Pacific long- and short-beaked common dolphins, it is possible that nuclear genotypes will similarly demonstrate zero contemporary gene flow between the forms of *Delphinus*. This notion is reinforced by the distinctiveness of the external morphology and cranial morphometrics, both of which result from nuclear gene expression, and can thus be considered as proxies of nuclear differentiation.

In our study, control region diagnosability was 99%, and Nei's  $d_A$  was 0.009. Although these values exceed the 95% diagnosability and 0.004 Nei's  $d_A$  thresholds for subspecies delimitation suggested by Taylor et al. (2017), Nei's  $d_A$  does not exceed their 0.02 threshold recommended for species delimitation. It should be noted that the quantitative guidelines suggested by Taylor et al. (2017) are intended for studies where mtDNA is the only, or primary, line of evidence for making taxonomic decisions. This is recognized in their flowchart (fig. 3 in Taylor et al., 2017), where cases that meet the subspecies thresholds, but do not meet the species threshold, can still be considered as species if other lines of evidence support species status. In this study, we have provided strong morphometric evidence of species-level differentiation that also corresponds to external color pattern and geography. Additionally, using full mitogenomes from six short-beaks and 12 long-beaks from California, and 10 long-beaks from Peru, Urrutia Osorio et al. (see Footnote 1) recently demonstrated reciprocal monophyly of the two forms and estimated a divergence time in the eastern Pacific of about 1.5 MYA. Thus, in light of the Taylor et al. (2017) guidelines, the mtDNA results support species-level recognition of the two forms of *Delphinus* in the eastern Pacific.

## 5.5 | Life history

Life history of ENP long-beaks is not well known, as studies before 1994 generally mixed the two common dolphin species together, and only a few studies have been conducted since then. Longevity is not well studied, and in a sample of 41 specimens from the Gulf of California, the oldest had only 21 GLGs (Gallo-Reynoso et al., 2014). Vidal and Gallo-Reynoso (2012) presented evidence that suggests that long-beaks in the Gulf of California grow larger than those off California (and thus may represent separate populations), and in fact they may be the largest common dolphins in the world. They reportedly reach lengths of at least 252cm (females) and 265cm (males) (Vidal & Gallo-Reynoso, 2012).

Several differences in reproductive parameters have been found between ENP long-beaked and short-beaked common dolphins (Chivers et al., 2016). The mean birth date for calves is in winter (December 12) for short-beaks and in spring (March 6) for long-beaks. Also, the percentage of calves in groups (6.9% for short-beaks and 4.5% for long-beaks) and average age at which calves swim independently (14.0 months for short-beaks and 11.1 months for long-beaks) are higher in the short-beaked species. The nearly 3-month offset in peak calving (and thus presumably mating as well) may provide a mechanism for reproductive isolation of the two species and may inhibit potential interbreeding. Also, based on large samples ( $n = 130$ ), the percentage of females that are pregnant (28.1% in short-beaks and 22.1% in long-beaks) may be higher for the short-beaked animals (Kellar et al., 2014). It is possible that only females (but not males) of the two lineages have different reproductive timing, though this appears to us very unlikely. All of these elements argue for a significant degree of reproductive isolation between the two species in the ENP.

## 6 | SPECIES REDESCRIPTIONS AND TAXONOMIC TREATMENT

Order Artiodactyla Owen, 1848

  Infraorder Cetacea Brisson, 1762

    Odontoceti Flower, 1867

      Family Delphinidae Gray, 1821

        Genus *Delphinus* Linnaeus, 1758

*Delphinus bairdii* Dall, 1873

### Synonymy

*Delphinus bairdii* Dall, 1873:12. Original description.

### Holotype and Type Locality

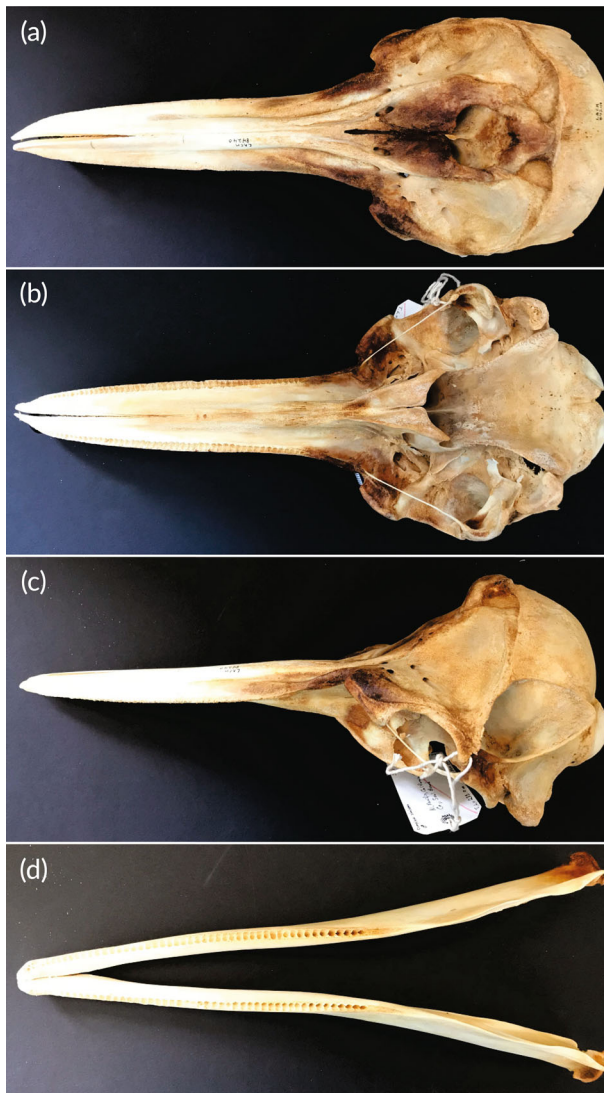
The species was described, based on two specimens collected off Point Arguello, California, by C. M. Scammon on 29 October 1872 (Dall, 1873, 1874). One specimen (a skeleton) was apparently sent to the United States National Museum (Smithsonian Institution), but there was no record of its arrival, even after a thorough search by Poole and Schantz (1942) and more recently by J. G. Mead (personal communication, July 30, 2021). Both type specimens are apparently lost. Heyning and Perrin (1994) therefore proposed a neo-type (LACM 84240; Figure 11), a complete skeleton, and illustrated both the external appearance and skull of that specimen (figs. 8 and 18 in Heyning & Perrin, 1994). There is also a control region sequence in GenBank (OQ409275, SWFSC 198467).

### Diagnosis<sup>3</sup>

The eastern Pacific endemic *Delphinus bairdii* can be distinguished from the parapatric *D. delphis* by the following external characters: longer beak, greater body length, more slender body, and relatively smaller flippers and dorsal fin (Heyning & Perrin, 1994). Beak length can reach up to 175mm (Heyning & Perrin, 1994). Body length of adults ranges from 193–265cm (Heyning & Perrin, 1994; Gallo-Reynoso et al., 2014; Leander et al., 2021; Vidal & Gallo-Reynoso, 2012; this study). *D. bairdii* also has a longer and relatively narrower skull. Condylbasal length of adults ranges from 415–514mm (Heyning & Perrin, 1994; this study). Rostral length/zygomatic width ratios range from 1.50 to 1.83, and eastern Pacific specimens and ratios >1.476 can be considered to be *D. bairdii* (this study). Tooth counts are 47–62 per tooth row (this study). Color pattern components that are diagnostic include a more muted pattern overall, with a slightly darker thoracic patch. There is a wide stripe from the gape to the anus, which merges and blends with the flipper stripe. This creates a darkened face (especially in older animals), in which the eye and lip patches show less contrast with the rest of the face (Heyning & Perrin, 1994; this study). Light patches may occur on the flippers and dorsal fin, but generally only in larger animals (T.A.J., personal observation). Because there were shared control region and cytochrome *b* haplotypes between *D. bairdii* and *D. delphis* in this study, there were no fixed differences or fully diagnostic mtDNA sites. However, the Random Forest model based on the concatenated control region and cytochrome *b* sequences in this study can correctly classify over 99% of the *D. bairdii* specimens (249 out of 251). Fifteen sites were identified as being important to this classification, two of which were nearly fixed.

