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Eastern North Atlantic Strandings Validate Genetic Patterns in Pygmy and Dwarf Sperm Whales (Kogiidae)

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ABSTRACT

Pygmy (*Kogia breviceps*) and dwarf (*Kogia sima*) sperm whales are among the least studied cetaceans due to their elusive behavior and low detectability at sea. Molecular approaches are therefore essential to clarify their taxonomy, population structure, and conservation status. We present new mitochondrial DNA data from stranded *K. breviceps* and *K. sima* specimens collected across the eastern North Atlantic, a region previously not represented in genetic studies. We analyzed fragments of the mitochondrial cytochrome *b* gene and control region from 56 individuals and integrated these data with publicly available sequences to place regional diversity within a global phylogeographic framework. Population genetics, phylogenetics, and haplotype network analyses showed a weak or absent population structure in *K. breviceps* across its range, whereas *K. sima* was consistently separated into Atlantic–Mediterranean and Indo-Pacific lineages, characterized by high genetic divergence. Eastern North Atlantic samples clustered within the Atlantic lineage and showed moderate genetic diversity, with a few locality-specific haplotypes identified. Overall, our results expand the genetic baseline for Kogiidae species in the eastern North Atlantic and support previous evidence of cryptic diversity within *K. sima*. Despite observational limitations, the relatively high genetic diversity observed in the two species provides cautiously optimistic indications of population health in this elusive cetacean family.

1 | Introduction

Despite their ecological importance and evolutionary distinctiveness, many cetacean species remain poorly known. The pygmy sperm whale, *Kogia breviceps* (de Blainville 1838), and the dwarf sperm whale, *Kogia sima* (Owen 1866), are among the least understood, with limited information available on their biology, ecology, and conservation (McAlpine 2009). Historically, a single species (*K. breviceps*) was recognized by most authors and included in the sperm whale family (Physeteridae), until morphological and genetic evidence confirmed the presence of two distinct species (Handley 1966; Ross 1979; Chivers et al. 2005), now ascribed to the family Kogiidae (Gill 1871).

The two species share many morphological features, including an overall appearance, a small-medium size, and the characteristic

'false gill' located posterior to the eyes (Best 2007). However, they also exhibit some consistent differences in their skull bones, lower jaw dental formula, total body length, and size, shape, and position of the dorsal fin (Handley 1966; McAlpine 2009). Based on the analysis of their gut content, kogiid species show an overall dietary overlap, mostly consisting of cephalopods but also of fish and crustaceans (Wang et al. 2002; Staudinger et al. 2014; Matsuda et al. 2023). However, some differences in terms of prey composition, abundance, and size can be observed, and these may reflect different niches occupied by the two species (e.g., Wang et al. 2002). Little is known about the ecology of kogiids, but *K. breviceps* may have a more offshore distribution and may feed in deeper water than *K. sima* (Willis and Baird 1998). This, together with the morphological differences in the jaw, may lead to the selection of different prey items and therefore reduce niche overlap.

Both species are characterized by cryptic and elusive behavior, and therefore rarely observed at sea. When at the surface, they are visible just in calm sea conditions. If approached by boats they tend to dive for a long time, and when they feel threatened they can release a red-brownish gastrointestinal fluid (Willis and Baird 1998; Covelo and López 2021; Dávila et al. 2026). Additionally, both species seem to be solitary or occurring in small groups of varying age and sex (McAlpine 2009). All these characteristics make *Kogia* species difficult to sight and identify in the field and, therefore, most of the available knowledge on the species comes from post-mortem examinations of stranded animals, with the exception of a few sites around the world (e.g., MacLeod et al. 2004; Baird 2005; Baird et al. 2022).

Kogia species are protected under several international frameworks, as summarized by Maio et al. (2017), and they are assessed as 'Least Concern' by the IUCN Red List, even if the available information on both species is limited and the population trends are unknown, especially for the European populations, which are currently listed as 'data deficient'. Therefore, additional information is required, especially from the understudied localities in which they are known to occur, in order to comprehensively assess their conservation status.

