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Phylogenetic Relationships Among Eastern Pacific Common Dolphins (*Delphinus* spp.)

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Abstract

Common dolphins in the eastern Pacific are currently recognized as separate subspecies, a long-beaked form (*Delphinus delphis bairdii*) and a short-beaked form (*Delphinus delphis delphis*), which are sympatric across portions of their ranges in waters off California. While the taxonomic status of these forms is still unclear, several studies have shown that they represent different evolutionary trajectories. Most of this work has been conducted on common dolphins in the Eastern North Pacific. In this study, the phylogenetic relationship of these two forms was examined, in addition to long-beaked common dolphins occurring off Peru in the Eastern South Pacific, using complete mitochondrial genomes. Peruvian and Californian long-beaked common dolphins formed a monophyletic clade with respect to short-beaked common dolphins from California and common dolphins from Senegal and the Black Sea. This clade of eastern Pacific long-beaked common dolphins was estimated to have zero connectivity with the Californian short-beaked form. Within the long-beaked clade, Peruvian long-beaked common dolphins were monophyletic, although Californian long-beaked dolphins were paraphyletic. These results are consistent with long-beaked common dolphins in the eastern Pacific being a species distinct from short-beaked common dolphins in the same region. Furthermore, evidence showed that Peruvian long-beaked common dolphins may represent a separate subspecies.

Key Words: *Delphinus*, phylogenetics, taxonomy, mitogenomes

Introduction

The common dolphin (*Delphinus delphis*) is one of the most abundant, widespread, and genetically diverse dolphins in the world (Evans, 1994; Heyning & Perrin, 1994; Rosel et al., 1994; Amaral et al., 2007; Perrin, 2018). For years, phylogenetic studies have attempted to elucidate questions regarding the evolution and classification of this species (Rosel et al., 1994; LeDuc et al., 1999; Natoli et al., 2006; Cunha et al., 2015; Perrin, 2018). Most of this work has been focused on understanding relationships among forms that differ largely by length of the rostrum, often referred to as long- and short-beaked common dolphins. Currently, the Society for Marine Mammalogy (SMM) recognizes a single global species of common dolphins, *Delphinus delphis* (Committee on Taxonomy, 2024), composed of four subspecies: (1) *D. d. delphis* Linnaeus, 1758 (the nominate common dolphin, a globally distributed form that includes both long- and short-beaked populations), (2) *D. d. bairdii* Dall, 1873 (the Eastern North Pacific long-beaked common dolphin), (3) *D. d. ponticus* Barabash, 1935 (the Black Sea common dolphin, a short-beaked form), and (4) *D. d. tropicalis* van Bree, 1971 (the Indo-Pacific common dolphin, an exceedingly long-beaked form).

Both long- and short-beaked common dolphins are present in warm-temperate and tropical waters of the Pacific Ocean (Perrin, 2018), where they are often found sympatrically in the eastern Pacific along California, western Baja California, and Peru (Figure 1). In the Eastern North Pacific (ENP), both forms can be found in California and northern Mexico, where long-beaked common

