Received: 8 May 2023 | Accepted: 8 May 2024

DOI: 10.1111/mms.13144

ARTICLE

Marine Mammal Science

Common dolphin (*Delphinus delphis*) mitochondrial genomes from Senegal reveal geographic structure across the North Atlantic but provide no support for global long-beaked clade

Madeleine A. Becker[1,2,3,4] | Katherine R. Murphy[5] | Frederick I. Archer[6] | Thomas A. Jefferson[6,7] | Lucy W. Keith-Diagne[8] | Charles W. Potter[1] | M. Fernanda Urrutia-Osorio[9] | Ibrahima Ndong[8] | Michael R. McGowen[1]

[1]Division of Mammals, Department of Vertebrate Zoology, Smithsonian National Museum of Natural History, Washington, District of Columbia

[2]Smithsonian-Mason School of Conservation, Front Royal, Virginia

[3]Center for Conservation Genomics, Smithsonian's National Zoo and Conservation Biology Institute, Washington, District of Columbia

[4]School of Systems Biology, George Mason University, Fairfax, Virginia

[5]Laboratories of Analytical Biology, Smithsonian National Museum of Natural History, Washington, District of Columbia

[6]Southwest Fisheries Science Center, National Marine Fisheries Service, NOAA, La Jolla, California

[7]Clymene Enterprises, Lakeside, California

[8]African Aquatic Conservation Fund, Ngazobil, Senegal

[9]Scripps Institute of Oceanography, University of California San Diego, La Jolla, California

Correspondence
Michael R. McGowen, Smithsonian National Museum of Natural History, Division of Mammals, MRC-108, 10th Street & Constitution Avenue NW, Washington, DC 20560.
Email: mcgowenm@si.edu

Funding information
Division of Ocean Sciences, Grant/Award Number: OCE-1560088

Abstract

The common dolphin (*Delphinus delphis*) is a widely distributed species exhibiting extensive morphological diversity, with previous taxonomies recognizing multiple *Delphinus* species primarily based on relative beak length. We sequenced mitochondrial genomes of *D. delphis* morphotypes from multiple regions, calculated mitogenome nucleotide diversity ($\pi = 0.00504$), dated *Delphinus* mitogenome diversification to 1.27 mya, and conducted phylogenetic and

population-level analyses focusing on morphotype and geographic origin. We present the first *Delphinus* sequencing data from Senegal, at the edge of where long- and short-beaked dolphins co-occur in the Atlantic, but only recovering stranded dolphins with long or indeterminate beak lengths. While we detected little genetic structure across most of the North Atlantic, fixation indices demonstrate that Senegalese dolphins are distinct. Geography did not reliably predict phylogeny, with few monophyletic localities, but we do infer a monophyletic group of long-beaked dolphins from California, Peru, and possibly China. However, neither Senegalese long-beaked dolphins nor long-beaked *D. d. tropicalis* are closely related to Pacific long-beaked dolphins, providing no support for a worldwide long-beaked clade (formerly *D. capensis*). Our findings reveal a distinctive Senegal *Delphinus* population and provide a foundation for global genomic analyses to further investigate the evolution of *Delphinus* morphotypes.

KEYWORDS
Delphinus, genetic structure, mitogenomics, museum specimens, phylogeography, taxonomy

1 | INTRODUCTION

The common dolphin, *Delphinus delphis*, is one of the most abundant, widespread, and well-studied delphinid species in tropical and warm-temperate waters, yet its taxonomy has been in flux over the past 30 years (Perrin, 2018). Although the Society for Marine Mammalogy Committee on Taxonomy currently recognizes only one species of *Delphinus*, two species, *Delphinus delphis* Linnaeus, 1758 (short-beaked common dolphin) and *Delphinus capensis* Gray, 1828 (long-beaked common dolphin), were recognized as recently as 2015. Others suggested that an even longer-beaked *Delphinus* morph from the coastal Indo-Pacific should be considered a separate species, *D. tropicalis* van Bree, 1971 (Amaha, 1994; Rice, 1998; van Bree, 1971; van Bree and Gallagher, 1978), before it was listed as a subspecies of *D. capensis* on account of morphological similarity (Jefferson & Van Waerebeek, 2002). While relative beak size, measured as the ratio between rostral length and zygomatic width, has served as a primary character for species diagnosis (Amaha, 1994; Banks & Brownell, 1969; Evans, 1975; Heyning & Perrin, 1994; Jefferson & Van Waerebeek, 2002; van Bree & Gallagher, 1978), geographic variation in size, external coloration, tooth count, and skeletal characters like vertebral count are also often incorporated into taxonomic study.

Today, phylogenetic relationships among the various beak morphotypes (short-beaked, long-beaked, ultra-long-beaked *tropicalis*) and subspecies within the genus *Delphinus* remain unresolved on a global scale. The 1994 resurrection and redescription of *D. capensis* as a separate long-beaked species was based on a robust morphological data set of Californian specimens (Heyning & Perrin, 1994) that was further supported by molecular analysis (Rosel et al., 1994), demonstrating clear distinction of eastern North Pacific Ocean (ENP) long-beaked dolphins from ENP short-beaked dolphins, as well as reciprocal monophyly between the two groups.

Heyning and Perrin (1994) then paired these findings with a global review of morphological studies to extrapolate that this distinction constituted a global clade of long-beaked *Delphinus*. However, continued investigation into *Delphinus* morphology has resulted in less consistent distinctions outside of the ENP region. Skull measurements from Australia and New Zealand (Amaha, 1994; Jordan, 2012), South America (Cunha et al., 2015; Esteves & Oviedo, 2007; Tavares et al., 2010), South Africa (Bell et al., 2002; Ngqulana et al., 2019; Samaai et al., 2005), and western Europe (Murphy et al., 2006) demonstrate phenotypic variability among short- and long-beaked dolphins that does not parse into the two diagnostic categories created by Heyning and Perrin (1994) for ENP *Delphinus* populations. Recent morphometric analysis on a global scale has demonstrated the divergence of ultra-long-beaked *D. d. tropicalis* and distinction of *D. d. bairdii*, but also revealed parallel differentiation of northern versus southern short-beaked skull shapes in the Atlantic and Pacific Oceans (Nicolosi & Loy, 2021), shedding further light on the complexity of categorizing range-wide morphotypes.

Additionally, mounting molecular evidence from outside of the ENP region has not supported a worldwide long-beaked clade and has demonstrated the necessity for sampling more areas within the global distribution of common dolphins (Cunha et al., 2015; Farías-Curtidor et al., 2017; Kingston et al., 2009; Natoli et al., 2006; Stockin et al., 2014). Accordingly, *D. capensis* has been synonymized with *D. delphis* until further genetic studies shed light on the possibility of distinct, diagnosable species within *Delphinus* (Committee on Taxonomy, 2023). Currently, there are four recognized subspecies of *D. delphis*, which display different morphological characters including coloration and rostrum length: (1) the common dolphin, *D. d. delphis* Linnaeus, 1758; (2) the eastern North Pacific long-beaked common dolphin, *D. d. bairdii* Dall, 1873; (3) the Indo-Pacific common dolphin, *D. d. tropicalis* van Bree, 1971; and (4) the Black Sea common dolphin, *D. d. ponticus* Barabash, 1935, a small, short-beaked dolphin endemic to the Black Sea. Despite this updated taxonomic framework, uncertainty persists concerning subspecies relationships, ranges, and validity, including whether the distinct ENP long-beaked *bairdii* group warrants subspecies or species status (Cunha et al., 2015).

Another motivation for expanded genetic sampling of *Delphinus* is to examine population structure across the Atlantic Ocean. Some studies of *Delphinus* have documented fine scale genetic structure in the populations of Australasia (Barceló et al., 2021; Möller et al., 2011) and the Indian Ocean (Gray et al., 2021), while others have observed population differentiation between ocean basins (Amaral et al., 2012a; Mirimin et al., 2009; Natoli et al., 2006, 2008; Tonay et al., 2020). However, several genetic studies of specimens in the North Atlantic Ocean have not found *D. delphis* population structure that is comparable to that of other local cetacean species (Amaral et al., 2012b; Mirimin et al., 2009; Natoli et al., 2006), with one analysis of 433 samples across Europe describing an "atypical panmixia" (Moura et al., 2013). The reasons for this uncommon phenomenon are poorly understood, although the abundance, large populations, high genetic diversity, and long-distance dispersal of this species are likely factors (Ball et al., 2017).

The objective of this study was to expand *Delphinus* sequencing to whole mitochondrial genomes (mitogenomes) in the Atlantic and leverage publicly available sequences to investigate phylogeography and genetic structure on a global scale. Namely, we wanted (1) to test whether mitogenomes reflect broad-scale *Delphinus* geographic distribution, with closer relationships between specimens collected from the same general regions than between ocean basins; (2) to test whether beak morphs from disparate regions share a recent common ancestor or represent independent lineages; (3) to construct a time-calibrated tree of *D. delphis* mitochondrial lineages; and (4) to compare sequences from Senegal with other North Atlantic populations. To answer these questions, we sequenced 31 mitogenomes of stranded *Delphinus* from Senegal, an understudied area with high *Delphinus* abundance (Correia et al., 2020) and reported co-occurrence of short- and long-beaked forms (Van Waerebeek, 1997; Van Waerebeek et al., 2000), but no large-scale attempts at genetic sequencing. We also sequenced mitogenomes of 13 individuals from the western North Atlantic (WNA), three from Peru in the eastern South Pacific (ESP), and three from the eastern tropical Pacific (ETP). Combining these with nine previously published *Delphinus* mitogenomes of both long- and short-beaked morphs (Alexander et al., 2013; Biard et al., 2017; Lee et al., 2018; McGowen et al., 2020; Xiong et al., 2009), we have assembled the largest data set of complete *Delphinus* mitochondrial genomes to date, through which we address questions surrounding common dolphin taxonomy and population structure.

2 | METHODS

2.1 | Sample collection and identification

Tissue samples were collected opportunistically from common dolphin strandings in Senegal ($n = 31$) in 2018–2019 by L.K.D. and I.N. of the African Aquatic Conservation Fund (with the assistance of M.R.M. and C.W.P.) using the research permit issued to LKD from the Senegal Ministry of the Environment, Direction of Water and Forestry. All samples were imported legally into the United States and deposited in the Smithsonian National Museum of Natural History (NMNH) Division of Mammals (Table S1); this included three individuals with vouchered skulls. Where possible, all Senegalese individuals were identified as long-beaked morphs based on rostral length/zygomatic width (RL/ZW) ratio if a skull was present (Heyning & Perrin, 1994) or beak length/total body length (BL/TBL) ratio (<6.9% for short-beaked dolphins, >6.9 for long-beaked; Jefferson et al., 2015). In most cases, stranded Senegalese animals were juveniles ($n = 29$), and often decomposed or otherwise not intact, meaning that beak morph identification was sometimes tenuous or impossible. In all cases where it was possible to measure either RL/ZW or BL/TBL ratios, we determined individuals were long-beaked morphs ($n = 6$; Table S2) and categorized the rest as "unknown" in downstream analyses. We were only able to document coloration pattern in two juvenile individuals, USNM 594604 and USNM 594610, both of which had a dark flipper-to-anus stripe (Figure S3a,b), which can be indicative of individuals from the eastern North Atlantic (Amaha, 1994). Other individuals were too decomposed to document coloration in life (Figure S3c,d). There seems to be a high prevalence of long-beaked morphs among bycaught and stranded specimens in Senegal (Cadenat et al., 1959; Van Waerebeek, 1997), although both morphs are likely present in Senegal based on RL/ZW ratios (Van Waerebeek et al., 2000).