Both species are considered cosmopolitan, occurring from temperate to tropical waters, even though *K. sima* seems to prefer warmer regions (Moura et al. 2016; Plön and Baird 2022). Direct sightings of the species are only reported from Hawaii (Baird 2005; Baird et al. 2022), the Canary Islands (Martín et al. 2024), the Azores (Benak et al. 2025), the Caribbean Sea (Dunphy-Daly et al. 2008; Kiszka et al. 2024), and the Gulf of Mexico (Baumgartner et al. 2001). Strandings, instead, demonstrate a broad distribution across the Atlantic, Indian, and Pacific Oceans (McAlpine 2009). Recently, environmental DNA has also proven effective in detecting *Kogia* species, allowing the detection of *K. breviceps* in multiple water samples collected in the western Mediterranean (Valsecchi et al. 2026).

Given their elusive nature and the difficulties of identifying stranded individuals morphologically, molecular approaches have become essential for species identification and for population studies. Genetic analyses confirmed the presence of at least two species of *Kogia* (Chivers et al. 2005) and revealed contrasting patterns of population structure between them. Specifically, *K. breviceps* showed no evidence of population structure based on mitochondrial cytochrome *b* gene (*cytb*) and control region (CR) markers (Chivers et al. 2005; Nishida et al. 2023; Plön et al. 2023). In contrast, *K. sima* was separated into two well-defined genetic lineages, one from the Atlantic and Mediterranean regions and the other from the Indo-Pacific (Chivers et al. 2005; Nishida et al. 2023; Plön et al. 2023; Maio et al. 2024). These findings led to the hypothesis that the two populations may represent different species (Chivers et al. 2005).

In this context, the eastern North Atlantic remains one of the least studied regions from a genetic perspective, despite numerous historical records of strandings. These records come from several countries, including Ireland, the Netherlands, France, Spain, Portugal, and Scotland (Berrow and Rogan 1997; Fraser 1974; Duguy 1966; Duguy and Budker 1972; Penas-Patiño and Piñeiro-Seage 1989; Sequeira et al. 1992, 1996; Santos et al. 2006). The aim of our study was to analyze new genetic data from specimens stranded along Scotland, France, Portugal, the continental coasts of Spain and the Canary Islands. This allowed us to assess the local genetic diversity in the eastern North Atlantic region and to place these new data within the global phylogeographic context of both *Kogia* species.

2 | Material and Methods

2.1 | Sampling, DNA Extraction and Sequencing

A total of 56 tissue samples of *Kogia* spp. (50 *K. breviceps*, including 27 males, 22 females, and 1 un-sexed fetus; 6 *K. sima*, including 4 males and 2 females) were obtained from strandings that occurred in the eastern North Atlantic, namely the Canary Islands ($n = 19$), Portugal ($n = 10$), France ($n = 10$), Scotland ($n = 4$), and continental Spain ($n = 13$) (Figure 1; Table S1). All samples were obtained from animals stranded between 1995 and 2024. Tissue samples were preserved in different ways, including 70% ethanol ($n = 14$), 98% ethanol ($n = 26$), 96% ethanol ($n = 13$), and 20% DMSO saturated with NaCl ($n = 3$). All samples were obtained from skin and/or muscle tissue.

Total genomic DNA (gDNA) was extracted using the DNeasy Blood and Tissue Kit (Qiagen, Hilden, Germany) or the Euroclone spinNAker Universal Genomic DNA kit (Euroclone, Milan, Italy). Prior to extraction, samples were incubated with 20 μL proteinase K (20 mg/mL) at 56°C for 2–3 h or overnight, depending on their state of preservation; tougher, desiccated samples received extended incubation to ensure complete lysis. Samples stored in DMSO were rinsed and soaked in Milli-Q water for 2 h before overnight lysis with proteinase K.