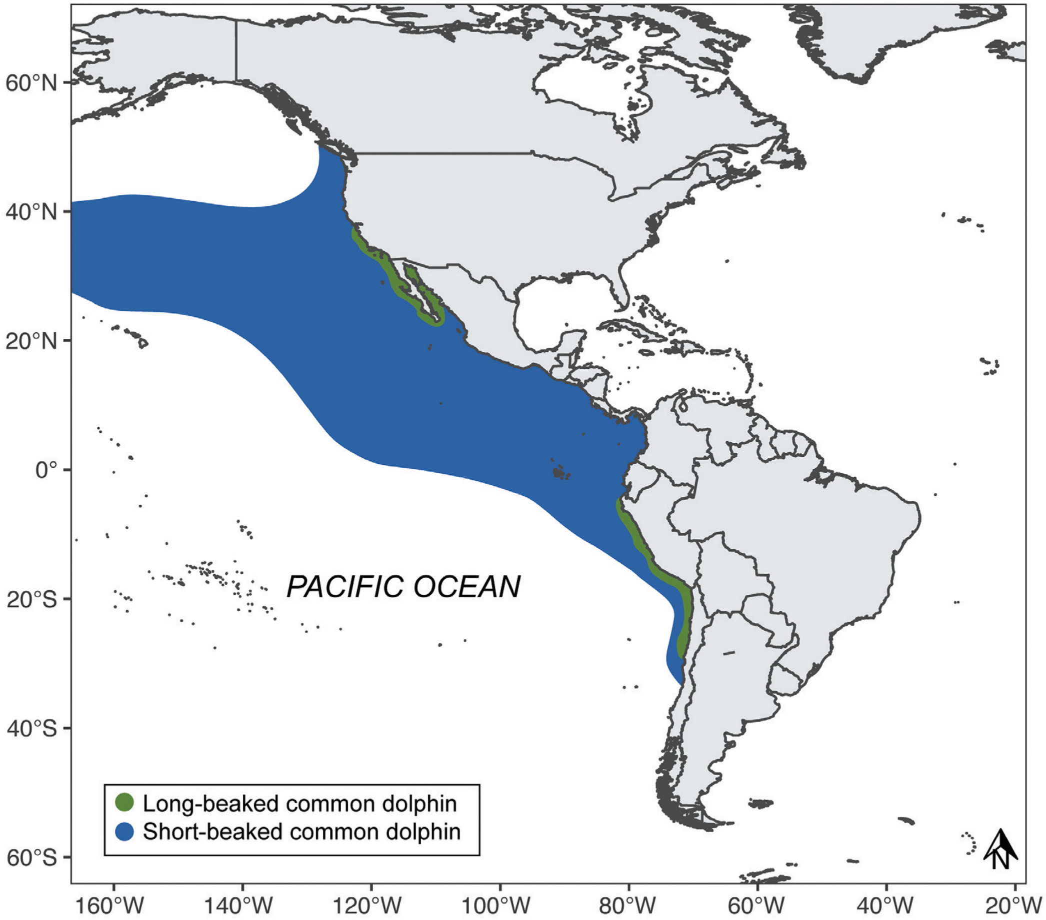


Figure 1. Distribution of long- and short-beaked common dolphins (*Delphinus* spp.) in the eastern Pacific

dolphins (*D. d. bairdii*) are commonly distributed in coastal waters and short-beaked common dolphins (*D. d. delphis*) tend to occur more offshore (Banks & Brownell, 1969; van Bree & Purves, 1972; Heyning & Perrin, 1994; Rosel et al., 1994; Cunha et al., 2015; Perrin, 2018). A similar trend seems to be evident in the Eastern South Pacific (ESP), where both long- and short-beaked and common dolphins are observed along Peru (Llapapasca et al., 2018; Santillán et al., 2023).

Long-beaked common dolphins in the ENP were first described as a distinct species of common dolphin by Dall (1873), referred to as *D. bairdii* (though Dall's reason for considering them a different species had more to do with geography than morphology). The differentiation of this form was based on its rostrum length and slenderness (length ratio of rostrum/greatest skull width), which was different from specimens from the Atlantic Ocean (Dall, 1873; Miller, 1936; Banks & Brownell, 1969). Additionally, Banks & Brownell (1969) suggested that a "*bairdii*-like" population inhabited the ESP, where long-beaked common dolphins are mainly found in Peruvian waters, between 4° and 18° S (Llapapasca et al., 2018; Pacheco et al., 2019; Santillán et al., 2023).

Based largely on an examination of a series of skulls and color pattern differences, Heyning & Perrin (1994) described ENP long-beaked common dolphins as *Delphinus capensis* Gray, 1828, as skull measurements and tooth counts of the type specimen for that species, collected from the Cape of Good Hope (Eastern South Atlantic), were similar to long-beaked common dolphins from California and the name had priority over other named long-beaked common dolphin species. Species-level differentiation of the ENP long- and short-beaked common dolphins was also supported by an analysis of mitochondrial DNA control region and cytochrome *b* sequences (Rosel et al., 1994).