<sup>3</sup>Outside of the eastern Pacific Ocean, although most common dolphin populations are relatively short-beaked forms, there are long-beaked populations of *D. delphis*, which overlap and even exceed *D. bairdii* in many features. For instance, beak length is exceedingly long in *D. delphis tropicalis*, and reaches at least 9.7% of total length (Jefferson & Van Waerebeek, 2002). Body length can be up to 256 cm in *D. d. tropicalis* (Jefferson & Van Waerebeek, 2002), 260 cm in Japanese long-beaks (Amaha, 1994), and up to 258 cm in short-beaks from the eastern North Atlantic (Murphy et al., 2006; Perrin & Reilly, 1984). Condylbasal length extends to 575 mm in *D. d. tropicalis* (Jefferson & Van Waerebeek, 2002), and to at least 543 mm in a long-beaked population off South Africa (Jefferson & Van Waerebeek, 2002). The greatest ratios of rostral length/zygomatic width occur in the *tropicalis* subspecies (1.60–2.06; Jefferson & Van Waerebeek, 2002), though other long-beaked populations also come close to or exceed the values for *D. bairdii*: up to 1.80 off South Africa, 1.77 in Brazil and southern Australia, and 1.76 in Japan (Esteves & Oviedo, 2007; Jefferson & Van Waerebeek, 2002; Ngqulana et al., 2019; Westgate, 2005). The highest tooth counts among common dolphin populations/forms also occur in the *D. d. tropicalis* subspecies, reaching as many as 67 teeth per row, and Japanese long-beaks may have up to 60 teeth per row (Jefferson & Van Waerebeek, 2002).





**FIGURE 11** Dorsal (a), ventral (b), lateral (c), and dorsal mandible (d) views of the skull of the neotype specimen for *D. bairdii* Dall, 1873 (LACM 84240).

### Geographic Variation

Other than some subjective impressions of geographic differences in color patterns (with dolphins in southern Baja California, Mexico, supposedly showing more bold patterning and distinct stripes and blazes), no studies have provided further evidence for geographic color variation in the species. In reviewing extensive data from many different sources (i.e., morphology, genetics, distribution, movements, ecology), Dizon et al. (1994) found no evidence to separate the eastern Pacific long-beaked common dolphins into separate stocks for management. However, since then evidence has come to light that *D. bairdii* populations in the Gulf of California are larger than other populations of the species. Of over 140 specimens measured from the northern and central Gulf of California, females reached 252 cm and males 265 cm in total length (Gallo-Reynoso et al., 2014; Vidal & Gallo-Reynoso, 2012). By comparison, California specimens of *D. bairdii* are only known to grow to lengths of 237 for females and 243 for males (Heyning & Perrin, 1994; this study). The Gulf of California specimens are not only the largest known among eastern Pacific

long-beaked common dolphins they are the largest specimens of *Delphinus* (either species) known from anywhere in the world (Vidal & Gallo-Reynoso, 2012). This is strongly suggestive of a distinct stock or geographic form in the Gulf of California. The results of Urrutia Osorio et al. (see Footnote 1) suggest that the Peruvian population of long-beaks may deserve subspecific status, but this remains to be further investigated.

### Distribution and Habitat

*Delphinus bairdii* normally occurs from around the Monterey Bay and San Francisco Bay areas, California, southwards to just south of the tip of Baja California, and then northwards throughout the entire Gulf of California (see Hamilton et al., 2009). There are increasingly frequent records further north than the traditional limits in central California. This includes at least seven stranding records and multiple sightings of small groups of 5–20 individuals over several years in Washington State, particularly in Puget Sound (Shuster et al.; S. Norman, pers. comm.); six sightings, one stranding, and one bycatch record for British Columbia (Ford, 2005, 2014; though note that the report of *D. bairdii* from British Columbia by Guiget, 1954 was actually a specimen of *D. delphis*; Ford, 2014); and a series of sighting records of a single probable long-beaked common dolphin from in and around Prince William Sound, Alaska (at nearly 61°N; D. Anderson, in litt.). In the past, records north of the San Francisco Bay area have been considered extralimital strays, but with the warming of ocean waters off the west coast of North America, it is possible that those north to at least Washington State are representative of a northward range extension (Shuster et al., 2018).

There is another population of long-beaked common dolphins off the coast of Peru and Chile, which is separated from Californian/Mexican population(s) by a >2,500 km hiatus. Long-beaked common dolphins have been sighted along the entire coast of Peru, from 3°30'S to 18°21'S (Hamilton et al., 2009; Llapapasca et al., 2018). These animals also range south into Chilean waters, at least occasionally (Bernal et al., 2003; Sanino et al., 2003). Although records are known from as far south as approximately 33°S (Bernal et al., 2003), due to poor survey coverage, the typical range limits in Chile are not known. The presumed range of *D. bairdii*, based on available records, is shown in Figure 12.

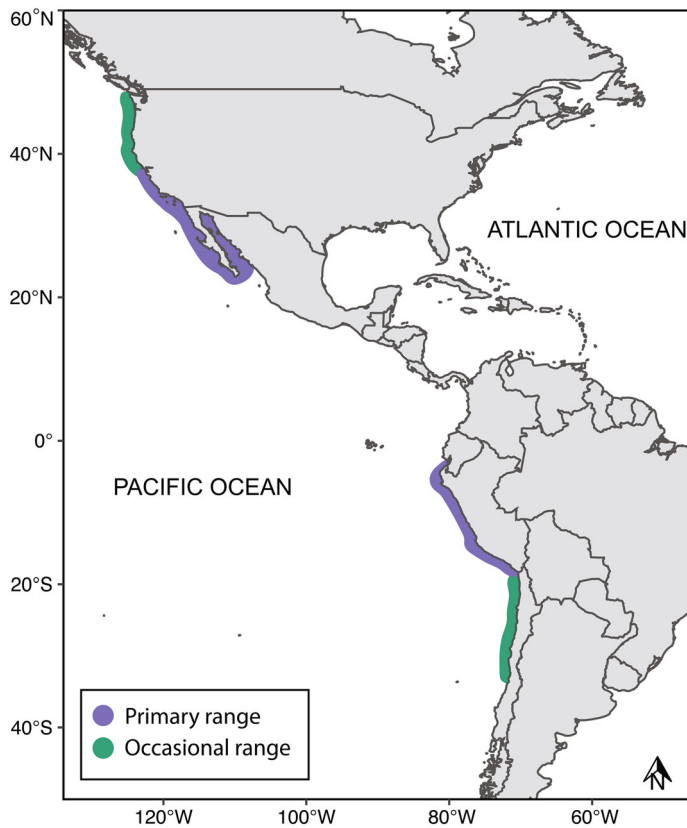
Evans (1982) called the long-beaked form the “northern neritic long-snouted population” and showed its distribution only extending south to about 20°N. He also found that short- and long-beaked animals overlapped in distribution but did not appear to form mixed schools (Evans, 1982), a point also raised by Heyning and Perrin (1994). The ENP long-beaked common dolphin has a restricted nearshore range over and near the continental shelf, being limited to within about 100 nmi (185 km) from the coast (Dizon et al., 1994; Perrin et al., 1985). Groups have often been observed from land, within a few hundred meters of the coastline in California and Mexico (T.A.J., personal observation). Known range states are limited to the United States, Mexico, Canada, Peru, and Chile, although western Pacific long-beaks require further investigation.

### Etymology

The species name, *bairdii*, is in honor of Spencer F. Baird (1823–1887), who was Commissioner of Fish and Fisheries, Secretary of the Smithsonian Institution, and a great supporter of marine mammal studies. We suggest the common name “eastern Pacific long-beaked common dolphin,” due to the fact that the species’ typical range is apparently restricted to the US state of California, Baja California, and the Gulf of California, Mexico; as well as Peru/Chile.

### Conservation Status

*Delphinus bairdii* is currently not listed on the IUCN Red List of Threatened and Endangered Species. The species is currently covered under *D. delphis*, which is listed as Least Concern (Braulik et al., 2021b). If the status of the species were assessed against the IUCN Red List criteria, it is likely that *D. bairdii* would be classified as Least Concern. Long-beaked common dolphins are quite abundant within their range, often being reported as the first- or second-most abundant cetacean species in Mexican waters of the Gulf of California (see Breese & Tershy, 1993; Salvadeo et al., 2009; Silber et al., 1994; Urban, 2010; Vidal & Gallo-Reynoso, 2012). Estimates of abundance from California and the west coast of Baja were made from a ship survey in 2009, and it was estimated that 183,396 (CV = 0.41) individuals are found off California, and 95,786 (CV = 0.47) off the west coast of Baja (Carretta et al., 2011). A more recent abundance estimate for the US west coast of 83,379 (CV = 0.216) is considered more accurate than the



**FIGURE 12** Presumed range of *D. bairdii* in the eastern Pacific Ocean. Shading shows both primary range (where surveys indicate regular occurrence), and occasional range (where there are very few records, or survey data are not available).