A fragment of the mitochondrial cytochrome *b* gene (*cytb*) and the mitochondrial control region (CR) were amplified from the gDNA by polymerase chain reaction (PCR). The *cytb* region was amplified using primers slightly modified from Kocher et al. (1989) and Martin and Palumbi (1993),

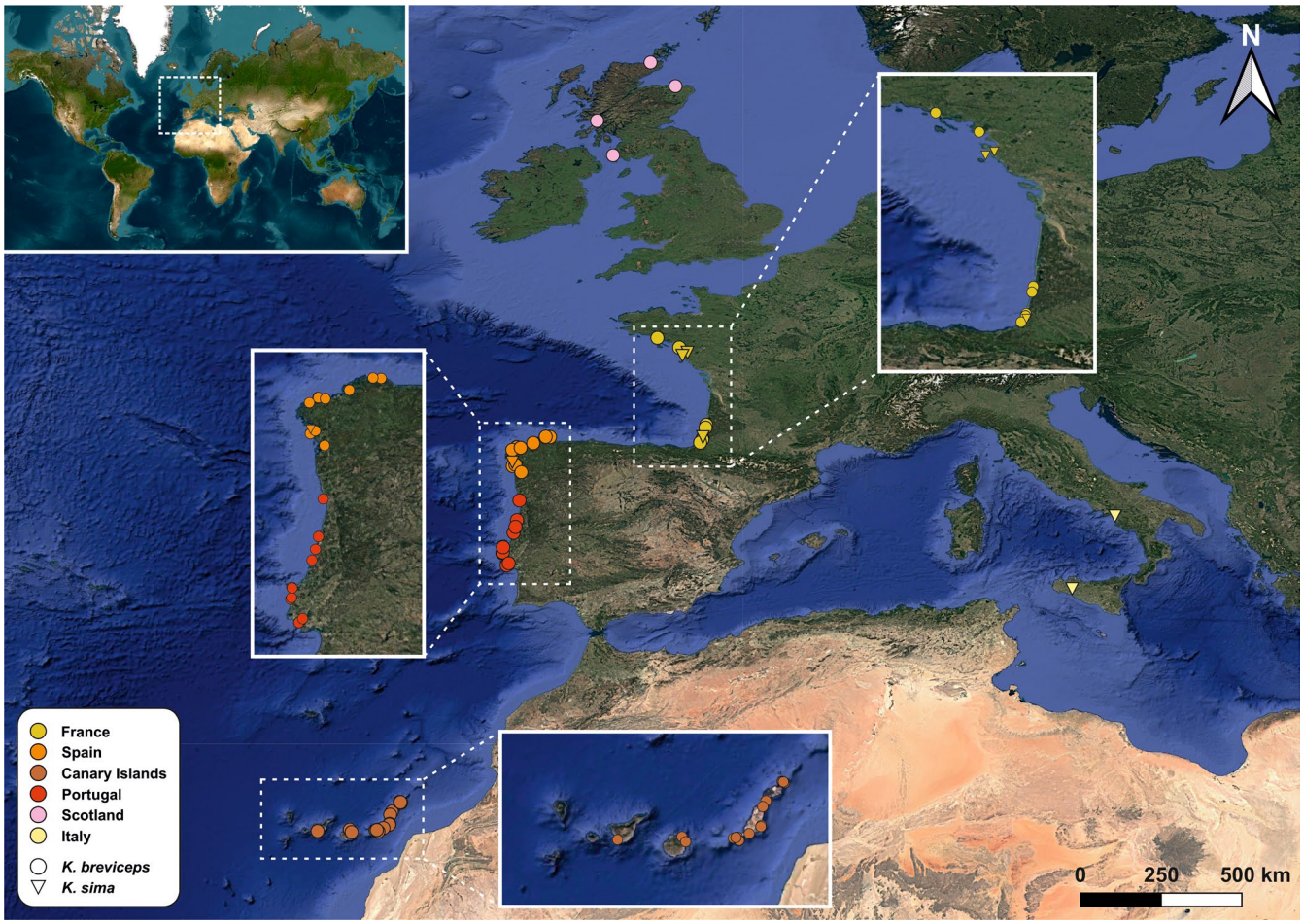

FIGURE 1 | Map of stranding localities, colored by country, for both newly sequenced eastern North Atlantic specimens and the Mediterranean sequences mined from GenBank (yellow). Circles and triangles represent strandings of *K breviceps* and of *K. sima*, respectively.

namely K-CytB2F (5′-CAGAATGATATTTGGCCTCA-3′) and K-CytB1R (5′-TGACTTGAAAAATCATCGTTG-3′). The CR region was amplified using the primer H16343 (5′-CCTGAAGTAAGAACCAGATG-3′) from Rosel et al. (1994) and the primer L15812 (5′-CCTCCCTAAGACTCAAGG-3′) from Chivers et al. (2005). Each PCR was performed in a volume of 25 μL using the Wonder Taq kit (Euroclone, Milan, Italy), and included 1.5 units of Wonder Taq polymerase, 1X Wonder Taq reaction buffer (containing 1 mM dNTPs and 3 mM $MgCl_2$), 0.4 μM of each primer, 16.2 μL of Milli-Q water, and 2.5 μL of DNA template. PCR cycles consisted of an initial denaturation for 3 min at 95°C, 40 cycles of denaturation (30 s at 96°C), annealing (30 s at 52.5°C for *K. breviceps* and 30 s at 47.5°C for *K. sima*), extension (30 s at 72°C for *K. breviceps* and 45 s at 72°C for *K. sima*), and a final extension at 72°C for 5 min.