However, later genetic analyses with a greater number of samples and geographical coverage indicate that ENP long-beaked common dolphins are not closely related to those occurring in the Eastern South Atlantic and South Africa from where the type specimen of *D. capensis* was originally described (Natoli et al., 2006; Amaral et al., 2007; Cunha et al., 2015). Thus, although the accumulated evidence suggests that the two forms of common dolphins occurring in the ENP are highly differentiated and might be considered a different species (Amaral et al., 2007; Cunha et al., 2015), the ENP long-beaked common dolphin form should not be referred to as *D. capensis* (Perrin, 2018).

Based on an examination of 351 skulls, 755 control regions, and 370 cytochrome *b* sequences, along with a review of color pattern differences and distribution of the forms, Jefferson et al. (2024) proposed that long-beaked common dolphins in the ENP be recognized as *D. bairdii*, a species distinct from the nominate short-beaked common dolphin *D. delphis*. However, even in light of the evidence presented, this proposal did not receive sufficient support by the SMM Committee on Taxonomy to recognize long-beaked common dolphins as a distinct species. The primary concerns were the lack of supporting nuclear data and a need for inclusion of samples from a wider geographic range. Thus, the SMM Committee on Taxonomy (2024) still recognizes the ENP long-beak common dolphin as the subspecies *D. d. bairdii*.

Furthermore, the evolutionary lineage of the ENP counterpart form, the ESP long-beaked common dolphins, is also unclear. Due to the limited availability of biopsy samples and the absence of prior taxonomic studies, the relationship between long-beaked common dolphins in the ENP and the ESP remains unknown. Given the lack of connectivity between their distributions and the substantial distance separating them, it is unclear whether these two forms, despite both being long-beaked common dolphins, should be classified within the same taxon.

The aim of this study was to evaluate whether the long-beaked common dolphins from the ENP and the ESP share a common evolutionary lineage. In addition, the study determined the phylogenetic relationships and degree of genetic differentiation between ENP long- and short-beaked common dolphins using full mitogenome sequences.

Methods

Skin samples from 28 long- and short-beaked common dolphins were collected from stranded and biopsied individuals. Based on the identification of color pattern by experienced observers, 12 long-beaked common dolphins from California (LB-Cali), currently known as *D. d. bairdii*, and six short-beaked common dolphins from California (SB-Cali) were identified from stranded individuals by the Southwest Fisheries Science Center (SWFSC), the Santa Barbara Natural Museum of Natural History, and Sea World San Diego. Samples from ten dolphins from the coast of Peru (LB-Peru) were identified as long-beaked common dolphins from individuals biopsied by SWFSC (Figure 2). No samples from Peruvian short-beaked common dolphins were available for the study.

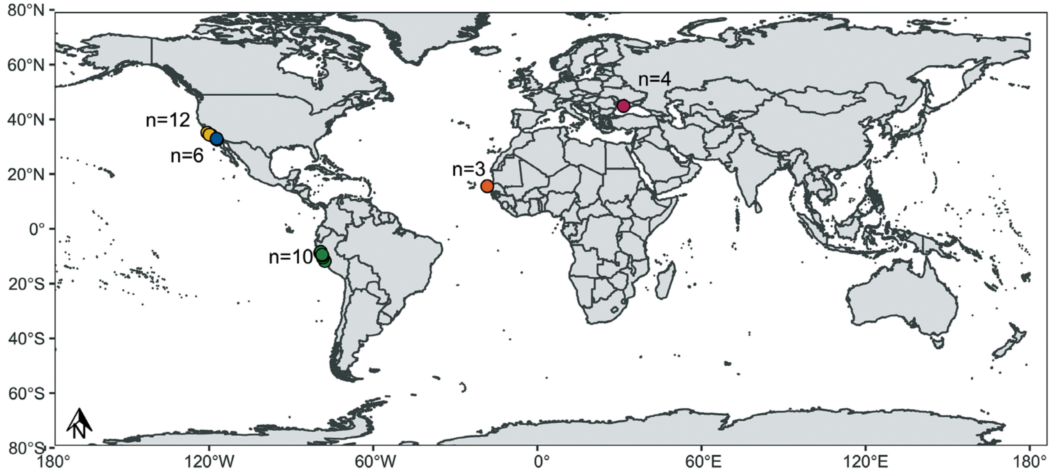


Figure 2. Location and number of sample collections: Black Sea (pink), LB-Cali (yellow), LB-Peru (green), SB-Cali (blue), and Senegal (orange).