We also included in our data set tissue samples representing regions outside Senegal (Figure 1, Table S1) from the Smithsonian National Museum of Natural History (NMNH) Division of Mammals, including short-beaked morphs from the western North Atlantic ($n = 13$; WNA) and eastern tropical Pacific ($n = 3$; ETP_sb). Additionally, we added three specimens of long-beaked morphs from Peru (Table S1) in the eastern South Pacific ($n = 3$; ESP_lb), which were collected, processed, and sequenced separately from the rest of the samples.

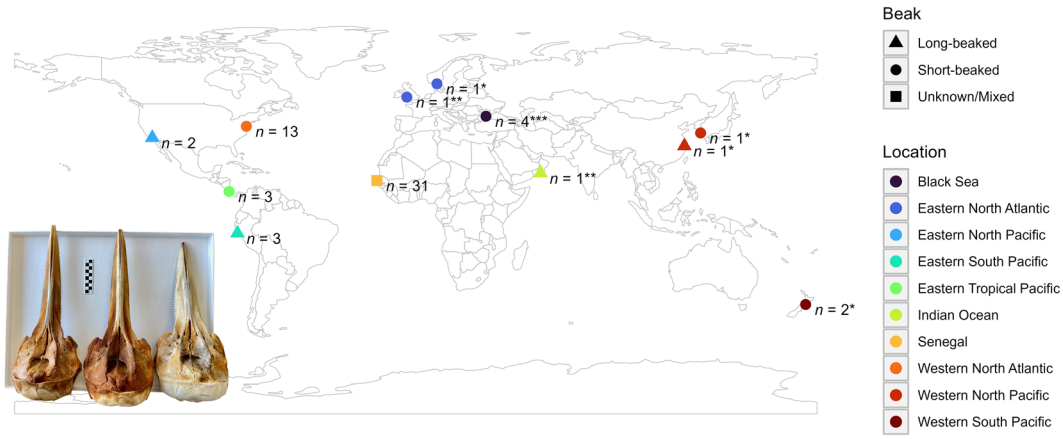

FIGURE 1 General localities of *Delphinus delphis* samples and sample sizes, including novel specimens and previously published sequences: *Sequences downloaded directly from GenBank, **Mitochondrial sequences bycaught from target capture data generated by McGowen et al. (2020), ***GenBank sequences derived from ancient samples (400–530 CE). Inset: Skulls of three *Delphinus* morphotypes (from left to right) ultra-long-beaked *D. delphis tropicalis* (USNM 550976, Somalia), long-beaked *D. delphis bairdii* (USNM 504278, Baja California, Mexico), and short-beaked *D. delphis delphis* (USNM 594196, North Carolina). Scale bar = 10 cm.

2.2 | DNA extraction, long-range PCR, library prep, and sequencing

Laboratory methods differed between different sample sets. For Senegalese and other NMNH samples ($n = 47$), we performed DNA extractions using DNeasy Blood and Tissue kits (Qiagen Sciences, Germantown, MD). Two overlapping segments of the complete mitogenome were amplified using long-range PCR with NEB Q5 Hot Start DNA polymerase and two primer pairs (LR1, product size 9.3 kB; LR2, product size 7.5 kB) designed to amplify delphinid dolphins as described in Morin et al. (2010). In cases where one or both segments failed to amplify, smaller segments (2.4–5.0 kB) were amplified using additional primer pairs (Table S4). While seven of our ten PCR primers were previously described in Morin et al. (2010), three (Ddel-LR2r, Ddel_Ttru-LR2.2f, Ddel-LR2.2r) were specifically designed for this study based on available reference sequences for *D. dephis* and *Tursiops truncatus*, but targeting the same sites as LR2 and LR2.2 from Morin et al. (2010) (Table S4). PCR products were cleaned with either ExoSAP-IT (Applied Biosystems, Waltham, MA) or with a QIAquick gel extraction kit (Qiagen) in cases of spurious PCR bands due to nonspecific primer binding. Clean amplicons were quantified using the Qubit dsDNA HS assay and pooled in equimolar ratios for each specimen. We then sheared pooled amplicons to a target size of 200 bp on a Covaris ME220 UltraSonicator. In five cases (specimens USNM 487807, 571320, 572175, 605113, 605119), we directly sheared genomic DNA (gDNA) to serve as input for library construction for whole-genome sequencing, as long-range PCR was not successful. We constructed Illumina libraries for 5 ng of sheared amplicons or 100 ng of sheared gDNA using NEBNext Ultra II DNA kits with dual indexing. Libraries were quantified using the Qubit dsDNA HS assay, sized with a high sensitivity D1000 tape run on an Agilent 2100 Tapestation, and then equimolarly pooled. The resulting pools were submitted for sequencing (paired-end, 2×150 bp) on the Illumina MiSeq with V2 chemistry at the Smithsonian NMNH Laboratories for Analytical Biology (LAB).

For Peruvian samples, genomic DNA was extracted using sodium chloride precipitation (Miller et al., 1988) or the NucleoMag Tissue Extraction Kit (Macherey-Nagel, Inc., Bethlehem, PA). A capture array was designed as in Hancock-Hanser et al. (2013), with mitogenomes of 11 species (Table S4), each at 20 copies on the array. 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 8–14 libraries to reduce impact of index-hopping during postcapture amplification (Kircher et al., 2012). Individual libraries were quantified using real time qPCR using Bio-Rad iTaq universal SYBR supermix (Bio-Rad Laboratories, Inc., Hercules, CA) and KAPA standards (KAPA Biosystems, Wilmington, MA) made for Illumina primers. After hybridization and final amplification of the post hybridized-product, the library was quantified as above and diluted to 4 nM for loading on a MiSeq 2×75 v3 kit flowcell per manufacturer's instructions (Illumina, San Diego, CA). The library was sequenced using paired end reads with 75 cycles each.

2.3 | Additional sequences

To increase the scope of our data set, we added previously published *Delphinus* partial or complete mitogenome sequences ($n = 9$) to our novel mitochondrial genomes (Table S1), including four ancient (400–530 CE) short-beaked *D. delphis ponticus* from the Black Sea (BLS), one short-beaked dolphin from Denmark in the eastern North Atlantic (ENA), one *capensis*-type long-beaked morph from China in the western North Pacific (WNP), two mitogenomes of short-beaked morphs from the western South Pacific (WSP), and the *D. delphis* annotated reference mitogenome, which is derived from a short-beaked morph from South Korea in the WNP (Alexander et al., 2013; Biard et al., 2017; Lee et al., 2018; Xiong et al., 2009). We also extracted four additional mitogenomes from target capture data: two partial mitogenomes from *capensis*-type long-beaked morphs in the eastern North Pacific (ENP_lb), one partial mitogenome from a *tropicalis*-type long-beaked morph in the Indian Ocean (IND_lb), and one complete mitogenome from an ENA short-beaked morph from the United Kingdom (McGowen et al., 2020). Lastly, we also added as outgroups complete mitogenomes from five closely related delphinine species:

Lagenodelphis hosei, *Tursiops aduncus*, *T. truncatus*, *Stenella attenuata*, and *S. coeruleoalba* (Lee et al., 2019, 2018; Xiong et al., 2009). Table S1 provides details of locality data and GenBank numbers for these mitogenomes; Figure 1 displays broad localities for all *Delphinus* individuals.

To expand our sample size for downstream population-level analyses, we also downloaded from NCBI GenBank ($n = 329$) previously sequenced partial control region haplotypes from the North Atlantic, Mediterranean, and Black Sea (Biard et al., 2017; Kingston et al., 2009; Mirimin et al., 2009; Natoli et al., 2008; Quérouil et al., 2010; Rosel et al., 1994; Viricel et al., 2014) and analyzed them with our novel sequences (see 2.6 | Population genetics analyses and Table S1).

2.4 | Mitochondrial assembly

Novel sequence read quality was determined with FastQC version 0.11.5 (Andrews, 2010) and aggregated with MultiQC version 1.7 (Ewels et al., 2016). Low quality bases and adapters were removed with Trimmomatic version 0.33 (Bolger et al., 2014). Quality checking and trimming were performed on the Smithsonian Institution High Performance Computing Cluster. Trimmed reads were imported into Geneious 11.1.5 (https://www.geneious.com) and mapped to the *D. delphis* mitogenome annotated reference sequence MH000365.1 (Lee et al., 2018) using the Geneious mapper with fast and medium sensitivity settings. Ambiguous bases and sites with coverage <5 were assigned as missing data (Ns). We also generated the four *Delphinus* mitogenomes from the target sequence capture study of McGowen et al. (2020) by mapping trimmed reads to MH000365.1 with the same parameters. Assembly of reads for Peruvian specimens was done through the custom R pipeline described in Archer et al. (2013). As in that paper, the first approximately 400 bp of the control region was replaced with Sanger sequenced versions to eliminate ambiguities from alignment and base calling in the Peruvian mitogenome assembly pipeline. We aligned all sequences (including those obtained from GenBank; $n = 68$) using MAFFT version 7.388 (Katoh & Standley, 2013) with default parameters. All assembled mitochondrial sequences have been deposited in NCBI GenBank (PP375135-PP375181, PP623004-PP623006, PP727284, PP761274, PP761277, PP761279).

2.5 | Phylogenetic and divergence dating analyses

Prior to building phylogenetic trees, we separated our mitogenome data into separate partitions including three separate coding positions in each protein coding gene, individual rRNA and tRNA genes, and the control region. Positions that overlapped between genes were included in the larger partition and not duplicated. We used this delimitation to find the best substitution model for each partition with ModelFinder (Kalyaanamoorthy et al., 2017) in the IQTree v2.1.2 module (Minh et al., 2020) on the CIPRES Science Gateway v3.3 (Miller et al., 2011). Partitions were analyzed using default parameters, a gamma model of evolution, corrected Akaike information criterion (AICc) model selection, linked branch lengths, and a greedy search algorithm (Lanfear et al., 2012). We then conducted a maximum likelihood (ML) analysis with IQTree v2.1.2 (Chernomor et al., 2016; Minh et al., 2020) using our best partition scheme from ModelFinder ($n = 16$), 1,000 Ultrafast bootstrap replicates (Hoang et al., 2018), and *L. hosei*, *T. aduncus*, *T. truncatus*, *S. attenuata* and *S. coeruleoalba* as outgroups.

We also conducted a Bayesian phylogenetic analysis using MrBayes v3.2.7a (Ronquist & Huelsenbeck, 2003) on CIPRES with the same partition scheme, two Monte Carlo Markov chains and 10 million generations; the first 25% of output trees were discarded as burn-in. Posterior probability support scores are derived from the 50% majority rule consensus tree, rooted after the analysis. We used the ggtree v3.3.1 package (Yu et al., 2017) in R (R Core Team, 2021) to manipulate and annotate the resulting ML and Bayesian trees.

To test the likelihood of a monophyletic long-beaked group (the former *Delphinus capensis* species) fitting the given mitogenomic data, we performed an approximately unbiased (AU) test (Shimodaira, 2002) in IQTree with

10,000 RELL replicates. AU tests were conducted on two hypothetical topologies showing long-beaked monophyly on different geographical scales: one with an Indian + Pacific long-beaked clade (i.e., the six dolphins from the Pacific Ocean and '*tropicalis*') and another topology containing a clade of all long-beaked individuals including all samples from Senegal (whether identified as long-beaked or unknown morphotype). We performed additional AU tests with the same parameters to test the likelihood of monophyly for each of the Atlantic populations (SEN, WNA, BLS, ENA).