Amplification products were verified by 1% agarose gel electrophoresis and sent to Macrogen Europe (Milan, Italy), where they were purified and Sanger-sequenced in both directions using the amplification primers on an ABI 3730xl DNA Analyzer (Applied Biosystems, Waltham, MA, USA). The chromatograms were visually checked and assembled using Geneious Prime (Biomatters, Auckland, New Zealand), and *cytb* sequences were translated to check for the presence of stop codons. Sequences were deposited in GenBank with the accession numbers PX692166–PX692267.

2.2 | Data Analysis

The sequences were compared with those deposited in NCBI GenBank using BLAST, to assess the species identity of the specimens and to check for possible contamination. All the available *cytb* and CR sequences for *Kogia* species were downloaded from NCBI GenBank, along with original sampling metadata (Table S2). Country-level sampling information was used when available, otherwise broader locality categories were assigned (i.e., Atlantic, western North Atlantic, and Indo-Pacific) and sequences without geographical information were removed from the datasets. For *K. breviceps,* sequences were overall retrieved from Australia (*cytb*: 18; CR: 4), Indonesia (CR: 1), Japan (CR: 30), New Caledonia (*cytb*: 2), New Zealand (*cytb*: 42; CR: 36), Peru (*cytb*: 1), South Africa (*cytb*: 29; CR: 3) and from the more general areas western North Atlantic (*cytb*: 8; CR: 73), Atlantic (*cytb*: 18; CR: 4), and Indo-Pacific (*cytb*: 16; CR: 32). For *K. sima*, sequences were retrieved from Australia (*cytb*: 3; CR: 3), Chile (*cytb*: 1), China (*cytb*: 1; CR; 1), India (*cytb*: 1), Italy (*cytb*: 3; CR: 2), Japan (CR: 37); New Caledonia (CR: 4), South Africa (*cytb*: 26; CR: 1), Thailand (CR: 2), and from the more general areas

western North Atlantic (*cytb*: 6; CR: 26), Atlantic (*cytb*: 5), and Indo-Pacific (*cytb*: 15; CR: 13).