Tissues from biopsies and stranded animals were preserved frozen at -20° or -80°C in a 20% salt-saturated DMSO solution or in 100% ETOH in the SWFSC's Marine Mammal and Sea Turtle Research Collection (MMaSTR). Genomic DNA was extracted using sodium chloride precipitation (Miller et al., 1988) or the NucleoMag Tissue Extraction Kit (Macherey-Nagel, Inc., Bethlehem, PA, USA).

A capture array was designed as in Hancock-Hanser et al. (2013), with mitogenomes of 11 species, for use in capture enrichment of mitogenome DNA from multiple odontocete species (Table S1; this supplemental table is available in the "Supplemental Material" section of the *Aquatic Mammals* website), each at 20 copies on the array. The 60 bp probes were spaced every 15 bp so that every position in the sequences was represented four times in the probes. All the mitogenome sequences were modified to include a 40 bp overlap at both ends of the linearized sequence to allow for probe design across the artificial break point in the circular mitogenome.

DNA library preparation and array capture were performed according to Hancock-Hanser et al. (2013) with a few exceptions. Libraries were dual indexed using all unique i7 indexes and shared i5 indexes for groups of eight to 14 libraries to reduce impact of index-hopping during post-capture amplification (Kircher et al., 2011). Individual libraries were quantified using real time qPCR utilizing Bio-Rad iTaq universal SYBR supermix (Bio-Rad Laboratories, Inc., Hercules, CA, USA) and KAPA standards (KAPA Biosystems, Wilmington, MA, USA) made for Illumina primers. After hybridization and final amplification of the post hybridized product, the library was quantified as above and diluted to 4nM for loading on a MiSeq 1 × 150 v3 kit flow cell per manufacturer's instructions (Illumina, San Diego, CA, USA). The library was sequenced using paired end reads with 75 cycles each.

Assembly of the reads for each sample was done through the custom pipeline in *R*, Version 4.0.2 (R Core Team, 2020), described in Archer et al. (2013) using default settings. All reads were assembled to a *Delphinus* mitogenome from GenBank (Accession No. NC_012061). The first approximately 400 bp of the control region was replaced with Sanger sequenced versions (for methods, see Archer et al., 2013) to eliminate ambiguities from alignment and base calling in the pipeline.

The 'strataG' package for *R* (Archer et al., 2017) was used to calculate molecular diversity indices, such as haplotype and nucleotide diversity, proportion of unique haplotypes, and number of variable sites. In addition, pairwise levels of population differentiation were estimated with an analysis of molecular variance (AMOVA), Φ_{ST}, F_{ST}, and χ^2 using 1,000 permutations.

To provide further clarification of relationships among long- and short-beaked individuals worldwide, four Black Sea short-beaked common dolphin (*Delphinus delphis ponticus*) mitogenomes from Biard et al. (2017) were downloaded from Genbank (Accession Nos. MF669495, MF669496, MF669497, and MF669498), and three long-beaked common dolphin mitogenomes from Senegal were obtained from Becker et al. (2024). Phylogenetic relationships and divergence times in million years (Ma) among the three common dolphin populations (LB-Peru, LB-Cali, and SB-Cali) were reconstructed from a total of 35 mitogenome sequences under a Bayesian framework using *BEAST*, Version 1.10.4 (Suchard et al., 2018). Mitogenomes from the Black Sea (n = 4) and Senegal (n = 3) were only used in the phylogenetic analysis, with the purpose of showing global patterns of common dolphin differentiation and, therefore, were not used in the population structure analysis, which focused on the eastern Pacific.