We used BEAST2 v2.6.7 (Bouckaert et al., 2019) to date divergences within the phylogenetic tree of *Delphinus* mitogenomes following Louis et al. (2020). First, we downloaded 27 complete mitogenomes (2 phocoenids, 2 monodontids, 1 iniid, 22 delphinids; Table S5) and added these to four *Delphinus* mitogenomes (D_del_550846_SEN, England_ENA, MH000365_WNP, EU557094_WNP_LB) which represented mitogenomes with a common ancestor at the root of *Delphinus*. A phylogenetic tree of these 31 mitogenomes was created using IQTree with the same parameters described above with partitions using ModelFinder. We then dated the node inclusive of all *Delphinus* mitogenomes using a Yule prior, optimized relaxed clock model, and two log-normal calibration priors, one at the common ancestor of Monodontidae and Phocoenidae based on the minimum age of the phocoenid fossil *Salumophocaena stocktoni* (7.5 Ma; M = 1; S = 0.75; Geisler et al., 2011; Wilson, 1973) and the minimum age of Delphininae (excluding *Sotalia*) based on the minimum age of *Etruridelphis giulii* (3.98 Ma; M = 0.5; S = 0.3; Bianucci, 2013). We conducted the MCMC analysis for 50 million generations, discarding the first 25% as burn-in and summarizing post burn-in trees in TreeAnnotator v2.6.7, part of the BEAST2 package. We then used the date of 1.5556 Ma for the diversification of *Delphinus* as the input for another BEAST analysis of only *Delphinus* mitogenomes, excluding all mitogenomes with missing data for a total of n = 55 in the final BEAST2 dataset. For this analysis we used a constant population coalescent tree prior and strict clock model with a uniform rate prior, as suggested for intraspecific divergence dating analyses (Louis et al., 2020). We conducted the MCMC analysis and discarded trees as in the previous analysis.

2.6 | Population genetics analyses

For haplotype comparisons and analyses between populations, we used a subset of sequences ($n = 55$) restricted to localities with multiple complete mitochondrial genomes (SEN, WNA, BLS, ENA, ETP_sb, ESP_lb) and excluding one WNA sequence (USNM 550921) due to 24% missing data. The aligned sequences were imported into Arlequin v3.5.2.2 (Excoffier & Lischer, 2010) with PGDSpider v2.1.1.5 (Lischer & Excoffier, 2012). We used Arlequin to calculate the diversity and interpopulation fixation indices based on a Tamura and Nei model of substitution (Tamura & Nei, 1993), selected by a separate unpartitioned ModelFinder analysis (Kalyaanamoorthy et al., 2017) in IQTREE v2.1.2 (Minh et al., 2020). In Arlequin, we calculated pairwise values of Φ_{ST}, an estimated fixation index analogous to F_{ST} appropriate for molecular haplotype data (Excoffier et al., 1992; Holsinger & Weir, 2009), with 10,100 permutations. In addition, we calculated traditional haplotype frequency-based pairwise F_{ST} and nucleotide diversity (π) within populations. We also used DnaSP v6.12.03 (Rozas et al., 2017) to calculate d_A (Nei, 1987) to measure genetic divergence between populations, with sites containing alignment gaps excluded from this analysis. Lastly, we constructed a minimum-spanning haplotype network (Bandelt et al., 1995, 1999) in PopART (Leigh & Bryant, 2015) only comprising complete mitogenomes ($n = 49$).

To increase sample sizes and contextualize our North Atlantic mitogenomes with previous sequencing efforts in the region, we expanded our population-level analyses by downloading 329 partial mitochondrial control regions from GenBank representing *Delphinus* individuals from the North Atlantic, Mediterranean, and Black Seas (see Table S1 for accession numbers and original publications). We aligned these sequences with our SEN, WNA, and BLS mitogenomes in Geneious resulting in a 366 bp alignment, and calculated pairwise values of Φ_{ST} and F_{ST} in Arlequin with the same parameters as above with the following populations: France ($n = 6$), Ireland ($n = 22$), Canary Islands ($n = 21$), WNA ($n = 76$), Azores ($n = 100$), Madeira ($n = 52$), SEN ($n = 31$), BLS ($n = 11$), Tyrrenian Sea ($n = 5$), Alboran Sea ($n = 34$), Galicia (Spain) ($n = 30$), Portugal ($n = 17$), Ionian Sea ($n = 19$).

3 | RESULTS

3.1 | Mitogenome coverage and assembly

The number of reads that mapped to the *D. delphis* mitochondrial reference sequence ranged from 3,791 to 853,724 with mean coverage ranging from 33.5× to 12,851× (Table S6). Only three samples had mitogenome coverage below 100× (USNM 550846, 594608, 594613). All but four resulted in complete mitogenomes, with only one resulting in missing data above 1.4% (USNM 550921: 24% missing data; Table S6). Control regions of the mitogenome did not greatly differ in mean coverage from the mitogenome as a whole. Mapping target sequence capture data from McGowen et al. (2020), resulted in one complete mitogenome (D.del_SJR_ENA) and three partial mitogenomes: D. cap_79929_ENP (3,885 bp), D.cap_108471_ENP (4,672 bp), and D.del.trop_IND (2,792 bp). Partial mitogenomes derived from capture were included in phylogenetic analyses but were excluded from divergence-dating and all mitogenome-wide analyses due to large quantities of missing data.

3.2 | Phylogenetic analyses

Bayesian inference (MrBayes) and maximum likelihood (IQTree) analyses generated mitogenome trees with similar topologies (Figures 2 and S2a,b). Conflicts between methods involved closely related sequences with incredibly short branch lengths and low support values. Both Bayesian and ML trees demonstrate that long-beaked morphs (formerly *D. capensis*) do not form a clade, with or without the inclusion of long-beaked morphs from Senegal, as the ultra-long-beaked *tropicalis* individual (D.del.trop_IND) does not group with the other long-beaked samples from the eastern and western North Pacific. An approximately unbiased (AU) test in IQTree significantly rejected the monophyly of long-beaked morphs with ($p = 2.14e{-}44$) or without ($p = 1.25e{-}48$) Senegalese specimens. Nonetheless, long-beaked common dolphins in the eastern North Pacific, western North Pacific, and eastern South Pacific were recovered as monophyletic and well-supported, but nested within the total *D. delphis* clade. Known long-beaked morphs from Senegal did not group with long-beaked individuals from the Indian or Pacific Oceans.

Monophyly based on geographic origin generally was not recovered. While most SEN samples grouped in one cluster, one WNA sample was also included in this clade (D.del_571320_WNA) and other SEN samples were placed in positions throughout the tree. To rule out contamination, D.del_571320_WNA was re-extracted and resequenced with the same result. Similarly, WNA, BLS, ENA, and ENP (short-beaked) populations were all recovered as polyphyletic. In the Atlantic, approximately unbiased tests of alternate topologies were significantly rejected with $p < 0.001$. Only short-beaked WSP ($n = 2$) sequences formed a resolved monophyletic group, and no larger Pacific short-beaked clade was recovered. Peruvian mitogenomes may also be monophyletic, but this relationship was not well-supported in either Bayesian or ML trees.

3.3 | Divergence dating

The BEAST2 analysis dated the diversification of all *Delphinus* mitochondrial lineages to a mean date of ∼1.27 Mya (Figure 3). The most divergent lineage which contained mitogenomes from WNA and SEN started to diverge from other common dolphins at this time; this lineage likely contains *D. delphis tropicalis* according to ML and Bayesian analysis (Figure 2), although due to missing data, our sample was not included in the dating analysis. The Pacific long-beaked lineage diverged from other *Delphinus* ∼ 863 kya and split soon thereafter (∼737 kya) into a western Pacific and eastern Pacific clade (Figure 3). Most mitogenomes diverged after ∼641 kya with the predominantly Senegalese clade diversifying after ∼262 kya. Mitogenomes currently present in the Black Sea were found to exist ∼74.8 kya.

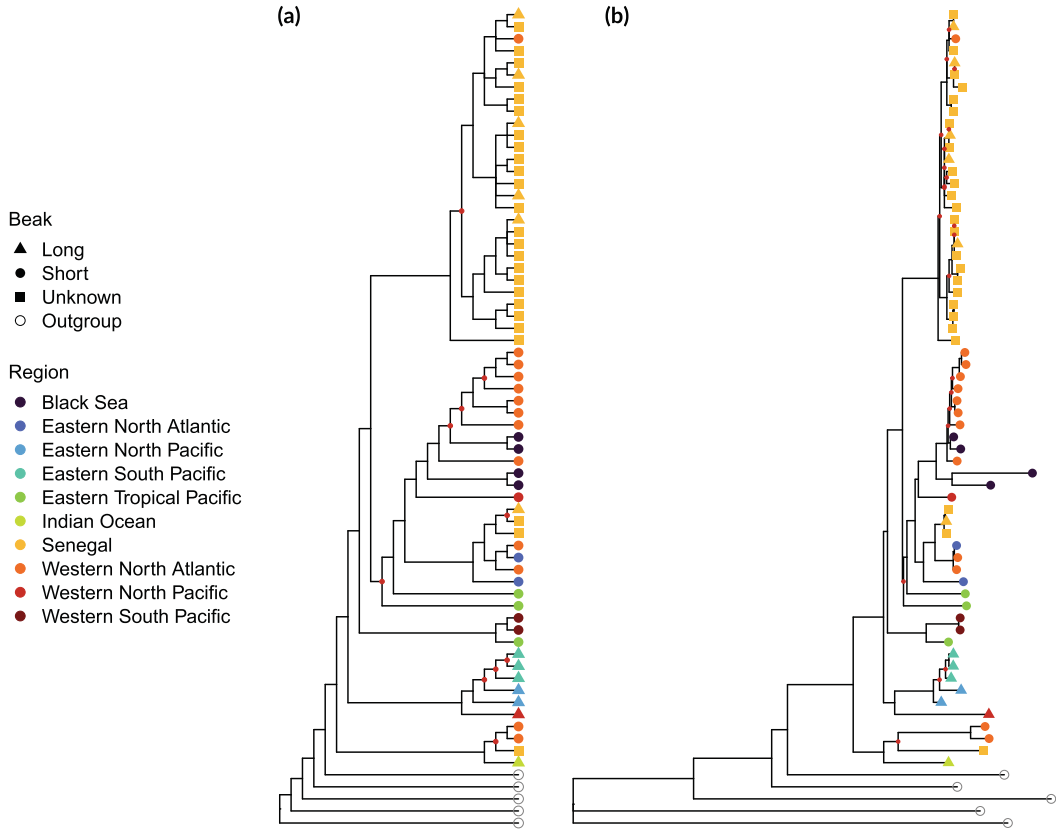

FIGURE 2 Phylogenetic trees of *Delphinus* mitogenomes and delphinid outgroups inferred with (a) Bayesian inference (MrBayes) and (b) maximum likelihood (IQTree). All unlabeled nodes are well-supported (support scores >95 for ML and posterior probability >0.95 for BI) while the nodes annotated with red dots are not supported. The supported topologies are almost identical between methods, except for differences in interpreting the incredibly short branch lengths between closely-related haplotypes in the majority-Senegal clade, which are largely collapsed into polytomies by MrBayes, but left as bifurcations with poor support in IQTree. See Figure S8 for tip labels by sample and clearer resolution between short branches.