For each molecular marker, the retrieved sequences were aligned to those obtained in this study using MAFFT 7.110 (Katoh and Standley 2013) with the E-INS-i option, and each alignment was visually checked and trimmed at both ends.

DnaSP 6 (Rozas et al. 2017) was used to infer genetic diversity indices, including % of variable sites, number of haplotypes, haplotype diversity, and nucleotide diversity. Specifically, for each species and molecular marker, indices were calculated for the entire species, at the ocean level (Atlantic and Indo-Pacific), at the eastern North Atlantic level, and, when more than one sequence was available, at a finer geographic scale (country of collection).

The presence of intra-specific population structure for each species and molecular marker was assessed with analysis of molecular variance (AMOVA) and pairwise Φ_{ST} statistics between pairs of localities. For *K. breviceps*, localities represented by fewer than five sequences were excluded, as were sequences lacking precise geographic information (i.e., those that could only be assigned to the Atlantic or Indo-Pacific regions). The remaining sequences were then grouped by locality and oceanic region (Atlantic and Indo-Pacific). For *K. sima*, most localities were represented by only a few sequences. Therefore, population structure was assessed only at the broader scale of oceanic region, by comparing Atlantic and Indo-Pacific sequences. AMOVAs and Φ_{ST} statistics were computed in Arlequin v. 3.5.2.2 (Excoffier and Lischer 2010) using Kimura 2-Parameter (K2P; Kimura 1980) distances, which account for different rates of transitions and transversions, 9999 permutations, and a significance level of 0.01. For comparison, also pairwise F_{ST} statistics were computed in Arlequin with 9999 permutations and a significance level of 0.01.

The *cytb* and CR alignments were then used to generate median-joining haplotype networks in PopART 1.7 (Leigh et al. 2015) for each species using default settings.

Midpoint-rooted maximum likelihood phylogeny reconstructions were inferred using RAxML 8.2.12 (Stamatakis 2014), after collapsing sequences into unique haplotypes. Substitution models were determined with ModelTest-NG (Darriba et al. 2020), resulting in the HKY + G model for *cytb* and the HKY + G + I model for CR, and node support was assessed with 1000 non-parametric rapid bootstrap replicates.

Finally, intra- and inter-specific K2P genetic distances were calculated for each species and molecular marker, as well as between Atlantic and Indo-Pacific clades of *K. sima*, using MEGA v11.0.1 (Tamura et al. 2021) with 1000 bootstrap replicates. Additionally, Nei's d_A was calculated between species and populations.

3 | Results

A total of 53 new sequences were obtained for *cytb* (49 *K. breviceps* and 4 *K. sima*) and 48 new sequences for CR (44 *K. breviceps* and 4 *K. sima*) (Table S1). Five samples allowed us to obtain only *cytb* sequences, whereas three samples preserved in DMSO or EtOH did not yield sequences for either the *cytb* or CR. All other samples were successfully sequenced at both regions. These new sequences resulted in 14 *cytb* and 34 CR haplotypes for *K. breviceps* and in 3 *cytb* and 4 CR haplotypes for *K. sima*. Including both publicly available GenBank sequences and sequences

TABLE 1 | Genetic diversity indices of *Kogia* species based on *cytb* and CR datasets, including number of sequences (*n*), percentage of variable sites (% Sv), number of haplotypes (H), haplotype diversity (*h*), and nucleotide diversity (π).