California estimate above (Carretta et al., 2023). For the Gulf of California, an older estimate (from surveys between 1986 and 1993) exists of 69,456, 95% CI [31,295, 154,153] long-beaked common dolphins (Gerrodette & Palacios, 1996). No estimates of abundance for the Peruvian population appear to exist.

Taken together, the above estimates suggest that the total global abundance of the eastern Pacific long-beaked common dolphin may be over 250,000 individuals. Clearly, as a species they are not endangered, and there is no evidence of depletion of the overall population. However, there has been no quantitative assessment of population trends for the species. The balance of evidence suggests that long-beaked common dolphins may be increasing in abundance, at least off the US west coast (Carretta et al., 2011, 2023). This is supported by the fact that strandings of the species have increased in southern California in recent years (1978–1986 and 1992–2008; Danil et al., 2010; Heyning & Perrin, 1994). However, it is unknown if these increases off California represent shifts of animals from Mexico, or actual increases in overall population size.

Long-beaked common dolphins are affected by human activities in various ways. Primary known threats include mortality in drift gill nets (Carretta et al., 2023), set gill nets (Carretta et al., 2023), sardine purse seines (Gallo-Reynoso, 1990), and blast trauma from US Navy underwater detonations (Danil & St. Leger, 2011). They may also be taken occasionally in ETP tuna purse seines, but this has not been confirmed, as the records do not always indicate if these were short-beaked or long-beaked (Carretta et al., 2023). There are anecdotal reports of large numbers of this species being taken for fishery bait in coastal areas of Baja California, Mexico (K. Forney, pers. comm.). Domoic acid intoxication is another factor that can sometimes cause mass mortality, such as was suspected to be the case in a

UME in southern California in 2002 (Torres de la Riva et al., 2009). In the upper Gulf of California in 1995, there was a large die-off of long-beaked common dolphins (and other species); the cause remains unknown but is thought to be related to some kind of toxic substance in the water (Vidal & Gallo-Reynoso, 2012). Toxic contaminants, such as DDT and its breakdown products, have been detected in tissues of specimens from the Gulf of California, but it is unknown how these pollutants are affecting the animals (Gallo-Reynoso et al., 2015). Their more coastal distribution may make them more vulnerable to oil spills. The Peruvian population is affected by incidental catches in fisheries, and more recently, some direct hunting (Van Waerebeek et al., 1997, 1999). The meat from these catches is sold at local fish markets for both human consumption and to bait fishing lines and nets. None of these issues appear to be threatening the species at present.

### *Delphinus delphis* Linnaeus, 1758

#### Synonymy

- Delphinus delphis* Linnaeus, 1758: 77. Original description.
- Delphinus vulgaris* Lacepede, 1804: 250. Junior synonym.
- Delphinus capensis* Gray, 1828:2. Junior synonym.
- Delphinus longirostris* G. Cuvier, 1829:288. Junior synonym.
- Delphinus novae-zelandiae* Quoy & Gaimard, 1830:149. Junior synonym.
- Delphinus loriger* Wiegmann, 1840:Pl. 362 (no text). Junior synonym.
- Delphinus zelandae* Gray, 1843. Junior synonym.
- Delphinus janira* Gray, 1846:41. Junior synonym.
- Delphinus forsteri* Gray, 1846:42. Junior synonym.
- Delphinus albimanus* Peale, 1849:33. Junior synonym.
- Delphinus fulvifasciatus* Jacquinot & Pucheran, 1853:37. Junior synonym.
- Delphinus frithii* Blyth, 1859. Junior synonym.
- Delphinus algeriensis* Loche, 1860:474. Junior synonym.
- Delphinus microps* Burmeister, 1866:101. Junior synonym.
- Delphinus major* Gray 1866:396. Junior synonym.
- Delphinus moorei* Gray 1866:396. Junior synonym.
- Delphinus walkeri* Gray 1866:397. Junior synonym.
- Delphinus pomeepra* Owen, 1866:23. Junior synonym.
- Eu[delphinus] tasmaniensis* Van Beneden & Gervais, 1880:604. Junior synonym.
- Delphinus dussumieri* Blanford, 1891:588. Junior synonym.
- Delphinus tropicalis* van Bree, 1971:345. Junior synonym.

#### Holotype and Type Locality

Linnaeus described *D. delphis* in his 10th edition of *Systema Naturae*, the starting point of our current taxonomic system for zoology (Linnaeus, 1758). Linnaeus based the type description on the information from “*Oceano Europaeo*” (probably in turn based mostly on observations of Mediterranean dolphins by Artedi, 1738). The species was described briefly, with no details or illustration provided and no type specimen was designated or collected.

#### Diagnosis

The following diagnosis applies only to short-beaked common dolphins in the eastern Pacific. *Delphinus delphis* can be distinguished from the parapatric *D. bairdii* by the following external characters: shorter beak, shorter body length, more robust body, and relatively larger flippers and dorsal fin (Heyning & Perrin, 1994). Beak length reaches up to about 140 mm (Heyning & Perrin, 1994). Body length of adults ranges from 164 to 237 cm (Heyning & Perrin, 1994; Leander et al., 2021; this study). Eastern Pacific *D. delphis* has a shorter and relatively wider skull. Condylbasal length of adults ranges from 386 to 447 mm (Heyning & Perrin, 1994; this study). Rostral length/zygomatic width ratios have been reported to range from 1.23–1.49 (Amaha, 1994; Heyning & Perrin, 1994), but we found that eastern Pacific specimens with ratios less than 1.476 can be considered to be *D. delphis* (this study). Tooth counts are in the range of 42–57 per tooth row (this study). The color pattern is more bold with light and dark areas more

contrasted overall, and a lighter thoracic patch, usually yellowish to ochre in color. There is no stripe from the gape to the anus (or if there is, its anterior portion is exceedingly faint). The flipper stripe is narrow and this creates a facial appearance in which the eye patch, lip patch, and flipper stripes appear distinct, and contrast boldly with the rest of the light-colored face. The white of the ventral field extends to above the level of the flipper stripe. Light patches are relatively common on the dorsal fin and flippers (Heyning & Perrin, 1994; this study). Since there were shared control region and cytochrome *b* haplotypes between *D. bairdii* and *D. delphis* in this study, there were no fixed differences or fully diagnostic mtDNA sites. However, the Random Forest model based on the concatenated control region and cytochrome *b* sequences in this study can correctly classify over 99% of the *D. delphis* specimens (114 out of 115). Fifteen sites were identified as being important to this classification, two of which were nearly fixed.

### Geographic Variation

There is extensive geographic variation in this species, with populations in different areas often varying in overall size, length of beak, body proportions, skull morphology, tooth counts, and coloration (see Amaha, 1994; Jefferson & Van Waerebeek, 2002). In particular, many coastal forms exist, which often have longer beaks and more muted or “muddy” color patterns (see Perrin, 1984). Unfortunately, the extents and limits of such variation are usually not well understood, and proper comparisons including both morphometric and molecular information are generally not available. One exception is the South African long-beaked population (previously recognized as part of the nominal species, *D. capensis*), which is relatively large, with a long rostrum, and bold (highly contrasting) color pattern, but the exact taxonomic status of this well-marked form is not fully resolved at this point. Long-beaked, coastal forms, which were previously thought to be closely related, are now generally thought to be separately derived from short-beaked, offshore ancestors (Cunha et al., 2015; Natoli et al., 2006). It thus appears that the long-beaked condition has arisen multiple times in the species’ evolutionary history, and thus its use as a taxonomic character is limited (Committee on Taxonomy, 2022). Since the eastern Pacific long-beaked common dolphin (*D. bairdii*, as redescribed above) does not occupy an early diverging position in the tree of Cunha et al., (2015), the implication from the best available evidence is that *D. delphis* (as redescribed here) is a paraphyletic species. The nominal species, *D. capensis*, which had been recognized since 1994 (see Heyning & Perrin, 1994), is no longer considered as valid (Committee on Taxonomy, 2022). Another exception is in the eastern Pacific, where based on differences in morphology, distribution, and reproductive timing, four to five management stocks have been identified (Dizon et al., 1994; Perrin et al., 1985; Perryman & Lynn, 1993). These include the Baja neritic form (which corresponds to *D. bairdii*, as redescribed above), Northern, Central, and Southern forms, and a possible Guerrero stock (Perrin et al., 1985). Recent molecular studies have also shown evidence of population divergence in the North Atlantic Ocean (Murphy et al., 2006; Westgate, 2007) and off Australia and New Zealand in the western South Pacific (Möller et al., 2011; Stockin et al., 2014), although these have not indicated any species or even subspecies-level differences, as of yet.