The program *jModelTest*, Version 2.1.10 (Guindon & Gascuel, 2003; Darriba et al., 2012) was used to select HKY + I as the best-fit model for nucleotide substitution for the data. Trees were generated using a Yule speciation process under a strict clock scenario. All trees were rooted to a reference sequence of striped dolphins (*Stenella coeruleoalba*; Genbank Accession No. NC_012053.1). A prior distribution on the time since most recent common ancestor (TMRCA) was specified between the striped dolphin and the genus *Delphinus* estimated by McGowen et al. (2009). The program was run with ten million MCMC iterations, with samples taken every 1,000 iterations and a "burn in" process of 10%. The software *Tracer*, Version 1.7.1 (Rambaut et al., 2018), was used to evaluate effective mixing and convergence to the posterior distribution, and the program *TreeAnnotator*, Version 1.10.4 (Suchard et al., 2018), was used to summarize the information from the produced trees into a single tree.

Bidirectional migration rates between three populations in the eastern Pacific were estimated under a HKY substitution model using an Isolation with Migration (IM) analysis with the software *IMa2* (Hey & Nielsen, 2004; Hey, 2010). Several short runs were conducted to improve mixing and to optimize parameters. The final run included one million burn-in steps, followed by ten million MCMC iterations saved every 100 steps, resulting in 100,000 saved genealogies under a geometric heating scheme. Effective sample size (ESS) values and plot trends were used to evidence good mixing and convergence.

Following the guidelines for cetacean subspecies and species delimitation (Taylor et al., 2017; Morin et al., 2023), net nucleotide divergence (Nei's d_A) was computed using 'strataG.' Percent diagnosability (PD) was calculated using a Random Forest model following Archer et al. (2017), with 10,000 trees, and sampling half of the smallest sample size per strata without replacement for each tree to create a balanced model.

Results

Genetic Diversity

Full mitochondrial DNA (16,376 bp) sequences were obtained from 28 common dolphin samples from California and Peru. The alignment of the 28 mitogenomes showed 347 variable sites, and a total of 25 different haplotypes were detected among the sequenced individuals in which almost all the samples had unique haplotypes (Table 1). The three putative populations showed high haplotype diversity (0.954 to 1.000), where the highest value was found within the SB-Cali population (Table 1). Only two haplotypes were shared: one between two individuals from Peru (LB-Peru-11880 and LB-Peru-11885), and the other among three long-beaked common dolphins from California (LB-Cali-65370, LB-Cali-79974, and LB-Cali-191186). Nucleotide diversity was greatest within the SB-Cali population (0.004), followed by the LB-Cali (0.002). The LB-Peru nucleotide diversity (0.0005) was an order of magnitude lower than the other two populations.

Phylogenetic Reconstruction

The Bayesian phylogenetic tree showed strong support for most nodes, with a posterior distribution greater than 0.90 in 77% of the nodes (Figure 3). The phylogenetic tree identified a well-supported clade (posterior probability = 1.0) containing all the sequences from the LB-Peru population. The LB-Cali population was paraphyletic, in which most sequences were more closely related to LB-Peru individuals than to other LB-Cali dolphins.

The SB-Cali population grouped together with high confidence, except for SB-Cali-78511 (Figure 3). The phylogenetic tree also revealed that short-beaked common dolphins from the eastern Pacific share a closer genetic relationship with long-beaked common dolphins from Senegal and short-beaked common dolphins from the Black Sea than with long-beaked common dolphins from their own ocean basin. In addition, the most surprising aspect of the phylogenetic analysis is that sequence SB-Cali-78511 was more distantly related to the other five SB-Cali sequences than individuals from the Black Sea and Senegal.

Thus, sample SB-Cali-78511 was further analyzed to find any assembly errors, but none were found. The six SB-Cali sequences showed a total of 201 variable sites. When the SB-Cali-78511 sequence was removed from the group, the number of variable sites decreased to 126, meaning that the SB-Cali-78511 accounted for 37% of all the variable sites in the SB-Cali clade. Specifically, SB-Cali-78511 showed 78 differences to the other five SB-Cali sequences, 76 of which were transitions and two transversions. For the 78 sites where differences were found, the average coverage was 70 reads, and the bases for those sites were called with an average frequency of 99%.