	cytb					CR				
	n	**% Sv**	**H**	***h***	π	***n***	**% Sv**	**H**	***h***	π
K. breviceps										
Total	184	14.2	52	0.884 ± 0.016	0.00578 ± 0.00032	224	19.0	144	0.993 ± 0.002	0.01628 ± 0.00045
Indo-Pacific	111	9.8	33	0.889 ± 0.020	0.00550 ± 0.00036	103	13.0	70	0.987 ± 0.004	0.01530 ± 0.00061
Atlantic	75	8.1	27	0.863 ± 0.029	0.00599 ± 0.00057	121	15.3	84	0.989 ± 0.003	0.01613 ± 0.00063
EN Atlantic	49	5.1	14	0.798 ± 0.043	0.00507 ± 0.00070	44	10.1	34	0.981 ± 0.010	0.01500 ± 0.00100
K. sima										
Total	65	11.4	24	0.841 ± 0.042	0.03251 ± 0.00364	93	18.8	66	0.990 ± 0.004	0.04328 ± 0.00176
Indo-Pacific	47	5.0	15	0.714 ± 0.073	0.00389 ± 0.00062	61	11.6	43	0.986 ± 0.005	0.01584 ± 0.00111
Atlantic	18	2.3	9	0.863 ± 0.054	0.00726 ± 0.00065	32	7.2	23	0.962 ± 0.022	0.01068 ± 0.00164
EN Atlantic	7	1.3	3	0.714 ± 0.107	0.00669 ± 0.00130	6	0.8	4	0.800 ± 0.161	0.00278 ± 0.00084

Note: The eastern North Atlantic group (EN Atlantic) is a subset of the 'Atlantic' group.

generated in this study, the final alignment of *cytb* sequences was 302 bp long and included 184 sequences for *K. breviceps* and 65 sequences for *K. sima*, while the final alignment of CR sequences was 361 bp long and included 224 sequences for *K. breviceps* and 93 sequences for *K. sima*.

The 184 *cytb* and 224 CR *K. breviceps* sequences resolved into 52 and 144 haplotypes, respectively, whereas the 65 *cytb* and 93 CR *K. sima* sequences resolved into 24 and 66 haplotypes, respectively (Table 1). Haplotype and nucleotide diversity indices indicated that both species are characterized by a relatively high intraspecific diversity (Table 1). These indices varied among localities for both genetic markers and species (Table 1, Table S3), but clear locality-specific patterns could not be assessed, mostly due to variable sample sizes (Table S3) and to the lack of precise geographic information for several sequences. Nucleotide and haplotype diversity were overall higher for CR datasets compared to *cytb* datasets (Table 1). Total haplotype diversity was comparable between species, and lowest values were found when considering eastern North Atlantic sequences alone. Regarding nucleotide diversity indices, the total *K. sima* dataset showed values six to three times higher than *K. breviceps* for *cytb* and CR, respectively (Table 1), likely reflecting the presence of a second cryptic subspecies or species within the *K. sima* group (i.e., Chivers et al. 2005). However, when *K. sima* was considered as subdivided into its Atlantic and Indo-Pacific groups, the nucleotide diversity values were comparable to those of *K. breviceps*. Regarding eastern North Atlantic samples, nucleotide diversity for *K. breviceps* was consistent with other localities, whereas for *K. sima* the nucleotide diversity of the CR dataset was much lower than for other groups (Table 1).

AMOVAs revealed that for *K. breviceps* (*cytb*) most of the genetic variation was found within localities (97.83%), with low and non-significant variation among oceans and among localities ($\Phi_{ST}=0.0217$, $p=0.088$) (Table 2a). For *K. breviceps* (CR), variation was also mainly within localities (94.02%), with a small but significant overall structure ($\Phi_{ST}=0.0598$, $p<0.01$) (Table 2b). In contrast, *K. sima* showed strong genetic structure, with most of the variation occurring among oceans (93.86% for *cytb* and 82.23% for CR), and highly significant differentiation (*cytb*: $\Phi_{ST}=0.9386$, $p<0.0$; CR: $\Phi_{ST}=0.8223$, $p<0.01$) (Table 2c,d). Pairwise Φ_{ST} and F_{ST} for *K. breviceps* were not significant, apart from a comparison between Portugal and New Zealand ($\Phi_{ST}=0.1248$, $p=0.0046$) when considering the *cytb* dataset (Table S4). For the CR dataset, most comparisons were non-significant, with low but significant differentiation limited to contrasts involving New Zealand vs. Canary Islands, Spain, and western North Atlantic when considering Φ_{ST} (Φ_{ST} spanning 0.0906 and 0.0952), and contrast involving New Zealand vs. Canary Islands and western North Atlantic and Japan vs. Canary Islands when considering F_{ST} (F_{ST} values spanning 0.0174–0.0345) (Table S4).