3.4 | Population genetics and diversity

Mitochondrial haplotype diversity between and among populations was high, with no shared haplotypes among populations and only three pairs of shared haplotypes within the Senegalese population (D.del_594605_SEN and D.del_594622_SEN, D.del_594634_SEN and D.del_594635_SEN, D.del_594606_SEN and D.del_594618_SEN). A minimum-spanning haplotype network of the complete mitogenomes demonstrates this scattered, high haplotype diversity, with a similar lack of clear geographic structure as in the phylogenetic analyses (Figure S3). Many haplotypes are highly diverged from one another, with over a hundred mutations between mitogenomes within the same putative population. The haplotypes of long-beaked dolphins from the ESP cluster together and are closely related to the WNP long-beaked dolphin haplotype; however, ESP_lb haplotypes are actually closer in number of steps to some haplotypes from Senegal (D.del_605113_SEN, D.del_594628_SEN, D.del_594633_SEN; 107–122 mutations) than the WNP haplotype (126 mutations). Nucleotide diversity (π) was also generally high across all mitogenomes (0.00504) and within populations (0.00254–0.00673), except for the ESP_lb population from Peru, whose diversity (0.000652) was an order of magnitude lower than for the other five populations analyzed (Table 1, Figure S4).

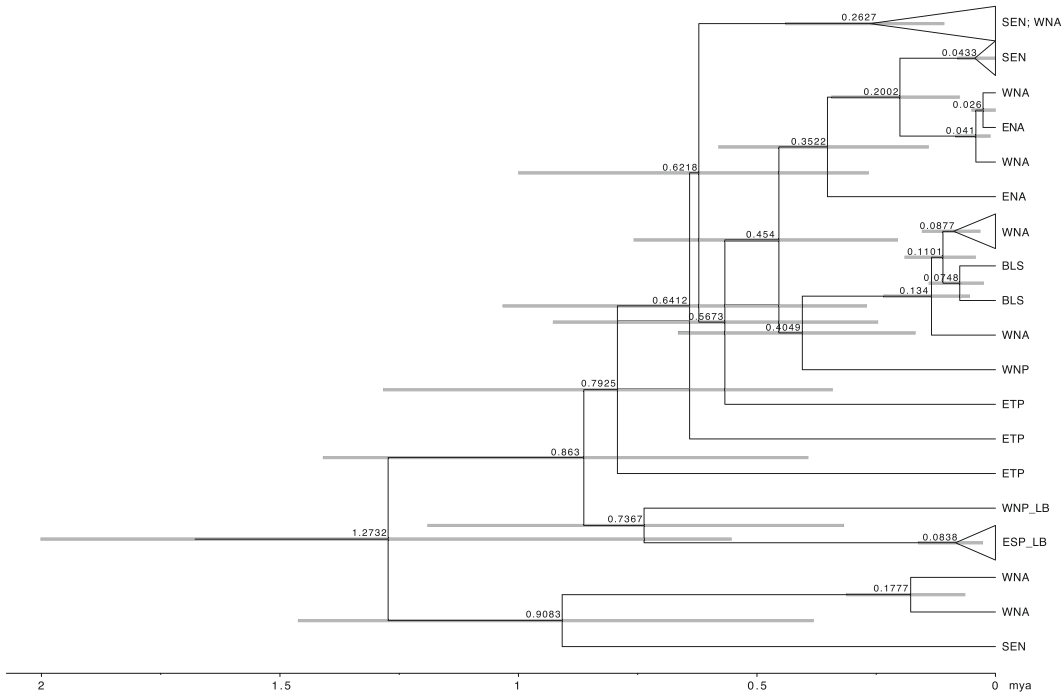

FIGURE 3 Divergence-dated Bayesian tree of *Delphinus* with some lineages collapsed, although the complete tree follows MrBayes (Figure 2a). Bars at nodes symbolize the 95% confidence intervals of dates of divergence, and numbers above each node are mean dates of divergence in millions of years ago (Mya). Scale at the bottom of the figures is in Mya. WNA = western North Atlantic, SEN = Senegal, BLS = Black Sea, ENA = eastern North Atlantic, ETP = eastern tropical Pacific, ESP_LB = eastern South Pacific (long-beaked), WNP_LB = western North Pacific (long-beaked).

TABLE 1 *Delphinus* mitogenome diversity by population.

Population	Number of polymorphic sites	Mean number of pairwise differences	Nucleotide diversity (π)
SEN ($n = 31$)	330	41.6 ± 18.6	0.00254 ± 0.00126
WNA ($n = 12$)	294	86.6 ± 40.1	0.00536 ± 0.00280
BLS ($n = 4$)	101	53.8 ± 29.7	0.00404 ± 0.00267
ENA ($n = 2$)	62	60.2 ± 42.9	0.00368 ± 0.00371
ETP_sb ($n = 3$)	170	110.2 ± 66.2	0.00673 ± 0.00504
ESP_lb ($n = 3$)	16	10.7 ± 6.7	0.000652 ± 0.000512
All ($n = 55$)	757	81.9 ± 35.8	0.00504 ± 0.00244

Note: SEN = Senegal, WNA = western North Atlantic, BLS = Black Sea, ENA = eastern North Atlantic, ETP_sb = eastern tropical Pacific (short-beaked), ESP_lb = eastern South Pacific (long-beaked).

This population also contained the fewest number of polymorphic sites and lowest mean number of pairwise differences (Table 1).

High haplotypic diversity made mitogenome haplotype-based comparisons inappropriate for investigating population structure, with pairwise F_{ST} values of 0 estimated among all measured populations. Sequence-based measurements of Φ_{ST} and Nei's d_A, by contrast, were more informative. Mitogenome divergence between SEN and WNA was moderate: $d_A = 0.00207$, (0.00208 ± 0.00095 with Jukes Cantor correction), below the species

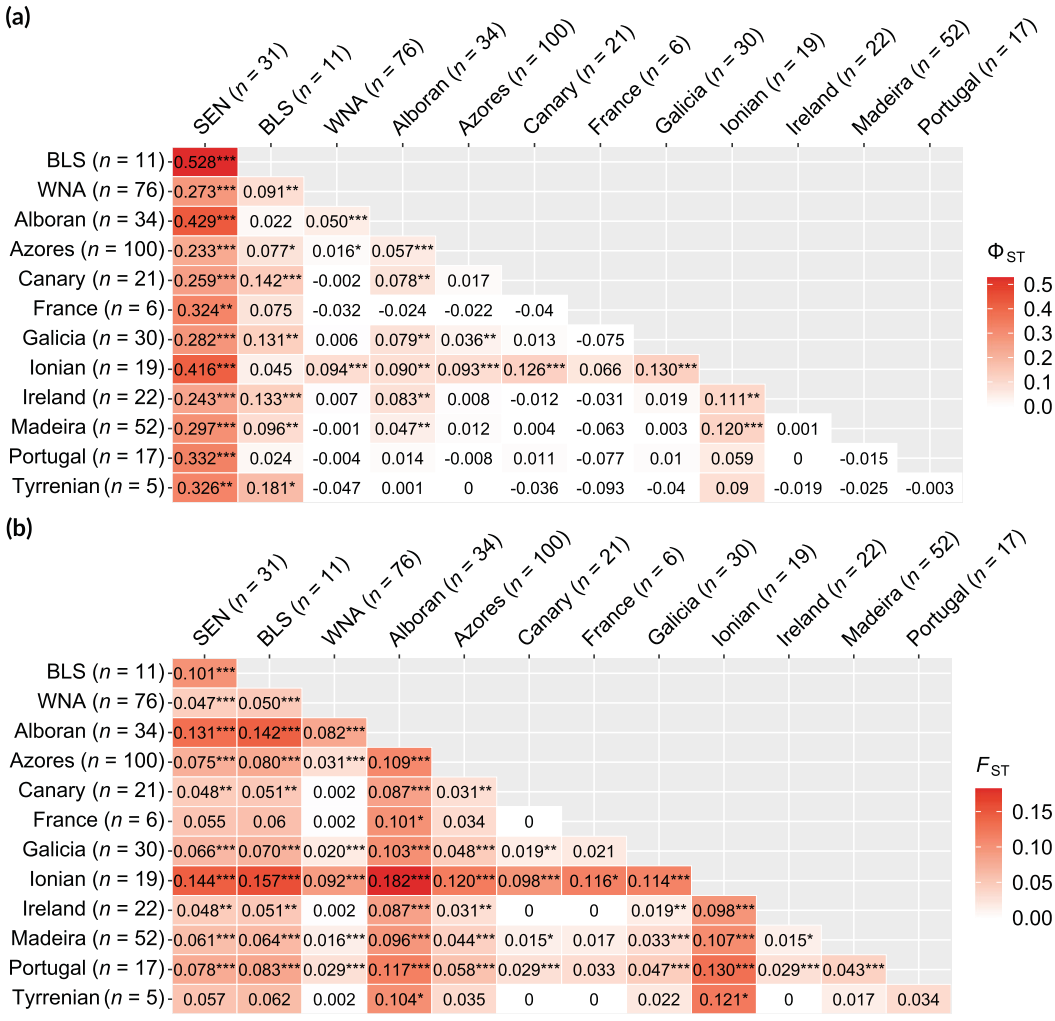

FIGURE 4 Heatmaps of pairwise population fixation indices for 366 bp partial control regions across the north Atlantic Ocean and the Mediterranean Sea incorporating previously published sequences. (a) Φ_{ST} estimated by haplotype frequency and genetic distance between haplotypes. (b) F_{ST} estimated by haplotype frequency only. $^{*}p < .05$, $^{**}p < .01$, $^{***}p < .001$. SEN = Senegal, BLS = Black Sea, WNA = Western North Atlantic.

delimitation threshold of $d_A = 0.008$ but comparable to divergence between accepted cetacean subspecies (Morin et al., 2023). Pairwise values of Φ_{ST} demonstrated that Senegalese mitogenomes are significantly differentiated from all other populations analyzed, while little differentiation exists between the other Atlantic regions (Table S7), though small and uneven sample sizes from BLS and ENA cloud this comparison. Calculations of Φ_{ST} and F_{ST} incorporating more populations and higher sample sizes from publicly available Atlantic and Mediterranean partial control region sequences (366 bp) displayed this same pattern with greater statistical power and geographic range (Figure 4a), with significant Φ_{ST} values ($p < .01$) between Senegal and other populations ranging from 0.233 to 0.528. Dolphins from the Black Sea and Mediterranean populations also exhibit significant differentiation from multiple other populations, with especially high pairwise values of F_{ST} (Figure 4). Fixation is generally lower between most Atlantic Ocean populations, though many pairwise F_{ST} estimations including Azores, Madeira, and Portugal are also significant.

Mitogenome-wide pairwise Φ_{ST} and d_A between populations suggest that long-beaked mitogenomes from Peru (ESP_lb) may also be highly differentiated from the other populations (Tables S7 and S8), but low sample size severely limits this analysis. Between short-beaked and Pacific long-beaked dolphin populations (WNA + ETP_sb + ENA vs. WNP_lb + ESP_lb), divergence was also moderate: $d_A = 0.00320$ (0.00322 ± 0.00166 with Jukes Cantor correction). Mitogenomes from Senegal were excluded from this analysis since the beak morphs of most individuals were categorized as unknown. A local comparison of ETP_sb vs. ESP_lb had high error due to low sample size, but the magnitude of the uncorrected figure of divergence was similar: $d_A = 0.00355$ (0.00357 ± 0.00295 with Jukes Cantor correction).

4 | DISCUSSION

4.1 | Systematics and taxonomy of the common dolphin

Our phylogenetic analyses show that complete mitogenomes do not support a single global long-beaked common dolphin clade (formerly identified as the species *Delphinus capensis*), with the *tropicalis* specimen from the Indian Ocean, and the Pacific and Senegalese long-beaked morphotypes scattered throughout the tree. This supports previous analyses of mitochondrial control region and cytochrome *b* data, which also uncovered the polyphyly of a long-beaked group, but in some cases with weaker support or fewer individuals (Amaral et al., 2007; Cunha et al., 2015; Farías-Curtidor et al., 2017; Gray et al., 2021; LeDuc et al., 1999; Natoli et al., 2006). Indeed, the nuclear phylogenomic analysis of McGowen et al. (2020) also did not support monophyly of long-beaked morphs, although only four individuals (three long-beaked, one short-beaked) were included in the analysis. Together, these results add further support refuting the hypothesis that a longer rostrum is evidence of global common ancestry in *Delphinus*.