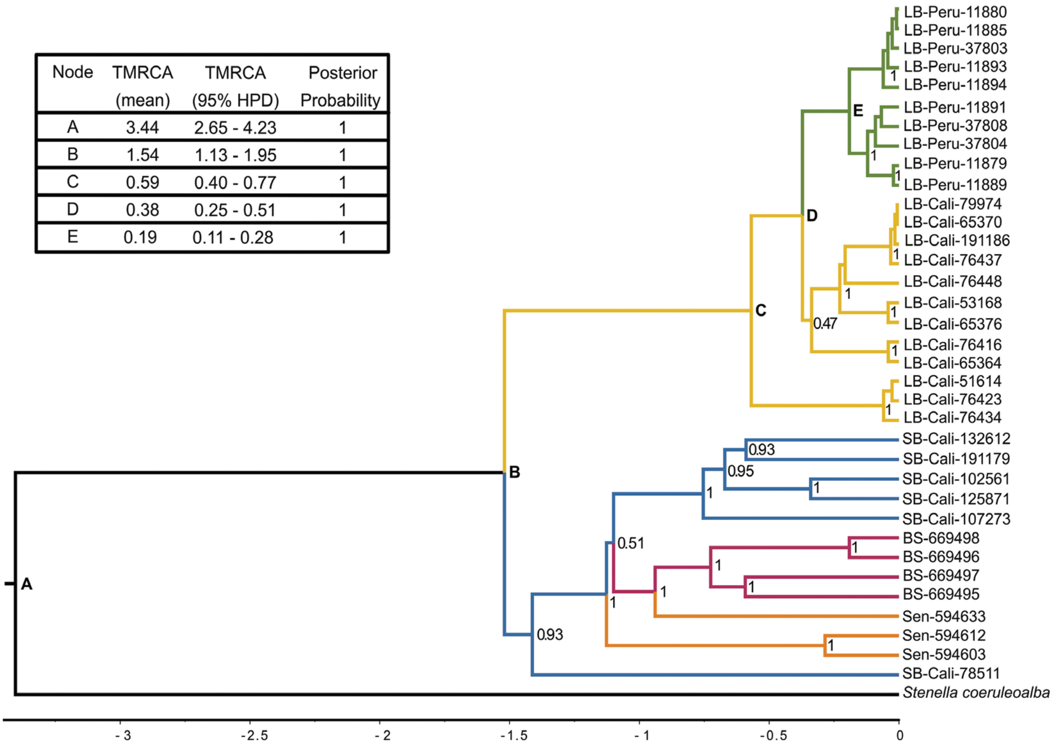
The time since most common recent ancestor (TMRCA) between both common dolphin forms and striped dolphins was estimated at around 3.44 Ma (95% HDP = 2.65 to 4.23 Ma), while the long- and short-beaked forms were estimated to have diverged around 1.54 Ma (95% HDP = 1.13 to 1.95 Ma).

Population Differentiation and Taxonomy

The three populations of common dolphins from the eastern Pacific showed significant genetic differentiation in the AMOVA analysis ($\Phi st = 0.3669$; $p < 0.0009$), but not for the F_{ST} and χ^2 analyses (Table 2). The strongest genetic differentiation resulted between the LB-Peru and SB-Cali samples, followed by LB-Cali

Table 1. Mitogenome (16,376 bp) summaries for the three common dolphin (*Delphinus* spp.) populations. N = number of sequences, N_H = number of unique haplotypes, P_H = proportion of unique haplotypes, h = haplotype diversity, π = nucleotide diversity, and VS = number of variable sites.

	N	N_H	P_H	h	π	VS
LB-Cali	12	10	0.750	0.954	0.002	91
LB-Peru	10	9	0.800	0.978	0.0005	28
SB-Cali	6	6	1.000	1.000	0.004	201
Total	28	25	0.821	0.989	0.004	347



Node	TMRCA (mean)	TMRCA (95% HPD)	Posterior Probability
A	3.44	2.65 - 4.23	1
B	1.54	1.13 - 1.95	1
C	0.59	0.40 - 0.77	1
D	0.38	0.25 - 0.51	1
E	0.19	0.11 - 0.28	1

Figure 3. Bayesian phylogenetic tree and TMRCA (time since most recent common ancestor) derived from *BEAST*. Numbers at each node correspond to the posterior probability.