Perrin and Brownell (1994) suggested that eventually dozens of stocks of common dolphins may be recognized. We concur with this speculation, and further suggest that several species and subspecies will become apparent with future taxonomic work on the genus *Delphinus*. Currently only four subspecies of common dolphins are listed by the SMM Taxonomy Committee (Committee on Taxonomy, 2022):

1. The nominate subspecies, *D. delphis delphis* Linnaeus, 1758, which is widely distributed in the Atlantic and Pacific oceans.
2. The Black Sea common dolphin, *D. delphis ponticus* Barabash, 1935, a dwarf form only found in the Black Sea. See Birkun (2008), Notobartolo and Birkun (2010) for more information.
3. The Indo-Pacific common dolphin, *D. delphis tropicalis* van Bree, 1971, an exceedingly long-beaked subspecies found in tropical and subtropical waters of the Indian and western Pacific oceans. See Jefferson and Van Waerebeek (2002) for more information.
4. The “eastern North Pacific common dolphin,” *D. delphis bairdii* Dall, 1873, a long-beaked form, which is here redescribed as a distinct species above.

## Distribution and Habitat

This panglobally distributed species of common dolphin has a very wide range, found in the North and South Pacific, North and South Atlantic, and Indian oceans (Evans, 1994; Perrin, 2017). The exact limits of the range are not well documented in many areas, but these animals are known to extend across entire ocean basins (e.g., the temperate North Pacific and North Atlantic), and occur in many enclosed or semi-enclosed bodies of water (e.g., the southern Gulf of California, Caribbean Sea, Mediterranean Sea, Black Sea, Persian Gulf, Red Sea, Gulf of Thailand, Sea of Japan, and Sea of Okhotsk (see Jefferson & Van Waerebeek, 2002; Perrin, 2017). Despite earlier indications to the contrary, common dolphins do not appear to be found anywhere in the Gulf of Mexico (see Jefferson et al., 2009).

The panglobal common dolphin occurs in both coastal and oceanic waters well beyond the continental shelf edge. In most areas, they favor deeper, offshore waters, but there are coastal populations in a number of areas (e.g., off Venezuela in the Caribbean, Brazil, West Africa, South Africa, throughout the northern rim of the Indian Ocean, and off China, Japan, and Korea; see Perrin, 2017). Common dolphins range from the tropics to cold temperate waters, being most common and most abundant in cool temperate waters, influenced by nutrient-rich upwelling (Jefferson et al., 2009; Perrin, 2017). Oceanographic features differ greatly throughout the range of the genus, and these (along with related differences in prey occurrence and behavior) help to shape *Delphinus* population genetic structure (Amaral et al., 2012).

## Etymology

The species name, *delphis*, is a tautological reference to the Latin name for the dolphin well-known to the ancient Greeks and Romans (i.e., *delphinus*, which is also used as the genus name). We suggest the common name “panglobal common dolphin” to be used for *D. delphis*, due to the fact that this species is found in the Atlantic, Pacific, and Indian oceans, and may be distributed nearly-continuously across each major ocean basin (at least in the Northern Hemisphere).

## Conservation Status

The panglobal common dolphin is probably the most abundant cetacean species on the planet, and the overall species is listed as Least Concern on the IUCN Red List (Braulik et al., 2021b), indicating that it is in no danger of extinction. Abundance has been estimated for many major portions of the species range in the Northern Hemisphere, but only for a few places in the Southern Hemisphere. In the Pacific Ocean, there are an estimated 1,428,000 off Japan and in the temperate central Pacific Ocean (Kanaji et al., 2017); 1,056,308 (CV = 0.207) off the US west coast (Carretta et al., 2023); and 2,963,000 in the ETP (Gerrodette & Forcada, 2002). In the Atlantic Ocean, 172,900 (CV=0.21) are estimated for the western Atlantic Ocean (Hayes et al., 2022); 467,000 for European waters (Hammond et al.<sup>4</sup>); more than 19,400 for the Mediterranean Sea (Cañadas, 2006); and several tens of thousands for the Black Sea (Birkun, 2008). In the southern part of the Indo-Pacific Ocean, there are an estimated 20,000–22,000 common dolphins in a small portion of southern Australia (Bilgmann et al., 2018), and 15,000–20,000 off southern Africa (Cockcroft & Peddemors, 1990). We could find no estimates for the northern Indian Ocean. Taken together, these estimates suggest that well over six million panglobal common dolphins inhabit the world's oceans.

Most populations of common dolphins do not appear to be in serious danger, but populations in the Mediterranean and Black seas have both declined, largely due to human activities. The Mediterranean population was once quite abundant, but experienced a large reduction in the mid-1900s (Bearzi et al., 2003). The decline is thought to have been caused by some hunting that occurred through the 1970s, but also influenced by effects of fishing activities (prey reduction and incidental catches). The Mediterranean population was classified as Endangered on the IUCN Red List (Bearzi et al., 2003). The Black Sea population also underwent a major reduction in the 20th century, but the cause in this case is well understood. Very large numbers of three species of small cetaceans (including

<sup>4</sup>Hammond, P. S., Lacey, C., Gilles, A., Viquerat, S., Börjesson, P., Herr, H., Macleod, K., Ridoux, V., Santos, M. B., Scheidat, M., Teilmann, J., Vingada, J., & Øien, N. (2017). *Estimates of cetacean abundance in European Atlantic waters in summer 2016 from the SCANS-III aerial and shipboard surveys*. Unpublished contract report to Miljø- og Fødevarerministeriet, Denmark; Agence des Aires Marines Protégées, France; Bundesamt für Naturschutz, Germany; Rijkswaterstaat, Netherlands; Havforskningsinstituttet, Norway; Sociedade Portuguesa de Vida Selvagem, Portugal; Instituto Español de Oceanografía, Spain; Havs- och vattenmyndigheten, Sweden; Department for Environment, Food and Rural Affairs, UK.

common dolphins) have been hunted in the Black Sea small cetacean fishery. With a reduction in numbers of up to 70%, the Black Sea common dolphin population has not recovered in recent years, despite restrictions on hunting (Birkun, 2008).

Primary threats to the species include incidental catches in fisheries, direct hunting, prey depletion, toxic contamination, and climate/habitat change (Braulik et al., 2021b). Direct hunting was significant in some areas in the past (primarily the Black Sea, where a large fishery took place in Turkish, Romanian, and Bulgarian waters; Birkun, 2008), but hunting pressure is now much reduced and is likely not a major threat at present. The primary threat to most populations these days is incidental catch in fisheries. The largest catches occur in purse seines (e.g., in the ETP, Braulik et al., 2021b; eastern tropical Atlantic, Simmons, 1968; and Indian Ocean, Braulik et al., 2021b), drift gill nets (e.g., off the US west coast, Carretta et al., 2023), and trawls (e.g., off the US east coast, Hayes et al., 2022; Europe, Northridge, 1991). Prey depletion is thought to be a significant factor in the Black Sea and Mediterranean (Bearzi et al., 2003, 2006). Contamination from toxic substances and climate/habitat change impacts are likely influential in many different areas, but have been identified as particularly problematic only for populations in the Mediterranean Sea (Bearzi et al., 2003, 2006). Other threats (such as vessel collisions, anthropogenic noise impacts, disturbance from dolphin watching, etc.), while certainly having effects on individuals, are probably not severe enough at present to cause significant population declines for most regions of the range.

## 7 | CONCLUSIONS

Although short- and long-beaked forms of common dolphins have been recognized in the Pacific Ocean (and elsewhere) for more than a century, their exact taxonomic status and nomenclature have been evasive and controversial. Much progress has been made in our understanding in the past several decades, but the close relationship of these two forms off western North and South America, as well as sampling limitations, have continued to hinder our understanding. This study both reviews relevant work to date on the issue and provides important new analyses of skeletal morphometrics and molecular genetic characters, which shed new light on the relationship between the two geographic forms in the eastern Pacific Ocean. The two forms occur in partial sympatry yet appear to typically maintain separate schools (excepting the occasional case), which provides another piece of evidence for their being on separate evolutionary tracks and avoiding interbreeding. The results provide convincing evidence that within the eastern Pacific (both north and south of the equator), short- and long-beaked forms are on distinct evolutionary pathways and have evolved to an extent deserving of distinct species status, *D. delphis* and *D. bairdii*, respectively. Although relatively closely related, gene flow between them appears to be extremely rare (despite their partial sympatry), and diagnostic differences are evident. Further, our analyses suggest, for the first time, that long-beaked common dolphins off Peru (and Chile) may be deserving of subspecific status within *D. bairdii*. Additional work is needed to confirm this and to clarify nomenclature.