Nonetheless, the few Pacific long-beaked dolphins (ENP, ESP, WNP) included in this study form a well-supported monophyletic group nested within the rest of *Delphinus*. The distinctiveness of ENP long-beaked dolphins, currently identified as *D. delphis bairdii*, is well established by morphological and molecular data (Banks & Brownell, 1969; Cunha et al., 2015; Gray et al., 2021; Heyning & Perrin, 1994; Kingston & Rosel, 2004; Nicolosi & Loy, 2021; Rosel et al., 1994; Segura-García et al., 2016). We did not infer any support for a close relationship between long-beaked samples in the ENP/ESP and short-beaked common dolphins collected from the eastern tropical Pacific, which supports other analyses of genetic isolation between these morphs in the eastern Pacific (Rosel et al., 1994; Segura-García et al., 2016), although our sample size is admittedly small. Furthermore, the long-beaked WNP dolphin from China (D.cap_NC012061_WNP) did not group with the short-beaked dolphin from South Korea in closer geographic proximity (D.del_MH000365_WNP). While high genetic variation within geographic populations could be a contributing factor, these results suggest ESP long-beaked dolphins could possibly be members of the same long-beaked ENP lineage, and that establishing the full range of *D. delphis bairdii* requires further investigation. Wider sampling of *Delphinus* throughout the Pacific can provide a clearer picture of how long-beaked members of *Delphinus* are related to one another and to short-beaked morphs in the Pacific Ocean.

Despite finding a monophyletic long-beaked clade in the Pacific, our phylogenetic analyses show that Pacific long-beaked dolphins are not reciprocally monophyletic with the rest of *Delphinus*. Researchers have explained the paraphyly of *D. delphis* with respect to the ENP long-beaked clade as an artifact of introgression and incomplete lineage sorting (LeDuc et al., 1999), or as a signal of incipient speciation (Kingston et al., 2009; Natoli et al., 2006). Observations show that long- and short-beaked dolphins in the ENP reside in different habitats (coastal versus offshore) and have distinct reproductive periods that may restrict gene flow (Chivers et al., 2016). Especially in sympatric populations, these traits are compelling evidence of speciation, but our limited number of mitogenomes do not shed further light on this open question. Global studies of *Delphinus* using nuclear data such as RADseq or whole genome sequencing along with morphological analysis will likely be needed to confirm the level of gene flow between morphotypes in the Pacific Ocean and investigate the taxonomic status of this distinct lineage. Recent and upcoming studies by a subset of authors from the current

paper will further elucidate the taxonomic status of the eastern Pacific long-beaked common dolphin (Jefferson et al., 2024; Urrutia-Osorio et al., 2024).

Our only sample of the ultra-long-beaked *D. d. tropicalis* was included in the most divergent lineage of *Delphinus*, grouping with three samples from the North Atlantic: two short-beaked WNA morphs and one an unknown morph from Senegal (Figure 2). A similar clade joining *tropicalis* and North Atlantic individuals from Scotland and the Iberian Peninsula was also recovered by Amaral et al. (2007) using cytochrome *b*, which they termed "Clade X". McGowen et al. (2020) found the same *D. d. tropicalis* individual to group with a North Atlantic short-beaked common dolphin using nuclear exonic data, although the mitogenome of that individual (D.del_SJR_ENA) does not seem to be closely related (Figure 2, Table S6). Recent microsatellite and control region data for a substantial number of *D. d. tropicalis* from Oman and Pakistan found significant differentiation in these populations from other common dolphins analyzed (Gray et al., 2021). Again, more nuclear data on a genomic scale will be needed to resolve the status of *tropicalis* within the wider worldwide *Delphinus* group, and decipher the origins of the enigmatic Clade X.

The factors potentially driving evolution of ecomorphs in *Delphinus* are complex and not fully understood. Different feeding habits are a possible functional explanation (Bell et al., 2002; Murphy et al., 2006; Natoli et al., 2006; Pinela et al., 2011; Westgate, 2007), and may also explain the distinctiveness and high variability of skull characters in the Mediterranean (Nicolosi & Loy, 2021). Even exclusively in short-beaked forms, global morphometric analysis has suggested parallel north-to-south evolutionary trends across the Atlantic and Pacific Oceans, with different sets of characters leading to similarly larger, compact skulls in the north and slender rostra in southern stocks (Nicolosi & Loy, 2021). In addition to acknowledging feeding ecology, Nicholosi & Loy (2021) connected this geographic convergence to Bergman's rule based on their sampling localities, suggesting that temperature is another factor shaping *Delphinus* skull morphology. Long-beaked dolphins are also generally restricted to coastal waters while short-beaked dolphins span pelagic ranges (Perrin, 2018), so differential habitat use and relative isolation may also contribute to repeated differentiation. Offshore and coastal ecotypes are hardly unique to *Delphinus*; coastal and pelagic forms of *Tursiops* show considerable genetic and morphometric differentiation in the Atlantic (Costa et al., 2021, 2022; Fruet et al., 2017; Louis et al., 2014). *Stenella longirostris* and *S. attenuata* also show ecomorphological differentiation (Leslie & Morin, 2018; Perrin, 1975, 1998). Coastal western Atlantic *Tursiops*, including both *Tursiops erebennus* and *Tursiops truncatus gephyreus*, exhibit a lower level of genetic diversity than their pelagic counterparts, *Tursiops truncatus truncatus* (Costa et al., 2021; Fruet et al., 2017; Louis et al., 2014), suggesting recent founder events in WNA and WSA coastal *Tursiops* (Costa et al., 2021; Louis et al., 2014). This is an interesting parallel to the long-beaked *Delphinus* from the ESP, which have a much lower nucleotide diversity than all other populations analyzed. However, in Atlantic/Mediterranean *Delphinus*, differential habitat use is not as clear, since ecological niche modeling shows that coastal waters are critical habitat even for short-beaked dolphins (Correia et al., 2019; Giménez et al., 2018; Paradell et al., 2019). Comparable data for West Africa are less complete, but *Delphinus* habitat models predict more coastal habitat in southern Europe/North African waters (Correia et al., 2019) while predicting offshore habitat suitability in Namibia (De Rock et al., 2019), making connections between morphotype and habitat use in Senegal even more difficult to infer.

Our phylogenetic analyses also found that the Black Sea endemic *D. delphis ponticus*, an endangered subspecies with distinct coloration, is polyphyletic and nests within western North Atlantic samples. However, these samples represent the ancient DNA sequences downloaded from GenBank and two of these sequences (MF669495.1, MF669497.1) showed poorer quality compared with many of the modern samples analyzed, also explaining their longer branch lengths in the maximum likelihood tree (Figure 2b). Recent analyses of modern *D. delphis* mitochondrial control regions in the Atlantic, Mediterranean, and Black Sea have also found that these populations share haplotypes, suggesting recent connectivity across these bodies of water (Gray et al., 2021; Tonay et al., 2020). This is in contrast with the two other cetacean species that inhabit the Black Sea, the harbor porpoise (*Phocoena phocoena*) and the common bottlenose dolphin, which both show evidence of isolation and/or differentiation (Ben Chehida et al., 2020; Fontaine et al., 2014; Moura et al., 2020; Viaud-Martinez et al., 2008), albeit the harbor porpoise's absence in the Mediterranean differs from both dolphins' continuous distribution.

Lastly, the relationship between short- and long-beaked common dolphins in Senegal requires further investigation. Senegal is an appropriate setting for studying the evolution of short- and long-beaked morphs, as both types have been documented (Van Waerebeek, 1997; Van Waerebeek et al., 2000). However, the definition of these two morphotypes were based on measurements of individuals from California and may not correlate well with individuals in other regions, which may have been a factor in our inability to precisely identify many of our stranded dolphins as categorically short- or long-beaked (in addition to the challenges of recovering many degraded and juvenile individuals). In Angola, the external appearance of *Delphinus* is intermediate, rather than distinctively short- or long-beaked (Weir, 2011; Weir & Coles, 2007), and Pinela et al. (2011) found it difficult to differentiate between morphs using morphometrics and stable isotopes in Mauritania. It may be that morphotypes in West Africa do not reflect distinct genetic lineages. Many of our samples were of unknown morphotype, but those identified as the long-beaked morph did not form a monophyletic group (Figure 2), although the existence of a primarily Senegalese clade indicates that differentiation may be ongoing. Distinct grouping of long- and short-beaked morphs using the original criteria of Heyning and Perrin (1994) does not hold in many other regions with or without hypothesized beak morphs (Amaha, 1994; Bell et al., 2002; Cunha et al., 2015; Esteves & Oviedo, 2007; Murphy et al., 2006; Ngqulana et al., 2019; Pinela et al., 2011; Tavares et al., 2010), and global comprehensive morphometrics studies of adult specimens along with genetic analysis of the same individuals are necessary to address whether short- and long-beaked morphs in the same region form genetically distinctive groups.

4.2 | Population structure and diversity

Based on our analysis of complete *Delphinus* mitogenomes, Senegal contains a genetically differentiated population. However, haplotypes in this population are not monophyletic and demonstrate potential connectivity throughout the Atlantic Ocean and beyond. Most sequences from Senegal grouped in one large clade which started to diversify ~263 kya, although this group also included one sequence from the western North Atlantic (Figure 3). Furthermore, topologies show other Senegalese mitogenomes spread out across the *Delphinus* tree: three in a separate nested monophyletic group with WNA and ENA sequences and another Senegalese sequence in the most divergent cluster, Clade X (Figure 2). WNA, ENA, and BLS also did not form monophyletic groups, with AU tests evaluating the likelihood of geographic clades significantly rejected. Though phylogeny does not strictly mirror geography for Senegalese dolphins, pairwise Φ_{ST} and F_{ST} calculations nonetheless indicate that this is a significantly distinct population from each of the other *Delphinus* groups across the North Atlantic (Figure 4). The differentiation of isolated Black Sea and Mediterranean populations is well-established, and their high haplotype frequency-derived F_{ST} values reflect comparatively recent isolation, while significant Φ_{ST} values incorporating genetic distance between Senegal and other populations may suggest longer-term evolutionary divergence. In contrast, haplotype fixation between populations from the Atlantic Ocean was lower in magnitude or nonsignificant. These results are further supported by our mitogenome phylogenies and previous research, in which even significant genetic structure detected across the North Atlantic was minimal (Mirimin et al., 2009; Moura et al., 2013; Natoli et al., 2008), except for comparisons using sequence data from another West African locality, Mauritania (Natoli et al., 2006). Interestingly, Mirimin et al. (2009) found significant structure in females, but not males, and by most metrics in mtDNA but not nuclear microsatellite data. Amaral et al. (2007) also discovered differentiation among populations off western Europe only when males and females were analyzed separately. Our analyses were restricted to the mitochondrial genome, and many sequences originated from highly decomposed and/or juvenile stranded dolphins, thereby making sexing and similar downstream comparisons difficult in many specimens. Further genome-wide analysis may be useful in testing this sex-biased dispersal and inferring how it has contributed to genetic structure across the Atlantic Ocean. Short-beaked *Delphinus delphis*, especially in the Atlantic Ocean, are highly mobile and pelagic with a high potential for long-distance dispersal (Natoli et al., 2006). This feature offers a possible explanation for the WNA sequence found within our otherwise Senegalese clade. Additional factors, like the large population sizes of

Delphinus (Perrin, 2018), relatively high genetic diversity, and historic or ongoing gene flow also likely contribute to the lack of geographically determined clades in our phylogenetic trees. Indeed, overall nucleotide diversity (π) in common dolphin mitogenomes analyzed here (0.00504) is greater than in most other delphinids as measured by Louis et al. (2020). It is closest to both *S. attenuata* (>0.0055) and *S. longirostris* ($\sim$0.005), both global species with distinct morphotypes and large population sizes.