Table 2. Population differentiation between three common dolphin populations in the eastern Pacific: χ^2, F_{ST}, Φst, Nei's d_A, and percent diagnosability (PD). For χ^2, only *p* values are shown. The last column shows the 95% confidence interval for the PD.

	χ^2 *p* value	F_{ST}	F_{ST} *p* value	Φst	Φst *p* value	d_A	PD (%)	PD (%) 95% CI
LB-Cali vs LB-Peru	0.096	0.034	0.068	0.344	0.001	0.0007	100	69-100
LB-Cali vs SB-Cali	0.269	0.025	0.269	0.622	0.001	0.0042	100	69-100
LB-Peru vs SB-Cali	0.487	0.012	0.487	0.713	0.001	0.0046	100	66-100

and SB-Cali, and then between LB-Peru and LB-Cali. Bidirectional migration between the three common dolphin populations was close to zero. Since *IMa2* estimates mutation rate-scaled parameters, migration rates were later converted to demographic estimates as the number of migrants per generation, assuming a generation time for common dolphins of 15 y (Taylor et al., 2007) and the mutation rate of 1.18×10^{-3} substitutions per site/generation estimated by the *BEAST* analysis conducted previously (Table 3).

For cetacean taxonomic delimitation using mitogenomes, Morin et al. (2023) proposed Nei's d_A values greater than 0.0006 for subspecies, and 0.008 for species classification and percent diagnosability (PD) greater than 95% for both delimitations. All pairwise comparisons for nucleotide divergence and diagnosability were found to fall within the suggested subspecies threshold values. However, for species delineation, all pairwise comparisons failed to meet the proposed threshold value for Nei's d_A but met the threshold for PD (Table 2).

Table 3. Bidirectional scaled migration rates (*m*) and number of migrants per generation between the three eastern Pacific populations of common dolphins. Parentheses show the 95% highest posterior density interval.

	m	Migrants per generation
LB-Peru <> LB-Cali	0.009 (0.001-0.104)	0.000
LB-Peru <> SB-Cali	0.027 (0.001-0.120)	0.000
SB-Cali <> LB-Cali	0.000 (0.000-0.135)	0.000

Discussion

Common dolphins in the ENP are currently recognized as two different subspecies, the long-beaked (*D. d. bairdii*) and the short-beaked (*D. d. delphis*) (Committee on Taxonomy, 2024). In this analysis, long-beaked common dolphins from Peru and California form a monophyletic clade with respect to short-beaked common dolphins from California and the Black Sea, and long-beaked common dolphins from Senegal. Additionally, although Nei's d_A is lower than the subspecies-species threshold suggested for mitogenomes by Morin et al. (2023), Pacific long- and short-beaked common dolphins are 100% diagnosable based on mtDNA. The estimated divergence time between long- and short-beaked common dolphins in the North Pacific based on mitogenome sequences (1.54 Ma; 95% HPDI = 1.13 to 1.95 Ma) is similar to that found in other recently diverged odontocete sister species (McGowen et al., 2009; Amaral et al., 2012; Braulik et al., 2019; Morin et al., 2023), and the estimated migration rate between the forms is zero. Thus, this study supports recognizing long- and short-beaked common dolphins in the Pacific as separate species, with both the Peruvian and Californian long-beaked form belonging to the same taxon, likely representing *Delphinus bairdii* Dall, 1873 (Banks & Brownell, 1969; Jefferson et al., 2024).

The present article is limited by its exclusive use of mitochondrial DNA, requiring the inclusion of nuclear DNA for result clarity. The small sample size compromises statistical robustness, emphasizing the need for a larger sample. While species-level insights are offered, the study suggests that additional samples and nuclear data are essential to refine the conclusions, ensuring a more comprehensive and reliable understanding of the different forms of common dolphins in the eastern Pacific.

Previous studies have shown that ENP long-beaked common dolphins are genetically differentiated from common dolphins in other parts of the world (Rosel et al., 1994; Kingston & Rosel, 2004; Natoli et al., 2006; Amaral et al., 2007; Jefferson et al., 2024). Using 1,140 bp of cytochrome *b*, Cunha et al. (2015) found ENP long-beaked common dolphins to be paraphyletic with respect to the ENP short-beaked form. The authors attributed this finding to ancestral shared polymorphisms or incomplete lineage sorting between recently diverged species. However, the use of the full mitogenome in our study provides greater phylogenetic resolution at this scale (Morin et al., 2010, 2023; Archer et al., 2013).