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## ORCID

Thomas A. Jefferson  <https://orcid.org/0000-0001-6817-2747>

Frederick I. Archer  <https://orcid.org/0000-0002-3179-4769>

## REFERENCES

- Amaha, A. (1994). Geographic variation of the common dolphin, *Delphinus delphis* (Odontoceti: Delphinidae) [Doctoral dissertation]. Tokyo University of Fisheries.
- Amaral, A. R., Beheregaray, L. B., Bilgmann, K., Freitas, L., Robertson, K. M., Sequeira, M., Stockin, K. A., Coelho, M. M. & Moller, L. M. (2012). Influences of past climatic changes on historical population structure and demography of a cosmopolitan marine predator, the common dolphin (genus *Delphinus*). *Molecular Ecology*, 21(19), 4854–4871. <https://doi.org/10.1111/j.1365-294X.2012.05728.x>
- Archer, F. (2022a). *rfPermute: Estimate permutation p-values for Random Forest importance metrics* (R package version 2.5.1) [Computer software]. <https://github.com/EricArcher/rfPermute>
- Archer, F. (2022b). *sprex: Species richness and extrapolation* (R package version 1.4.2) [Computer software]. <https://github.com/EricArcher/sprex>
- Archer, F. I., Martien, K. K., & Taylor, B. L. (2017a). Diagnosability of mtDNA with Random Forests: Using sequence data to delimit subspecies. *Marine Mammal Science*, 33(51), 101–131. <https://doi.org/10.1111/mms.12414>
- Archer, F. I., Adams, P. E., & Schneiders, B. B. (2017b). STRATAG: An R package for manipulating, summarizing and analysing population genetic data. *Molecular Ecology Resources*, 17, 5–11. <https://doi.org/10.1111/1755-0998.12559>
- Artedi, P. (1738). *Ichthyologia: Sive, Opera Omnia de Piscibus, Scilicet: Bibliotheca Ichthyologica. Philosophiaichthyologica. Genera Piscium. Synonymia Specierum. Descriptiones Specierum. Omnia in hoc Genereperfectiora, Quam Antea Ulla. Lugduni Batavorum: Apud Conradum Wishoff.*
- Banks, R. C. & Brownell, R. L. (1969). Taxonomy of the common dolphins of the eastern Pacific Ocean. *Journal of Mammalogy*, 50(2), 262–271. <https://doi.org/10.2307/1378342>
- Bearzi, G., Reeves, R. R., Notarbartolo Di Sciara, G., Politi, E., Canadas, A., Frantzis, A., & Mussi, B. (2003). Ecology, status and conservation of short-beaked common dolphins *Delphinus delphis* in the Mediterranean Sea. *Mammal Review*, 33(3–4), 224–252. <https://doi.org/10.1046/j.1365-2907.2003.00032.x>
- Bearzi, G., Politi, E., Agazzi, S., & Azzellino, A. (2006). Prey depletion caused by overfishing and the decline of marine megafauna in eastern Ionian Sea coastal waters (central Mediterranean). *Biological Conservation*, 127(4), 373–382. <https://doi.org/10.1016/j.biocon.2005.08.017>
- Becker, E. A., Forney, K. A., Miller, D. L., Fiedler, P. C., Barlow, J., & Moore, J. E. (2020). *Habitat-based density estimates for cetaceans in the California Current Ecosystem based on 1991–2018 survey data* (NOAA Technical Memorandum NMFS-SWFSC-638). U.S. Department of Commerce.
- Bernal, R., Olavarria, C., & Moraga, R. (2003). Occurrence and long-term residency of two long-beaked common dolphins, *Delphinus capensis* (Gray 1828), in adjacent small bays on the Chilean central coast. *Aquatic Mammals*, 29(3), 396–399.
- Bilgmann, K., Parra, G. J., & Möller, L. M. (2018). Occurrence, distribution and abundance of cetaceans off the western Eyre Peninsula in the Great Australian Bight. *Deep Sea Research Part II: Topical Studies in Oceanography*, 157–158, 134–145. <https://doi.org/10.1016/j.dsr2.2017.11.006>
- Birkun, A. A., Jr. (2008). *Delphinus delphis* ssp. *ponticus*. *The IUCN Red List of Threatened Species* 2008: e.T133729A3875256. <https://doi.org/10.2305/IUCN.UK.2008.RLTS.T133729A3875256.en>
- Braulik, G. T., Archer, F. I., Khan, U., Imran, M., Sinha, R. K., Jefferson, T. A., Donovan, C., & Graves, J. A. (2021a). Taxonomic revision of the South Asian River dolphins (*Platanista*): Indus and Ganges River dolphins are separate species. *Marine Mammal Science*, 37(3), 1022–1059. <https://doi.org/10.1111/mms.12801>
- Braulik, G. T., Barnett, R. V., Islas-Villanueva, V., Hoelzel, A. R., & Graves, J. A. (2015). One species or two? Vicariance, lineage divergence and low mtDNA diversity in geographically isolated populations of South Asian river dolphin. *Journal of Mammalian Evolution*, 22(1), 111–120. <https://doi.org/10.1007/s10914-014-9265-6>
- Braulik, G., Jefferson, T. A., & Bearzi, G. (2021b). *Delphinus delphis* (amended version of 2021 assessment). *The IUCN Red List of Threatened Species* 2021, e.T134817215A199893039. <https://doi.org/10.2305/IUCN.UK.2021-2.RLTS.T134817215A199893039.en>
- Breese, D., & Tershy, B. R. (1993). Relative abundance of Cetacea in the Canal de Ballenas, Gulf of California. *Marine Mammal Science*, 9(3), 319–324. <https://doi.org/10.1111/j.1748-7692.1993.tb00460.x>
- Breiman, L. (2001). Random forests. *Machine Learning*, 45, 5–32.