The lack of population structure in *Delphinus* across the eastern and western North Atlantic is not replicated in other areas of the dolphin's range. In fact, fine scale genetic structure is present in Australasia (Barceló et al., 2021; Möller et al., 2011), the Indian Ocean (Gray et al., 2021) and the Mediterranean/Black Sea (Natoli et al., 2008; Tonay et al., 2020)—although in the Australasian and Indian Ocean, this has been detected using nuclear derived data such as RADseq and microsatellites. Intrinsic factors such as different social structures and habitat preference, as well as extrinsic factors such as habitat fragmentation, could contribute to these differences in genetic structure globally (Mirimin et al., 2009). Prey availability also likely influences *Delphinus* genetic structure, with long-distance dispersal playing a key role for dolphins relying on prey with unreliable distributions, while they show more local fidelity when prey resources are predictable (Jefferson et al., 2009; Mason et al., 2016). In Senegal, long-beaked dolphins are more common than the short-beaked morphs (Cadenat et al., 1959; Van Waerebeek, 1997; Van Waerebeek et al., 2000), and we could not reliably identify any of the stranded individuals as short-beaked. Since long-beaked morphs tend to be more coastal and may disperse less than short-beaked dolphins, this difference in habitat usage between Senegalese and other Atlantic dolphins may be responsible for keeping North Atlantic ranges large and indistinct, while dolphins from coastal Senegal are on average more restricted and differentiated. Confusingly, while genetic data show that long-beaked morphs in Mauritania are also highly distinct from other global short-beaked populations (Natoli et al., 2006), stable isotope data of both morphs in Mauritania indicate that long-beaked morphs may be the ones feeding offshore more than short-beaked dolphins, or at least that they are preying on higher trophic levels (Pinela et al., 2011). Further research in West Africa could disentangle these puzzling results and may be very fruitful for understanding the broader interplay between niche segregation, local morphological adaptation, and genetic differentiation in *Delphinus* without the confounding factors of taxonomy found in the Pacific.

Due to small sample sizes, we cannot readily infer genetic structure in the eastern Pacific, though short-beaked dolphins from the ETP did exhibit less differentiation from Atlantic populations than did long-beaked dolphins from the ESP (Tables S7 and S8). Better understanding the drivers of population structure in *Delphinus* and how they intersect with taxonomic structure will require more robust examination of dolphins across *Delphinus*'s extensive global range. Global and local signatures of differentiation also have conservation applications; high dispersal may be more essential in some regions than others and preserving connectivity may enhance conservation outcomes for threatened/endangered populations of *Delphinus*, such as in the Mediterranean and Black Seas (Tonay et al., 2020).

4.3 | Conclusions

Novel mitochondrial data demonstrate that many *Delphinus* from Senegal comprise a genetically distinct group and that the Senegalese population is substantially differentiated from other North Atlantic *Delphinus* populations, an otherwise panmictic region. Neither mitogenomes of long-beaked dolphins in the Pacific, nor the ultra-long-beaked *D. d. tropicalis*, are closely related to long-beaked morphs in Senegal, strengthening the hypothesis that long beaks have independently evolved in populations of coastal-dwelling *Delphinus* around the globe. In the Pacific, long-beaked dolphins from California, Peru, and China (the latter based on only a single specimen) appear to form a nested monophyletic group, warranting deeper investigation into long-beaked dolphin relationships across the Pacific Ocean. In the future, genome-wide coverage may clarify *Delphinus* population connectivity and demographic history in these regions, and further paired genomic and morphometric analysis may elucidate the recurring evolution of the long-beaked morphotype.

ACKNOWLEDGMENTS

This study was supported by the Natural History Research Experience undergraduate intern program at NMNH, where MAB was an intern in Summer 2019. We would like to thank Chris Huddleston, Daniel DiMichele, John Ososky, Dietrich Gotzek, and Tom Sargent (NMNH), as well as Tomas Diagne (African Aquatic Conservation Fund) and Ellen Potter in assisting with collection of samples in Senegal. All Senegal specimens were legally imported into the United States using MMPA permit #20523 issued to Smithsonian National Museum of Natural History and Senegalese CITES export permits #1083 and #1189. All NMNH laboratory work was conducted in and with the support of the Laboratories of Analytical Biology (https://ror.org/05b8c0r92) of the NMNH. We thank Kelly Robertson for conducting all laboratory work at SWFSC. Funding for this study was provided by NMNH start-up funds to MRM. Additional thanks to Gene Hunt and Virginia Power for coordinating the NHRE program and to NSF for their NHRE sponsorship of MAB (OCE-1560088). We thank Jesús Maldonado as well as five anonymous reviewers for providing feedback on earlier versions of the manuscript.

AUTHOR CONTRIBUTIONS

Madeleine A. Becker: Formal analysis; visualization; writing – original draft; writing – review and editing. **Katherine R. Murphy:** Investigation; writing – original draft; writing – review and editing. **Frederick I. Archer:** Conceptualization; investigation; resources; writing – review and editing. **Thomas A. Jefferson:** Conceptualization; resources; writing – review and editing. **Lucy W. Keith-Diagne:** Conceptualization; funding acquisition; investigation; resources; writing – review and editing. **Charles W. Potter:** Investigation; resources; writing – review and editing. **M. Fernanda Urrutia-Osorio:** Resources; writing – review and editing. **Ibrahima Ndong:** Investigation; resources; writing – review and editing. **Michael R. McGowen:** Conceptualization; formal analysis; funding acquisition; investigation; resources; visualization; writing – original draft; writing – review and editing.

ORCID

Madeleine A. Becker https://orcid.org/0000-0003-2051-2911
Frederick I. Archer https://orcid.org/0000-0002-3179-4769
Thomas A. Jefferson https://orcid.org/0000-0001-6817-2747
Michael R. McGowen https://orcid.org/0000-0001-9192-3166

REFERENCES

Alexander, A., Steel, D., Slikas, B., Hoekzema, K., Carraher, C., Parks, M., Cronn, R., & Baker, C. S. (2013). Low diversity in the mitogenome of sperm whales revealed by next-generation sequencing. *Genome Biology and Evolution*, *5*(1), 113–129. https://doi.org/10.1093/gbe/evs126

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., Boutov, D., Freitas, L., Robertson, K. M., Sequeira, M., Stockin, K. A., Coelho, M. M., & Möller, L. M. (2012a). Seascape genetics of a globally distributed, highly mobile marine mammal: the short-beaked common dolphin (genus *Delphinus*). *PLoS ONE*, *7*(2), e31482. https://doi.org/10.1371/journal.pone.0031482

Amaral, A. R., Beheregaray, L. B., Bilgmann, K., Freitas, L., Robertson, K. M., Sequeira, M., Stockin, K. A., Coelho, M. M., & Möller, L. M. (2012b). 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

Amaral, A. R., Sequeira, M., Martínez-Cedeira, J., & Coelho, M. M. (2007). New insights on population genetic structure of *Delphinus delphis* from the northeast Atlantic and phylogenetic relationships within the genus inferred from two mitochondrial markers. *Marine Biology*, *151*(5), 1967–1976. https://doi.org/10.1007/s00227-007-0635-y

Andrews, S. (2010). *FastQC: a quality control tool for high throughput sequence data*. Babraham Bioinformatics, Babraham Institute, Cambridge, UK.

Archer, F. I., Morin, P. A., Hancock-Hanser, B. L., Robertson, K. M., Leslie, M. S., Bérubé, M., Panigada, S., & Taylor, B. L. (2013). Mitogenomic phylogenetics of fin whales (*Balaenoptera physalus* spp.): genetic evidence for revision of subspecies. *PLoS ONE*, *8*(5), e63396. https://doi.org/10.1371/journal.pone.0063396

Ball, L., Shreves, K., Pilot, M., & Moura, A. E. (2017). Temporal and geographic patterns of kinship structure in common dolphins (*Delphinus delphis*) suggest site fidelity and female-biased long-distance dispersal. *Behavioral Ecology and Sociobiology*, *71*(8), Article 123. https://doi.org/10.1007/s00265-017-2351-z

Bandelt, H.-J., Forster, P., & Röhl, A. (1999). Median-joining networks for inferring intraspecific phylogenies. *Molecular Biology and Evolution*, *16*(1), 37–48.

Bandelt, H.-J., Forster, P., Sykes, B. C., & Richards, M. B. (1995). Mitochondrial portraits of human populations using median networks. *Genetics*, *141*(2), 743–753.

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

Barceló, A., Sandoval-Castillo, J., Stockin, K. A., Bilgmann, K., Attard, C. R. M., Zanardo, N., Parra, G. J., Hupman, K., Reeves, I. M., Betty, E. L., Tezanos-Pinto, G., Beheregaray, L. B., & Möller, L. M. (2021). A matter of scale: population genomic structure and connectivity of fisheries at-risk common dolphins (*Delphinus delphis*) from Australasia. *Frontiers in Marine Science*, *8*, Article 616673. https://doi.org/10.3389/fmars.2021.616673

Bell, C., Kemper, C., & Conran, J. (2002). Common dolphins (*Delphinus delphis*) In southern Australia: a morphometric study. *Australian Mammalogy*, *24*, 1–10. https://doi.org/10.1071/AM02001

Ben Chehida, Y., Thumloup, J., Schumacher, C., Harkins, T., Aguilar, A., Borrell, A., Ferreira, M., Rojas-Bracho, L., Robertson, K. M., Taylor, B. L., Víkingsson, G. A., Weyna, A., Romiguier, J., Morin, P. A., & Fontaine, M. C. (2020). Mitochondrial genomics reveals the evolutionary history of the porpoises (Phocoenidae) across the speciation continuum. *Scientific Reports*, *10*(1), Article 15190. https://doi.org/10.1038/s41598-020-71603-9

Bianucci, G. (2013). *Septidelphis morii*, n. gen. et sp., from the Pliocene of Italy: new evidence of the explosive radiation of true dolphins (Odontoceti, Delphinidae). *Journal of Vertebrate Paleontology*, *33*(3), 722–740. https://doi.org/10.1080/02724634.2013.744757

Biard, V., Gol'Din, P., Gladilina, E., Vishnyakova, K., McGrath, K., Vieira, F. G., Wales, N., Fontaine, M. C., Speller, C., & Olsen, M. T. (2017). Genomic and proteomic identification of Late Holocene remains: Setting baselines for Black Sea odontocetes. *Journal of Archaeological Science: Reports*, *15*, 262–271. https://doi.org/10.1016/j.jasrep.2017.07.008

Bolger, A. M., Lohse, M., & Usadel, B. (2014). Trimmomatic: a flexible trimmer for Illumina sequence data. *Bioinformatics*, *30*(15), 2114–2120. https://doi.org/10.1093/bioinformatics/btu170

Bouckaert, R., Vaughan, T. G., Barido-Sottani, J., Duchêne, S., Fourment, M., Gavryushkina, A., Heled, J., Jones, G., Kühnert, D., De Maio, N., Matschiner, M., Mendes, F. K., Müller, N. F., Ogilvie, H. A., du Plessis, L., Popinga, A., Rambaut, A., Rasmussen, D., Siveroni, I., … Drummond, A. J. (2019). BEAST 2.5: An advanced software platform for Bayesian evolutionary analysis. *PLoS Computational Biology*, *15*(4), e1006650. https://doi.org/10.1371/journal.pcbi.1006650

Cadenat, J., Doutre, M., & Paraiso, F. (1959). Notes sur les Delphinidés ouest-africains (Notes on West African Delphinidae). *Bulletin de l'Institut Français d'Afrique Noire A*, *21*, 410–415.