TABLE 2 | Analysis of molecular variance (AMOVA) for *Kogia breviceps* and *K. sima* based on *cytb* and CR datasets.

Source of variation	d.f.	Sum of squares	Variance components	% of variation
(a) *K. breviceps* (*cytb*)				
Among oceans	1	1.536	0.00973	1.27
Among localities	6	5.169	0.00687	0.90
Within localities	137	102.325	0.74690	97.83
Total	144	109.029	0.76349	
Φ_{SC}: 0.0091 (0.223), Φ_{ST}: 0.0217 (0.088), Φ_{CT}: 0.0127 (0.1587)				
(b) *K. breviceps* (CR)				
Among oceans	1	16.881	0.16184	5.46
Among localities	5	15.374	0.01533	0.52
Within localities	172	478.905	2.78433	94.02
Total	178	511.16	2.96151	
Φ_{SC}: 0.0055 (0.286), Φ_{ST}: 0.0598 (0.000), Φ_{CT}: 0.0547 (0.048)				
(d) *K. sima* (*cytb*)				
Among oceans	1	288.135	11.04124	93.86
Within oceans	63	45.531	0.72271	6.14
Total	64	333.665	11.76394	
Φ_{ST}: 0.9386 (0.000)				
(e) *K. sima* (CR)				
Among oceans	1	523.019	12.39540	82.23
Within oceans	91	243.720	2.67824	17.77
Total	92	766.739	15.07365	
Φ_{ST}: 0.8223 (0.000)				

Note: Variance components and percentage of variation are reported for each hierarchical level. Φ statistics are shown with associated p values in parentheses. Significance was assessed at $p<0.01$.

In the *cytb* haplotype networks, *K. breviceps* showed the presence of two high-frequency haplotypes and several other haplotypes with lower frequency (Figure 2a). Most haplotypes diverged from each other by a single substitution and, overall, no geographic structure was observed. Moreover, except for some haplotypes represented by a single sequence and two haplotypes found in multiple sequences from New Zealand, all other haplotypes were shared by samples from different localities. Localities in the eastern North Atlantic showed three to six haplotypes each, with continental Spain, Portugal, and Scotland also showing one private haplotype each. The CR dataset resulted in a complex network, with several putative missing haplotypes and no clear geographic pattern, with eastern North Atlantic localities showing one to three private haplotypes (Figure S1).

The *K. sima* *cytb* and CR haplotype networks showed a clear separation between samples from the Atlantic and Mediterranean Sea and those from the Indo-Pacific, including