- Cañadas, A. (2006). *Towards conservation of dolphins in the Alboran Sea* [Doctoral dissertation]. Universidad Autonoma de Madrid.
- Carretta, J. V., Chivers, S. J., & Perryman, W. L. (2011). Abundance of the long-beaked common dolphin (*Delphinus capensis*) in California and western Baja California waters estimated from a 2009 ship-based line-transect survey. *Bulletin Southern California Academy of Sciences*, 110(3), 152–164. <https://doi.org/10.3160/0038-3872-110.3.152>
- Carretta, J. V., Oleson, E. M., Forney, K. A., Weller, D. W., Lang, A. R., Baker, J., Orr, A. J., Hanson, B., Barlow, J., Moore, J. E., Wallen, M., & Brownell, R. L., Jr. (2023). *U.S. Pacific marine mammal stock assessments: 2022* (NOAA Technical Memorandum NMFS-SWFSC 684). U.S. Department of Commerce.
- Chivers, S. J., Baird, R. W., McSweeney, D. J., Webster, D. L., Hedrick, N. M., & Salinas, J. C. (2007). Genetic variation and evidence for population structure in eastern North Pacific false killer whales (*Pseudorca crassidens*). *Canadian Journal of Zoology*, 85(7), 783–794. <https://doi.org/10.1139/Z07-059>
- Chivers, S. J., Perryman, W. L., Lynn, M. S., Gerrodette, T., Archer, F. I., Danil, K., Berman-Kowalewski, M., & Dines, J. P. (2016). Comparison of reproductive parameters for populations of eastern North Pacific common dolphins: *Delphinus capensis* and *D. delphis*. *Marine Mammal Science*, 32(1), 57–85. <https://doi.org/10.1111/mms.12244>
- Cockcroft, V. G., & Peddemors, V. M. (1990). Seasonal distribution and density of common dolphins *Delphinus delphis* of the south-east coast of southern Africa. *South African Journal of Marine Science*, 9, 371–377.
- Committee on Taxonomy. (2023). *List of marine mammal species and subspecies*. Society for Marine Mammalogy.
- Costa, A. P. B., Mcfee, W., Wilcox, L. A., Archer, F. I., & Rosel, P. E. (2022). The common bottlenose dolphin (*Tursiops truncatus*) ecotypes of the western North Atlantic revisited: an integrative taxonomic investigation supports the presence of distinct species. *Zoological Journal of the Linnaean Society*, 196, 1608–1636. <https://doi.org/10.1093/zoolinnean/zlac025>
- Cunha, H. A., De Castro, R. L., Secchi, E. R., Crespo, E. A., Lailson-Brito, J., Azevedo, A. F., Lazoski, C., & Sole-Cava, A. M. (2015). Molecular and morphological differentiation of common dolphins (*Delphinus* sp.) in the Southwestern Atlantic: Testing the two species hypothesis in sympatry. *PLoS ONE*, 10(11), e0140251. <https://doi.org/10.1371/journal.pone.0140251>
- Dall, W. H. (1873). Descriptions of three new species of Cetacea, from the coast of California. *Proceedings of the California Academy of Sciences*, 5, 12–14.
- Dall, W. H. (1874). Catalogue of the Cetacea of the North Pacific Ocean, with osteological notes, and descriptions of some new forms. In C. M. Scammon (Ed.), *The marine mammals of the northwestern coast of North America together with an account of the American whale-fishery* (pp. 281–308). Manessier Publishing Co.
- Danil, K., Chivers, S. J., Henshaw, M. D., Thieleking, J. L., Daniels, R., & St. Leger, J. A. (2010). Cetacean strandings in San Diego County, California, USA: 1851–2008. *Journal of Cetacean Research and Management*, 11(2), 163–184. <https://doi.org/10.47536/jcrm.v11i2.622>
- Danil, K., & St. Leger, J. A. (2011). Seabird and dolphin mortality associated with underwater detonation exercises. *Marine Technology Society Journal*, 45(6), 89–95. <https://doi.org/10.4031/MTSJ.45.6.5>
- Denwood, M. J. (2016). runjags: An R package providing interface utilities, model templates, parallel computing methods and additional distributions for MCMC models in JAGS. *Journal of Statistical Software*, 71(9), 1–25. <https://doi.org/10.18637/jss.v071.i09>
- Dizon, A. E., Perrin, W. F., & Akin, P. A. (1994). *Stocks of dolphins (Stenella spp. and Delphinus delphis) in the eastern tropical Pacific: a phylogeographic classification* (NOAA Technical Report NMFS 119). U. S. Department of Commerce.
- Esteves, M. A., & Oviedo, L. E. (2007). A potential morphotype of common dolphin (*Delphinus* spp.) on the northeast coast of Venezuela. *Aquatic Mammals*, 33(2), 229–234. <https://doi.org/10.1578/AM.33.2.2007.229>
- Evans, W. E. (1975). *Distribution, differentiation of populations, and other aspects of the natural history of Delphinus delphis Linnaeus in the northeastern Pacific* [Doctoral dissertation]. University of California, Los Angeles.
- Evans, W. E. (1982). Distribution and differentiation of stocks of *Delphinus delphis* Linnaeus in the northeastern Pacific. In *Mammals in the seas: Small cetaceans, seals, sirenians, and otters* (Vol. 4, pp. 45–66). FAO Fisheries Series, Rome, Italy.
- Evans, W. E. (1994). Common dolphin, white-bellied porpoise *Delphinus delphis* Linnaeus, 1758. In S. H. Ridgway & R. Harrison (Eds.), *Handbook of marine mammals, Volume 5: The first book of dolphins* (pp. 191–224). Academic Press.
- Flower, W. H. (1884). On the characters and divisions of the family Delphinidae. *Proceedings of the Zoological Society of London*, 32, 466–513.
- Ford, J. K. B. (2005). First records of long-beaked common dolphins, *Delphinus capensis*, in Canadian waters. *Canadian Field-Naturalist*, 119(1), 110–113. <https://doi.org/10.22621/cfn.v119i1.88>
- Ford, J. K. B. (2014). *Marine mammals of British Columbia*. Royal British Columbia Museum, Victoria, British Columbia, Canada.
- Gallo-Reynoso, J. P. (1990). The Gulf of California common dolphin. *Whalewatcher*, 24, 7–8.
- Gallo-Reynoso, J. P., Francisco, E. O., & Ortiz, C. L. (2014). Age estimation on long-beaked common dolphins, *Delphinus capensis*, from the Gulf of California. *Therya*, 5(2), 449–460. <https://doi.org/10.12933/therya-14-198>

- Gallo-Reynoso, J. P., Malek, T. B., Garcia-Hernandez, J., Moreno, L. V., & Segura-Garcia, I. (2015). Concentrations of DDE in blubber biopsies of free-ranging long-beaked common dolphin (*Delphinus capensis*) in the Gulf of California. *Bulletin of Environmental Contamination and Toxicology*, 94(1), 6–111. <https://doi.org/10.1007/s00128-014-1414-3>
- Gerrodette, T., & Forcada, J. (2002). *Estimates of abundance of western/southern spotted, whitebelly spinner and common dolphins, and pilot, sperm and Bryde's whales in the eastern tropical Pacific* (Administrative Report LJ-02-20). Southwest Fisheries Science Center.
- Gerrodette, T., & Palacios, D. M. (1996). *Estimates of cetacean abundance in EEZ waters of the eastern tropical Pacific*. (Administrative Report LJ-96-10). Southwest Fisheries Science Center.
- Gray, J. E. (1828). *Spicilegium Zoologica; or original figures and short systematic descriptions of new and unfigured animals*. Treuttel, Wurtz and Co.
- Guiget, C. J. (1954). A record of Baird's dolphin (*Delphinus bairdii* Dall) in British Columbia. *Canadian Field-Naturalist*, 68, 136.
- Hamilton, T. A., Redfern, J. V., Barlow, J., Ballance, L. T., Gerrodette, T., Holt, R. S., Forney, K. A., & Taylor, B. L. (2009). *Atlas of cetacean sightings for Southwest Fisheries Science Center Cetacean and Ecosystem surveys, 1986–2005* (NOAA Technical Memorandum NMFS-SWFSC 440). U.S. Department of Commerce.
- Hayes, S. H., Josephson, E., Maze-Foley, K., Rosel, P. E., & Wallace, J. (2022). *U.S. Atlantic and Gulf of Mexico marine mammal stock assessments 2021* (NOAA Technical Memorandum NMFS-NE 288). U.S. Department of Commerce.
- Hershkovitz, P. (1966). Catalog of living whales. *Bulletin of the United States National Museum*, 246.
- Heyning, J. E., & Perrin, W. F. (1994). Evidence for two species of common dolphins (genus *Delphinus*) from the eastern North Pacific. *Natural History Museum of Los Angeles County, Contributions in Science*, 442.
- Jefferson, T. A., & Van Waerebeek, K. (2002). The taxonomic status of the nominal dolphin species *Delphinus tropicalis* van Bree, 1971. *Marine Mammal Science*, 18(4), 787–818. <https://doi.org/10.1111/j.1748-7692.2002.tb01074.x>
- Jefferson, T. A., & Wang, J. Y. (2011). Revision of the taxonomy of finless porpoises (genus *Neophocaena*): The existence of two species. *Journal of Marine Animals and Their Ecology*, 4, 3–16.
- Jefferson, T. A., Fertl, D., Bolanos Jimenez, J., & Zerbini, A. N. (2009). Distribution of common dolphins (*Delphinus* spp.) in the western Atlantic Ocean: A critical re-examination. *Marine Biology*, 156(6), 1109–1124. <https://doi.org/10.1007/s00227-009-1152-y>
- Jordan, F., Murphy, S., Martinez, E., Amiot, C., van Helden, A., & Stockin, K. A. (2015). Criteria for assessing maturity of skulls in the common dolphin, *Delphinus* sp., from New Zealand waters. *Marine Mammal Science*, 31(3), 1077–1097. <https://doi.org/10.1111/mms.12229>
- Jost, L. (2007). Partitioning diversity into independent alpha and beta components. *Ecology*, 88(10), 2427–22439. <https://doi.org/10.1890/06-1736.1>
- Kanaji, Y., Yoshida, H., & Okazaki, M. (2017). Spatiotemporal variations in habitat utilization patterns of four Delphinidae species in the western North Pacific, inferred from carbon and nitrogen stable isotope ratios. *Marine Biology*, 164(4), Article 65.
- Katoh, K., Misawa, K., Kuma, K.-I., & Miyata, T. (2002). MAFFT: a novel method for rapid multiple sequence alignment based on fast Fourier transform. *Nucleic Acids Research*, 30(14), 3059–3066. <https://doi.org/10.1093/nar/gkf436>
- Kellar, N. M., Trego, M. L., Chivers, S. J., Archer, F. I., & Perryman, W. L. (2014). From progesterone in biopsies to estimates of pregnancy rates: Large scale reproductive patterns of two sympatric species of common dolphin, *Delphinus* spp. off California, USA and Baja, Mexico. *Bulletin of the Southern California Academy of Sciences*, 113(2), 58–80. <https://doi.org/10.3160/0038-3872-113.2.58>
- Kingston, S. E., & Rosel, P. E. (2004). Genetic differentiation among recently diverged delphinid taxa determined using AFLP markers. *Journal of Heredity*, 95(1), 1–10. <https://doi.org/10.1093/jhered/esh010>
- Leander, S. G. M., Durban, J. W., Danil, K., Fearnbach, H., Joyce, T. W., & Ballance, L. T. (2021). 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. *Marine Mammal Science*, 37(4), 1507–1513. <https://doi.org/10.1111/mms.12804>
- LeDuc, R. G., Perrin, W. F., & Dizon, A. E. (1999). Phylogenetic relationships among the Delphinid cetaceans based on full cytochrome *b* sequences. *Marine Mammal Science*, 15(3), 619–648. <https://doi.org/10.1111/j.1748-7692.1999.tb00833.x>
- Liaw, A., & Wiener, M. (2002). Classification and regression by randomForest. *R News*, 2(3), 18–22.
- Linnaeus, C. (1758). *Systema Naturae Per Regna Tria Naturae, Secundum Classes, Ordines, Genera, Species, cum Characteribus, Differentiis, Synonymis, Locis, Tomus I. Holmiae*, Impensis Direct, Laurtenii Salvii.
- Llapapasca, M. A., Pacheco, A. S., Fiedler, P., Goya, E., Ledesma, J., & Peña, C., & Vásquez, L. (2018). Modeling the potential habitats of dusky, commons and bottlenose dolphins in the Humboldt Current System off Peru: The influence of non-El Niño vs. El Niño 1997–98 conditions and potential prey availability. *Progress in Oceanography*, 168(5), 169–181. <https://doi.org/10.1016/j.pocean.2018.09.003>