Within the long-beaked clade, Peruvian long-beaked common dolphins were monophyletic, while Californian long-beaked common dolphins were paraphyletic with nine of 12 Californian long-beaked samples more closely related to Peruvian long-beaked common dolphins than to the other three Californian long-beaked dolphins. This pattern would be consistent with California as the source population for Peruvian long-beaked common dolphins was estimated to have diverged approximately 400 Kya (Figure 3). Additionally, our study indicates that there is no current gene flow between long-beaked common dolphins in these two regions, which is understandable given the great geographic distance (> 6,000 km) between them (see Hamilton et al., 2009). Thus, the monophyletic clade formed by Peruvian long-beaked common dolphins (Figure 3), in addition to meeting the subspecies threshold values for subspecies delimitation between the long-beaked form from Peru and California (Table 2), suggests that Peruvian long-beaked common dolphins may represent at a distinct evolutionary lineage at least at the subspecies level within the Pacific long-beaked taxon.

Other than the examination of two specimens from the coast of Peru (Banks & Brownell, 1969), taxonomic studies on Peruvian common dolphins have been scarce. The present study provides the first insights into the population structure and genetic differentiation of Peruvian long-beaked common dolphins. The nutrient-rich waters of the Humboldt Current make Peru's fisheries among the most important and productive fisheries in the world. The intense extraction of marine resources results in high mortality rates for Peruvian dolphins due to bycatch (Van Waerebeek et al., 2002; Mangel et al., 2010; Ayala et al., 2019). Ayala et al. (2019) reported that 25 vessels off the coast of Peru incidentally caught more than 1,000 dolphins in 2009. The results of this study suggest that Peruvian long-beaked common dolphins represent a distinct evolutionary lineage. Follow-up studies on this population are needed to assess its taxonomic and conservation status and to establish mitigation measures in this highly impacted area.

While differentiation between long- and short-beaked common dolphins in the eastern Pacific Ocean is clear, it is less so for relationships between the eastern Pacific short-beaked form and common dolphins in the Atlantic Ocean. The presence of the SB-Cali-78511 sequence at the base of a clade containing all other Californian short-beaked dolphins as well as samples of the endemic *D. d. ponticus* subspecies from the Black Sea and long-beaked common dolphins from Senegal suggests that there is considerable ancestral polymorphism within the eastern Pacific short-beaked form. Within California, Oregon, and Washington waters, the short-beaked common dolphin population is estimated at 1,056,308 (CV = 0.207) individuals (Carretta et al., 2022); thus, a large amount of genetic diversity is expected, which is unlikely to be fully represented by the six samples present in this study.

Within the Atlantic, Cunha et al. (2015) showed that long- and short-beaked cytochrome *b* sequences from the western South Atlantic had no genetic differences, with all corresponding to *D. delphis*. Natoli et al. (2006) found genetic differences in the mtDNA control region between populations in different sides of the Atlantic Ocean but no significant genetic differences between populations located on the same side of that ocean. A recent study of full mitogenome sequences showed significant population structure within Senegal as well as differentiation between common dolphins in Senegal and the rest of the North Atlantic (Becker et al., 2024). As the authors note, improved resolution of phylogenetic patterns in this region and globally will likely require nuclear genomic level data.

In summary, this study has demonstrated that Peruvian long-beaked common dolphins should be considered within the same taxon as long-beaked common dolphins from the ENP, which are all currently regarded as the subspecies *Delphinus delphis bairdii* (Committee on Taxonomy, 2024). Additionally, within that taxon, they represent a distinct evolutionary lineage. It is clear that full elucidation of the taxonomy of these forms awaits further studies.

Note: The supplemental table for this article is available in the "Supplemental Material" section of the *Aquatic Mammals* website: https://www.aquaticmammalsjournal.org/supplemental-material.

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