Chernomor, O., von Haeseler, A., & Minh, B. Q. (2016). Terrace aware data structure for phylogenomic inference from supermatrices. *Systematic Biology*, *65*(6), 997–1008. https://doi.org/10.1093/sysbio/syw037

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

Committee on Taxonomy. (2023). *List of marine mammal species and subspecies*. Society for Marine Mammalogy.

Correia, A. M., Gil, Á., Valente, R., Rosso, M., Pierce, G. J., & Sousa-Pinto, I. (2019). Distribution and habitat modelling of common dolphins (Delphinus delphis) in the eastern North Atlantic. *Journal of the Marine Biological Association of the United Kingdom*, *99*(06), 1443–1457. https://doi.org/10.1017/S0025315419000249

Correia, A. M., Gil, Á., Valente, R. F., Rosso, M., Sousa Pinto, I., & Pierce, G. J. (2020). Distribution of cetacean species at a large scale - Connecting continents with the Macaronesian archipelagos in the eastern North Atlantic. *Diversity and Distributions*, *26*(10), 1234–1247. https://doi.org/10.1111/ddi.13127

Costa, A. P. B., Fruet, P. F., Secchi, E. R., Daura Jorge, F. G., Simões Lopes, P. C., Di Tullio, J. C., & Rosel, P. E. (2021). Ecological divergence and speciation in common bottlenose dolphins in the western South Atlantic. *Journal of Evolutionary Biology*, *34*(1), 16–32. https://doi.org/10.1111/jeb.13575

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 Linnean Society*, zlac025. 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., & Solé-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

De Rock, P., Elwen, S., Roux, J., Leeney, R., James, B., Visser, V., Martin, M., & Gridley, T. (2019). Predicting large-scale habitat suitability for cetaceans off Namibia using MinxEnt. *Marine Ecology Progress Series*, *619*, 149–167. https://doi.org/10.3354/meps12934

Esteves, M., & Oviedo, L. (2007). A potential morphotype of common dolphin (*Delphinus* spp.) on the northeast coast of Venezuela. *Aquatic Mammals*, *33*, 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.

Ewels, P., Magnusson, M., Lundin, S., & Käller, M. (2016). MultiQC: summarize analysis results for multiple tools and samples in a single report. *Bioinformatics*, *32*(19), 3047–3048. https://doi.org/10.1093/bioinformatics/btw354

Excoffier, L., & Lischer, H. E. L. (2010). Arlequin suite ver 3.5: a new series of programs to perform population genetics analyses under Linux and Windows. *Molecular Ecology Resources*, *10*(3), 564–567. https://doi.org/10.1111/j.1755-0998.2010.02847.x

Excoffier, L., Smouse, P. E., & Quattro, J. M. (1992). Analysis of molecular variance inferred from metric distances among DNA haplotypes: application to human mitochondrial DNA restriction data. *Genetics*, *131*(2), 479–491.

Farías-Curtidor, N., Barragán-Barrera, D. C., Chávez-Carreño, P. A., Jiménez-Pinedo, C., Palacios, D. M., Caicedo, D., Trujillo, F., & Caballero, S. (2017). Range extension for the common dolphin (*Delphinus* sp.) to the Colombian Caribbean, with taxonomic implications from genetic barcoding and phylogenetic analyses. *PLoS ONE*, *12*(2), e0171000. https://doi.org/10.1371/journal.pone.0171000

Fontaine, M. C., Roland, K., Calves, I., Austerlitz, F., Palstra, F. P., Tolley, K. A., Ryan, S., Ferreira, M., Jauniaux, T., & Llavona, A. (2014). Postglacial climate changes and rise of three ecotypes of harbour porpoises, *Phocoena phocoena*, in western Palearctic waters. *Molecular Ecology*, *23*(13), 3306–3321.

Fruet, P. F., Secchi, E. R., Di Tullio, J. C., Simões-Lopes, P. C., Daura-Jorge, F., Costa, A. P. B., Vermeulen, E., Flores, P. A. C., Genoves, R. C., Laporta, P., Beheregaray, L. B., & Möller, L. M. (2017). Genetic divergence between two phenotypically distinct bottlenose dolphin ecotypes suggests separate evolutionary trajectories. *Ecology and Evolution*, *7*(21), 9131–9143. https://doi.org/10.1002/ece3.3335

Geisler, J. H., McGowen, M. R., Yang, G., & Gatesy, J. (2011). A supermatrix analysis of genomic, morphological, and paleontological data from crown Cetacea. *BMC Evolutionary Biology*, *11*(1), Article 112. https://doi.org/10.1186/1471-2148-11-112

Giménez, J., Cañadas, A., Ramírez, F., Afán, I., García-Tiscar, S., Fernández-Maldonado, C., Castillo, J. J., & de Stephanis, R. (2018). Living apart together: Niche partitioning among Alboran Sea cetaceans. *Ecological Indicators*, *95*, 32–40. https://doi.org/10.1016/j.ecolind.2018.07.020

Gray, H. W. I., Chen, I., Moura, A. E., Natoli, A., Nishida, S., Tanabe, S., Minton, G., Ponnampalam, L. S., Kiani, M. S., Culloch, R., Gore, M., Särnblad, A., Amir, O., Berggren, P., Collins, T., Willson, A. J., Baldwin, R., & Hoelzel, A. R. (2021). Comparative biogeography and the evolution of population structure for bottlenose and common dolphins in the Indian Ocean. *Journal of Biogeography*, *48*(7), 1654–1668. https://doi.org/10.1111/jbi.14102

Hancock-Hanser, B. L., Frey, A., Leslie, M. S., Dutton, P. H., Archer, F. I., & Morin, P. A. (2013). Targeted multiplex next-generation sequencing: advances in techniques of mitochondrial and nuclear DNA sequencing for population genomics. *Molecular Ecology Resources*, *13*(2), 254–268. https://doi.org/10.1111/1755-0998.12059

Heyning, J. E., & Perrin, W. F. (1994). Two forms of common dolphins (genus *Delphinus*) from the eastern North Pacific: evidence for two species. *Contributions in Science*, *442*, 1–35.

Hoang, D. T., Chernomor, O., von Haeseler, A., Minh, B. Q., & Vinh, L. S. (2018). UFBoot2: Improving the ultrafast bootstrap approximation. *Molecular Biology and Evolution*, *35*(2), 518–522. https://doi.org/10.1093/molbev/msx281

Holsinger, K. E., & Weir, B. S. (2009). Genetics in geographically structured populations: defining, estimating and interpreting FST. *Nature Reviews Genetics*, *10*(9), 639–650. https://doi.org/10.1038/nrg2611

Jefferson, T. A., Archer, F. I., & Robertson, K. M. (2024). The long beaked common dolphin of the eastern Pacific Ocean: Taxonomic status and redescription of *Delphinus bairdii*. *Marine Mammal Science*, e13133. https://doi.org/10.1111/mms.13133

Jefferson, T. A., Fertl, D., Bolaños-Jiménez, 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

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., Webber, M. A., & Pitman, R. L. (2015). Cetaceans. In T. A. Jefferson, M. A. Webber, & R. L. Pitman (Eds.), *Marine mammals of the world* (Second ed., pp. 24–357). https://doi.org/10.1016/B978-0-12-409542-7.50004-4

Jordan, F. F. (2012). *Skull morphometry of the common dolphin,* Delphinus *sp., from New Zealand waters* [Doctoral dissertation]. Massey University.

Kalyaanamoorthy, S., Minh, B. Q., Wong, T. K. F., von Haeseler, A., & Jermiin, L. S. (2017). ModelFinder: fast model selection for accurate phylogenetic estimates. *Nature Methods*, *14*(6), 587–589. https://doi.org/10.1038/nmeth.4285

Katoh, K., & Standley, D. M. (2013). MAFFT multiple sequence alignment software version 7: improvements in performance and usability. *Molecular Biology and Evolution*, *30*(4), 772–780. https://doi.org/10.1093/molbev/mst010

Kingston, S. E., Adams, L. D., & Rosel, P. E. (2009). Testing mitochondrial sequences and anonymous nuclear markers for phylogeny reconstruction in a rapidly radiating group: molecular systematics of the Delphininae (Cetacea: Odontoceti: Delphinidae). *BMC Evolutionary Biology*, *9*(1), 245. https://doi.org/10.1186/1471-2148-9-245

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

Kircher, M., Sawyer, S., & Meyer, M. (2012). Double indexing overcomes inaccuracies in multiplex sequencing on the Illumina platform. *Nucleic Acids Research*, *40*(1), e3–e3. https://doi.org/10.1093/nar/gkr771

Lanfear, R., Calcott, B., Ho, S. Y. W., & Guindon, S. (2012). PartitionFinder: Combined selection of partitioning schemes and substitution models for phylogenetic analyses. *Molecular Biology and Evolution*, *29*(6), 1695–1701. https://doi.org/10.1093/molbev/mss020

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

Lee, K., Lee, J., Cho, Y., Kim, H. W., Park, K. J., Sohn, H., Choi, Y.-M., Kim, H. K., Jeong, D. G., & Kim, J. H. (2019). First report of the complete mitochondrial genome and phylogenetic analysis of Fraser's dolphin *Lagenodelphis hosei* (Cetacea: Delphinidae). *Conservation Genetics Resources*, *11*(1), 47–50. https://doi.org/10.1007/s12686-017-0964-1

Lee, K., Lee, J., Cho, Y., Sohn, H., Choi, Y.-M., Lim, S. R., Kim, H. K., Yoon, S.-W., Jeong, D. G., & Kim, J. H. (2018). Characterization of the complete mitochondrial genome and phylogenetic analysis of the common dolphin *Delphinus delphis* (Cetacea: Delphinidae). *Mitochondrial DNA Part B*, *3*(2), 632–633. https://doi.org/10.1080/23802359.2018.1473720

Leigh, J. W., & Bryant, D. (2015). popart: full-feature software for haplotype network construction. *Methods in Ecology and Evolution*, *6*(9), 1110–1116. https://doi.org/10.1111/2041-210X.12410

Leslie, M. S., & Morin, P. A. (2018). Structure and phylogeography of two tropical predators, spinner (*Stenella longirostris*) and pantropical spotted (*S. attenuata*) dolphins, from SNP data. *Royal Society Open Science*, *5*(4), 171615. https://doi.org/10.1098/rsos.171615

Lischer, H. E. L., & Excoffier, L. (2012). PGDSpider: an automated data conversion tool for connecting population genetics and genomics programs. *Bioinformatics*, *28*(2), 298–299. https://doi.org/10.1093/bioinformatics/btr642

Louis, M., Skovrind, M., Samaniego Castruita, J. A., Garilao, C., Kaschner, K., Gopalakrishnan, S., Haile, J. S., Lydersen, C., Kovacs, K. M., Garde, E., Heide-Jørgensen, M. P., Postma, L., Ferguson, S. H., Willerslev, E., & Lorenzen, E. D. (2020). Influence of past climate change on phylogeography and demographic history of narwhals, *Monodon monoceros*. *Proceedings of the Royal Society B: Biological Sciences*, *287*(1925), Article 20192964. https://doi.org/10.1098/rspb.2019.2964

Louis, M., Viricel, A., Lucas, T., Peltier, H., Alfonsi, E., Berrow, S., Brownlow, A., Covelo, P., Dabin, W., Deaville, R., de Stephanis, R., Gally, F., Gauffier, P., Penrose, R., Silva, M. A., Guinet, C., & Simon-Bouhet, B. (2014). Habitat-driven population structure of bottlenose dolphins, *Tursiops truncatus*, in the North-East Atlantic. *Molecular Ecology*, *23*(4), 857–874. https://doi.org/10.1111/mec.12653

Mason, S., Salgado Kent, C., Donnelly, D., Weir, J., & Bilgmann, K. (2016). Atypical residency of short-beaked common dolphins (*Delphinus delphis*) to a shallow, urbanized embayment in south-eastern Australia. *Royal Society Open Science*, *3*(9), Article 160478. https://doi.org/10.1098/rsos.160478

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, M. A., Pfeiffer, W., & Schwartz, T. (2011). The CIPRES science gateway: a community resource for phylogenetic analyses. *Proceedings of the 2011 TeraGrid Conference: Extreme Digital Discovery*.