- Louis, M., Galimberti, M., Archer, F., Berrow, S., Brownlow, A., Fallon, R., Nykänen, M., O'Brien, J., Robertson, K. M., Rosel, P. E., Simon-Bouhet, B., Wegmann, D., Fontaine, M. C., Foote, A. D., & Gaggiotti, O. E. (2021). Selection on ancestral genetic variation fuels repeated ecotype formation in bottlenose dolphins. *Science Advances*, 7(44), eabg1245. <https://doi.org/10.1126/sciadv.abg1245>
- McGowen, M. R., Spaulding, M., & Gates, J. (2009). Divergence date estimation and comprehensive molecular tree of extant cetaceans. *Molecular Phylogenetics and Evolution*, 53(3), 891–906. <https://doi.org/10.1016/j.ympev.2009.08.018>
- McGowen, M. R., Tsagkogeorga, G., Álvarez-Carretero, S., Dos Reis, M., Struebig, M., Deaville, R., Jepson, P. D., Jarman, S., Polanowski, A., Morin, P. A., & Rossiter, S. J. (2020). Phylogenomic resolution of the cetacean tree of life using target sequence capture. *Systematic Biology*, 69(3), 479–501. <https://doi.org/10.1093/sysbio/syz068>
- Miller, G. S. (1936). The status of *Delphinus bairdii* Dall. *Proceedings of the Biological Society of Washington*, 49, 145–146.
- Miller, S. A., Dykes, D. D., & Polesky, H. F. (1988). A simple salting out procedure for extracting DNA from human nucleated cells. *Nucleic Acids Research*, 16(3), Article 1215. <https://doi.org/10.1093/nar/16.3.1215>
- Möller, L. M., Pedone, F., Simen, V., Allen, S., Bilgmann, K., Corrigan, S., & Beheregaray, L. B. (2011). Fine-scale genetic structure in short-beaked common dolphins (*Delphinus delphis*) along the East Australian Current. *Marine Biology*, 158(1), 113–126. <https://doi.org/10.1007/s00227-010-1546-x>
- Murphy, S., Herman, J. S., Pierce, G. J., Rogan, E., & Kitchener, A. C. (2006). Taxonomic status and geographical cranial variation of common dolphins (*Delphinus*) in the eastern North Atlantic. *Marine Mammal Science*, 22(3), 573–599. <https://doi.org/10.1111/j.1748-7692.2006.00037.x>
- Natoli, A., Canadas, A., Peddemors, V. M., Aguilar, A., Vaquero, C., Fernandez-Piqueras, P., & Hoelzel, A. R. (2006). Phylogeography and alpha taxonomy of the common dolphin (*Delphinus* sp.). *Journal of Evolutionary Biology*, 19, 943–954. <https://doi.org/10.1111/j.1420-9101.2005.01033.x>
- Nei, M. (1978). Estimation of average heterozygosity and genetic distance from a small number of individuals. *Genetics*, 89(3), 583–590. <https://doi.org/10.1093/genetics/89.3.583>
- Ngqulana, S. G., Plön, S., Galatius, A., Pistorius, P., & Hofmeyr, G. J. G. (2019). Cranial variation in common dolphins *Delphinus* spp. off South Africa, with the inclusion of information from the holotype of *Delphinus capensis*. *African Journal of Marine Science*, 41(3), 247–260. <https://doi.org/10.2989/1814232x.2019.1648318>
- Nicolosi, P., & Loy, A. (2019). Geometric morphometric methods as complementary tools to investigate variability in common dolphins (*Delphinus* sp.) using museum specimens. *Aquatic Conservation: Marine and Freshwater Ecosystems*, 31(S1), 22–35. <https://doi.org/10.1002/aqc.3042>
- Northridge, S. P. (1991). An updated world review of interactions between marine mammals and fisheries. *FAO Fisheries Technical Paper*, 251 (Suppl. 1).
- Notarbartolo Di Sciarra, G., & Birkun, A., Jr. (2010). *Conserving whales, dolphins and porpoises in the Mediterranean and Black Seas: An ACCOBAMS Status Report*. ACCOBAMS, Monaco.
- Paradis, E., & Schliep, K. (2019). ape 5.0: an environment for modern phylogenetics and evolutionary analyses in R. *Bioinformatics*, 35(3), 526–528. <https://doi.org/10.1093/bioinformatics/bty633>
- Pedersen, T., Hughes, S., Qiu, X. (2022). *densityClust: Clustering by fast search and find of density peaks* (R package version 0.3.2) [Computer software]. <https://CRAN.R-project.org/package=densityClust>
- Perrin, W. F. (1984). Patterns of geographical variation in small cetaceans. *Acta Zoologica Fennica*, 172, 137–140.
- Perrin, W. F. (2017). Common dolphin *Delphinus delphis*. In B. Würsig, J. G. M. Thewissen, & K. M. Kovacs (Eds.), *Encyclopedia of marine mammals* (3rd ed., pp. 205–209). Academic Press.
- Perrin, W. F. & Brownell, R. L., Jr. (1994). A brief review of stock identity in small marine cetaceans in relation to assessment of driftnet mortality in the North Pacific. *Reports of the International Whaling Commission, Special Issue 15*, 393–401.
- Perrin, W. F., Mead, J. G., & Brownell, R. L., Jr. (2009). *Review of the evidence used in the description of currently recognized cetacean subspecies* (NOAA Technical Memorandum NMFS-SWFSC 450). U.S. Department of Commerce.
- Perrin, W. F., & Reilly, S. B. (1984). Reproductive parameters of dolphins and small whales of the family Delphinidae. *Reports of the International Whaling Commission, Special Issue 6*, 97–133.
- Perrin, W. F., Scott, M. D., Walker, G. J., & Cass, V. L. (1985). *Review of geographical stocks of tropical dolphins (Stenella spp. and Delphinus delphis) in the eastern tropical Pacific* (NOAA Technical Report NMFS 28). U.S. Department of Commerce.
- Perrin, W. F., Yablokov, A. V., Barlow, J., & Mina, M. V. (1994). Comparison of the resolving power of metric and non-metric cranial characters in defining geographical populations of dolphins. *Contributions in Science*, 447.
- Perryman, W. L., & Lynn, M. S. (1993). Identification of geographic forms of common dolphin (*Delphinus delphis*) from aerial photography. *Marine Mammal Science*, 9(2), 119–137. <https://doi.org/10.1111/j.1748-7692.1993.tb00438.x>
- Pinela, A. M., Borrell, A. & Aguilar, A. (2011). Common dolphin morphotypes: Niche segregation or taxonomy? *Journal of Zoology*, 284(4), 239–247. <https://doi.org/10.1111/j.1469-7998.2011.00798.x>
- Plummer, M., Best, N., Cowles, K., & Vines, K. (2006). CODA: Convergence diagnosis and output analysis for MCMC. *R News* 6, 7–11.

- Poole, A. J. & Schantz, V. S. (1942). Catalog of the type specimens of mammals in the United States National Museum, including the biological surveys collection. *Bulletin of the United States National Museum*, 178, 1–703.
- Posada, D. (2008). jModelTest: Phylogenetic model averaging. *Molecular Biology and Evolution*, 25(7), 1253–1256. <https://doi.org/10.1093/molbev/msn083>
- R Core Team. (2022). *R: A language and environment for statistical computing* (Version 4.1.2) [Computer software]. R Foundation for Statistical Computing.
- Rodríguez, A., & Laio, A. (2014). Clustering by fast search and find of density peaks. *Science*, 344(6191), 1492–1496. <https://doi.org/10.1126/science.1242072>
- Rosel, P. E., Dizon, A. E., & Heyning, J. E. (1994). Genetic analysis of sympatric morphotypes of common dolphins (genus *Delphinus*). *Marine Biology*, 119(2), 159–167. <https://doi.org/10.1007/BF00349552>
- Salvadeo, C. J., Gomez-Gallardo, U. A., Lluch-Belda, D., & Urbán-R., J. (2009). The odontocete community and its environment in the southwestern Gulf of California. *Latin American Journal of Aquatic Mammals*, 7(1–2), 23–32. <https://doi.org/10.5597/lajam00130>
- Sambrook, J., Fritsch, E. F., & Maniatis, T. (1989). *Molecular cloning: a laboratory manual*. Cold Spring Harbor Laboratory Press.
- Sanino, G. P., Van Waerebeek, K., & Yáñez, J. (2003). Revisión de la distribución del género *Delphinus* y primeros registros documentados de *Delphinus capensis* en Chile [Reviewing of the distribution of the genus *Delphinus* and documented records of *Delphinus capensis* in Chile]. *Boletín del Museo Nacional de Historia Natural*, 52, 97–102. <https://doi.org/10.54830/bmnh.v52.2003.311>
- Scammon, C. M. (1874). *The marine mammals of the northwestern coast of North America together with an account of the American whale-fishery*. John H. Carmany and Co.
- Segura-García, I., Gallo-Reynoso, J. P., Chivers, S. J., Díaz-Gamboa, R., & Hoelzel, A. R. (2016). Post-glacial habitat release and incipient speciation in the genus *Delphinus*. *Heredity*, 117, 400–407. <https://doi.org/10.1038/hdy.2016.66>
- Shuster, L., Anderson, D., Huggins, J. L., Douglas, A. B., Harrison, N., Calambokidis, J., & S. Berta. (2018). *Dolphins in the Salish Sea: Are warmer water species expanding into our region?* Paper presented at Salish Sea Ecosystem Conference. <https://cedar.wvu.edu/ssec/2018ssec/allsessions/590>
- Silber, G. K., Newcomer, M. W., Silber, P. C., Perez-Cortes, M. H., & Ellis, G. M. (1994). Cetaceans of the northern Gulf of California: distribution, occurrence, and relative abundance. *Marine Mammal Science*, 10(3), 283–298. <https://doi.org/10.1111/j.1748-7692.1994.tb00483.x>
- Simmons, D. C. (1968). Purse seining off Africa's west coast. *Commercial Fisheries Review*, 30, 21–22.
- Stockin, K. A., Amaral, A. R., Latimer, J., Lambert, D. M., & Natoli, A. (2014). Population genetic structure and taxonomy of the common dolphin (*Delphinus* sp.) at its southernmost range limit: New Zealand waters. *Marine Mammal Science*, 30(1), 44–63. <https://doi.org/10.1111/mms.12027>
- Taylor, B. L., Archer, F. I., Martin, K. K., Rosel, P. E., Hancock-Hanser, B. L., Lang, A. R., Leslie, M. S., Mesnick, S.L., Morin, P.A., Pease, V.L., Perrin, W.F., Robertson, K. M., Parsons, K. M., Viricel, A., Vollmer, N. L., Cipriano, F., Reeves, R. R., Krützen, M., & Baker, C. S. (2017). Guidelines and quantitative standards to improve consistency in cetacean subspecies and species delimitation relying on molecular genetic data. *Marine Mammal Science*, 33(S1), 132–155. <https://doi.org/10.1111/mms.12411>
- Torres De La Riva, G., Johnson, C. K., Gulland, F. M. D., Langlois, G. W., Heyning, J. E., Rowles, T. K., & Mazet, J. K. (2009). Association of an unusual marine mammal mortality event with *Pseudo-nitzschia* spp. blooms along the southern California coastline. *Journal of Wildlife Diseases*, 45(1), 109–121. <https://doi.org/10.7589/0090-3558-45.1.109>
- True, F. W. (1889). Contributions to the natural history of the cetaceans, a review of the family Delphinidae. *Bulletin of the United States National Museum*, 36, 1–191 + plates.
- Urban, J. R. (2010). Marine mammals of the Gulf of California. In R. C. Brusca (Ed.), *The Gulf of California* (pp. 188–209). Arizona-Sonora Desert Museum.
- van Bree, P. J. H., & Purves, P. E. (1972). Remarks on the validity of *Delphinus bairdii* (Cetacea, Delphinidae). *Journal of Mammalogy*, 53(2), 372–374. <https://doi.org/10.2307/1379178>
- Van Waerebeek, K., Van Bresseem, M. F., Alfaro-Shigueto, J., Sanino, G. P., Montes, D., & Ontón, K. (1999). *A preliminary analysis of recent captures of small cetaceans in Peru and Chile*. Report SC/51/SM17 to the Scientific Committee of the International Whaling Commission.
- Van Waerebeek, K., Van Bresseem, M. F., Félix, F., Alfaro-Shigueto, J., García-Godos, A., Chávez-Lisambart, L., Ontón, K., Montes, D., & Bello R. (1997). Mortality of dolphins and porpoises in coastal fisheries off Peru and southern Ecuador in 1994. *Biological Conservation*, 81(1–2), 43–49. [https://doi.org/10.1016/S0006-3207\(96\)00152-8](https://doi.org/10.1016/S0006-3207(96)00152-8)
- Vidal, O., & Gallo-Reynoso, J. P. (2012). Composition by sex and size of long-beaked common dolphin (*Delphinus capensis*) from a die-off in the Gulf of California, Mexico. *Marine Biodiversity Records*, 5(3), e82. <https://doi.org/10.1017/S1755267212000395>

- Wang, J. Y., Frasier, T. R., Yang, S. C., & White, B. N. (2008). Detecting recent speciation events: The case of the finless porpoise (genus *Neophocaena*). *Heredity*, 101, 145–155. <https://doi.org/10.1038/hdy.2008.40>
- Westgate, A. J. (2005). *Population structure and life history of short-beaked common dolphins (Delphinus delphis) in the North Atlantic* [Doctoral dissertation]. Duke University.
- Westgate, A. J. (2007). Geographic variation in cranial morphology of short-beaked common dolphins (*Delphinus delphis*) from the North Atlantic. *Journal of Mammalogy*, 88(3), 678–688. <https://doi.org/10.1644/06-MAMM-A-177R.1>
- Xiong, Y., Brandley, M. C., Xu, S., Zhou, K., & Yang, G. (2009). Seven new dolphin mitochondrial genomes and a time-calibrated phylogeny of whales. *BMC Evolutionary Biology*, 9, Article 20. <https://doi.org/10.1186/1471-2148-9-20>
- Zhou, X., Guang, X., Sun, D., Xu, S., Li, M., Seim, I., Jie, W., Yang, L., Zhu, Q., Xu, J., Gao, Q., Kaya, A., Dou, Q., Chen, B., Ren, W., Li, S., Zhou, K., Gladyshev, V. N., Nielsen, R., ... Yang, G. (2018). Population genomics of finless porpoises reveal an incipient cetacean species adapted to freshwater. *Nature Communications*, 9, Article 1276. <https://doi.org/10.1038/s41467-018-03722-x>

## SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

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