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), 1215–1215. https://doi.org/10.1093/nar/16.3.1215

Minh, B. Q., Schmidt, H. A., Chernomor, O., Schrempf, D., Woodhams, M. D., von Haeseler, A., & Lanfear, R. (2020). IQ-TREE 2: New models and efficient methods for phylogenetic inference in the genomic era. *Molecular Biology and Evolution*, *37*(5), 1530–1534. https://doi.org/10.1093/molbev/msaa015

Mirimin, L., Westgate, A., Rogan, E., Rosel, P., Read, A., Coughlan, J., & Cross, T. (2009). Population structure of short-beaked common dolphins (*Delphinus delphis*) in the North Atlantic Ocean as revealed by mitochondrial and nuclear genetic markers. *Marine Biology*, *156*(5), 821–834. https://doi.org/10.1007/s00227-008-1120-y

Möller, L., Valdez, F. P., 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

Morin, P. A., Archer, F. I., Foote, A. D., Vilstrup, J., Allen, E. E., Wade, P., Durban, J., Parsons, K., Pitman, R., Li, L., Bouffard, P., Abel Nielsen, S. C., Rasmussen, M., Willerslev, E., Gilbert, M. T. P., & Harkins, T. (2010). Complete mitochondrial genome phylogeographic analysis of killer whales (*Orcinus orca*) indicates multiple species. *Genome Research*, *20*(7), 908–916. https://doi.org/10.1101/gr.102954.109

Morin, P. A., Martien, K. K., Lang, A. R., Hancock-Hanser, B. L., Pease, V. L., Robertson, K. M., Sattler, M., Slikas, E., Rosel, P. E., Baker, C. S., Taylor, B. L., & Archer, F. I. (2023). Guidelines and quantitative standards for improved cetacean taxonomy using full mitochondrial genomes. *Journal of Heredity*, *114*(6), 612–624. https://doi.org/10.1093/jhered/esad049

Moura, A. E., Natoli, A., Rogan, E., & Hoelzel, A. R. (2013). Atypical panmixia in a European dolphin species (*Delphinus delphis*): implications for the evolution of diversity across oceanic boundaries. *Journal of Evolutionary Biology*, *26*(1), 63–75. https://doi.org/10.1111/jeb.12032

Moura, A. E., Shreves, K., Pilot, M., Andrews, K. R., Moore, D. M., Kishida, T., Möller, L., Natoli, A., Gaspari, S., McGowen, M., Chen, I., Gray, H., Gore, M., Culloch, R. M., Kiani, M. S., Willson, M. S., Bulushi, A., Collins, T., Baldwin, R., … Hoelzel, A. R. (2020). Phylogenomics of the genus Tursiops and closely related Delphininae reveals extensive reticulation among lineages and provides inference about eco-evolutionary drivers. *Molecular Phylogenetics and Evolution*, *146*, Article 106756. https://doi.org/10.1016/j.ympev.2020.106756

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*(3), 943–954. https://doi.org/10.1111/j.1420-9101.2005.01033.x

Natoli, A., Cañadas, A., Vaquero, C., Politi, E., Fernandez-Navarro, P., & Hoelzel, A. R. (2008). Conservation genetics of the short-beaked common dolphin (*Delphinus delphis*) in the Mediterranean Sea and in the eastern North Atlantic Ocean. *Conservation Genetics*, *9*(6), 1479–1487. https://doi.org/10.1007/s10592-007-9481-1

Nei, M. (1987). *Molecular evolutionary genetics*. Columbia University Press.

Ngqulana, S., Plön, S., Galatius, A., Pistorius, P., & Hofmeyr, 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. (2021). 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

Paradell, O. G., López, B. D., & Methion, S. (2019). Modelling common dolphin (*Delphinus delphis*) coastal distribution and habitat use: Insights for conservation. *Ocean & Coastal Management*, *179*, Article 104836. https://doi.org/10.1016/j.ocecoaman.2019.104836

Perrin, W. F. (1975). Variation of spotted and spinner porpoise (genus *Stenella*) in the eastern Pacific and Hawaii. *Bulletin of the Scripps Institution of Oceanography*, *21*.

Perrin, W. F. (1998). Stenella longirostris. *Mammalian Species*, *599*, 1–7.

Perrin, W. F. (2018). Common dolphin: *Delphinus delphis*. In B. Würsig, J. G. M. Thewissen, & K. M. Kovacs (Eds.), *Encyclopedia of marine mammals* (Third ed., pp. 205–209). Academic Press. https://doi.org/10.1016/B978-0-12-804327-1.00095-9

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

Quérouil, S., Freitas, L., Cascão, I., Alves, F., Dinis, A., Almeida, J. R., Prieto, R., Borràs, S., Matos, J. A., & Mendonça, D. (2010). Molecular insight into the population structure of common and spotted dolphins inhabiting the pelagic waters of the Northeast Atlantic. *Marine Biology*, *157*, 2567–2580. https://doi.org/10.1007/s00227-010-1519-0

R Core Team. (2021). *R: a language and environment for statistical computing* (Version 4.0.5) [Computer software]. R Foundation for Statistical Computing.

Rice, D. W. (1998). *Marine mammals of the world: Systematics and distribution*. Special Publication Number 4, Society for Marine Mammalogy.

Ronquist, F., & Huelsenbeck, J. P. (2003). MrBayes 3: Bayesian phylogenetic inference under mixed models. *Bioinformatics*, *19*(12), 1572–1574. https://doi.org/10.1093/bioinformatics/btg180

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

Rozas, J., Ferrer-Mata, A., Sánchez-DelBarrio, J. C., Guirao-Rico, S., Librado, P., Ramos-Onsins, S. E., & Sánchez-Gracia, A. (2017). DnaSP 6: DNA sequence polymorphism analysis of large data sets. *Molecular Biology and Evolution*, *34*(12), 3299–3302. https://doi.org/10.1093/molbev/msx248

Samaai, T., Best, P., & Gibbons, M. (2005). The taxonomic status of common dolphins *Delphinus* spp. in South African waters. *African Journal of Marine Science*, *27*(2), 449–458. https://doi.org/10.2989/18142320509504103

Segura-García, I., Gallo, J. P., Chivers, S., Díaz-Gamboa, R., & Hoelzel, A. R. (2016). Post-glacial habitat release and incipient speciation in the genus *Delphinus*. *Heredity*, *117*(6), 400–407. https://doi.org/10.1038/hdy.2016.66

Shimodaira, H. (2002). An approximately unbiased test of phylogenetic tree selection. *Systematic Biology*, *51*(3), 492–508. https://doi.org/10.1080/10635150290069913

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

Tamura, K., & Nei, M. (1993). Estimation of the number of nucleotide substitutions in the control region of mitochondrial DNA in humans and chimpanzees. *Molecular Biology and Evolution*, *10*, 512–526. https://doi.org/10.1093/oxfordjournals.molbev.a040023

Tavares, M., Moreno, I. B., Siciliano, S., Rodríguez, D., De O. Santos, M. C., Lailson-brito, J., Jr., & Fabián, M. E. (2010). Biogeography of common dolphins (genus *Delphinus*) in the Southwestern Atlantic Ocean. *Mammal Review*, *40*(1), 40–64. https://doi.org/10.1111/j.1365-2907.2009.00154.x

Tonay, A. M., Uzun, B., Dede, A., Amaha Öztürk, A., Danyer, E., Aytemiz Danyer, I., Bilgin, S., Öztürk, B., & Bilgin, R. (2020). Population genetic structure of the short-beaked common dolphin from the Black Sea and the Turkish Straits System. *Mitochondrial DNA Part A*, *31*(6), 257–264. https://doi.org/10.1080/24701394.2020.1788008

Urrutia-Osorio M. F., Jefferson T. A., Morin P. A., Hancock-Hanser B. L., McGowen M. R., Becker M. A., and Archer F. I. (2024) *Phylogenetic relationships among eastern Pacific common dolphins* (Delphinus *spp*.) [Manuscript in preparation]. Scripps Institute of Oceanography.

van Bree, P. J. H. (1971). *Delphinus tropicalis*, a new name for *Delphinus longirostris* G. Cuvier, 1829. *Mammalia*, *35*, 345–346.

van Bree, P. J. H., & Gallagher, M. D. (1978). On the taxonomic status of *Delphinus tropicalis* van Bree, 1971 (Notes on Cetacea, Delphinoidea IX). *Beaufortia*, *28*(342), 1–8.

Van Waerebeek, K. (1997). *Long-beaked and short-beaked common dolphins sympatric off central-west Africa*. Report SC/49/SM46 to the Scientific Committee of the Internation Whaling Commission.

Van Waerebeek, K., Ndiaye, E., Djiba, A., & Diallo, M. (2000). *A survey of the conservation status of cetaceans in Senegal, the Gambia and Guinea-Bissau WAFCET-I Report*. Convention on the Conservation of Migratory Species of Wild Animals. UNEP/CMS Secretariat, Bonn, Germany.

Viaud-Martinez, K. A., Brownell, R. L., Komnenou, A., & Bohonak, A. J. (2008). Genetic isolation and morphological divergence of Black Sea bottlenose dolphins. *Biological Conservation*, *141*(6), 1600–1611. https://doi.org/10.1016/j.biocon.2008.04.004

Viricel, A., Pante, E., Dabin, W., & Simon-Bouhet, B. (2014). Applicability of RAD-tag genotyping for interfamilial comparisons: empirical data from two cetaceans. *Molecular Ecology Resources*, *14*(3), 597–605. https://doi.org/10.1111/1755-0998.12206

Weir, C. R. (2011). *Ecology and conservation of cetaceans in the waters between Angola and the Gulf of Guinea, with focus on the Atlantic humpback dolphin* (Sousa teuszii) [Dictoral dissertation]. University of Aberdeen.

Weir, C. R., & Coles, P. (2007). Morphology of common dolphins (*Delphinus* spp.) photographed off Angola. *17th Biennial Conference of the Society for Marine Mammalogy*, Cape Town, South Africa.

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

Wilson, L. E. (1973). A delphinid (Mammalia, Cetacea) from the Miocene of Palos Verdes Hills, California. *University of California Publications in Geological Sciences*, *103*, 1–34.

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*, 20. https://doi.org/10.1186/1471-2148-9-20

Yu, G., Smith, D. K., Zhu, H., Guan, Y., & Lam, T. T. (2017). GGTREE: an R package for visualization and annotation of phylogenetic trees with their covariates and other associated data. *Methods in Ecology and Evolution*, *8*(1), 28–36. https://doi.org/10.1111/2041-210X.12628

SUPPORTING INFORMATION

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

How to cite this article: 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. (2024). 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*, *40*(4), e13144. https://doi.org/10.1111/mms.13144