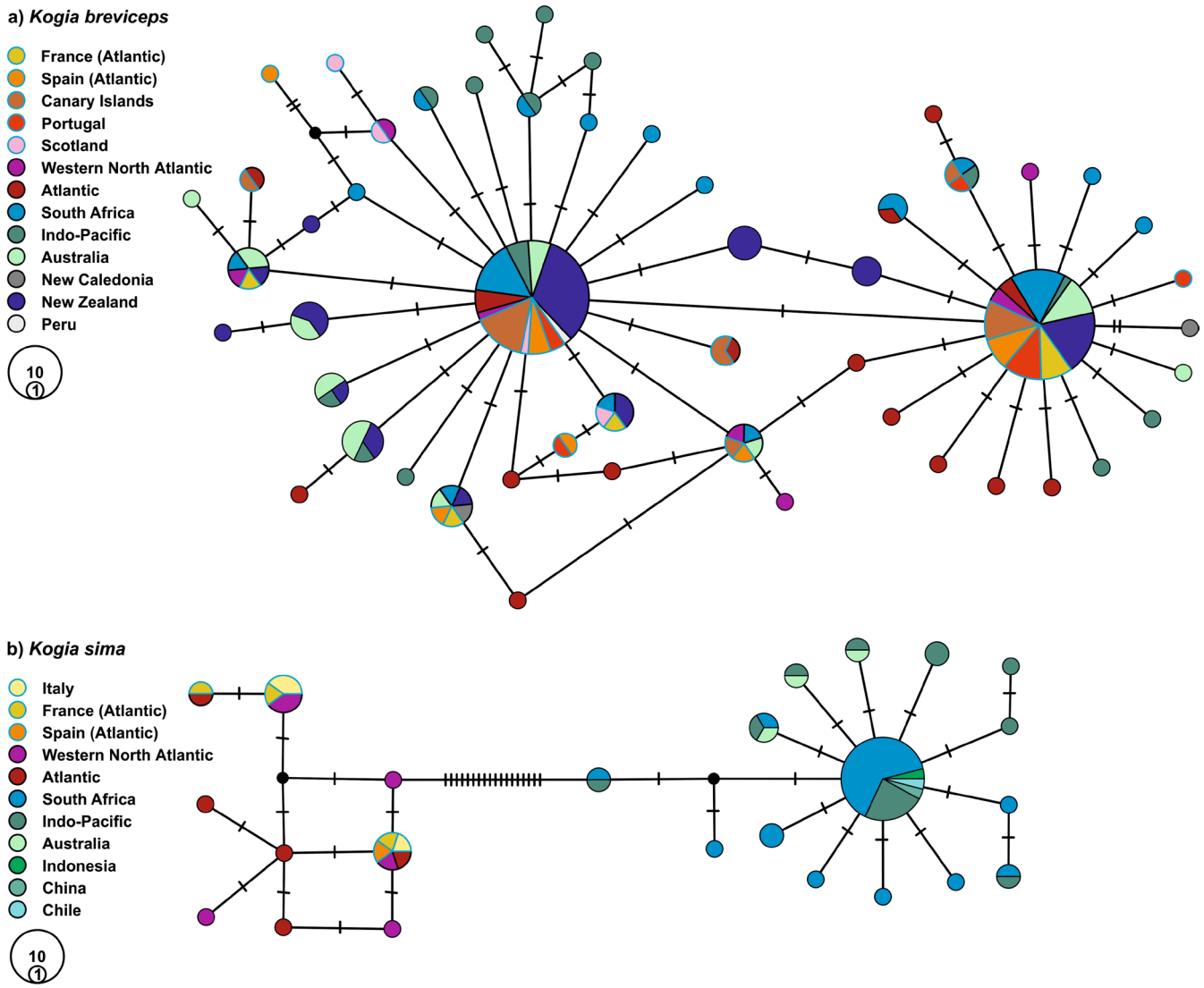

FIGURE 2 | Median-joining haplotype network based on *cytb* alignment of (a) *Kogia breviceps* and (b) *K. sima* sequences. The size of circles is proportional to the number of sequences carrying that specific haplotype. Perpendicular lines represent the number of substitutions between adjacent haplotypes. Small black circles represent putative missing haplotypes, while colors refer to geographic provenience, as indicated in the legend. Haplotypes with light blue outlines are those from eastern North Atlantic Ocean/Mediterranean Sea localities.

South Africa, with 18 and 21 substitutions occurring between the two haplogroups (Figure 2b, Figure S1). Although Chivers et al. (2005) reported that a *K. sima* specimen from St Helena Bay (South Africa) clustered within the Atlantic clade, it was not possible to identify the corresponding sequence due to the lack of geographical information in the original publication and in the associated GenBank metadata. Therefore, this sequence is assumed to be among those labeled as 'Atlantic' in the *K. sima* haplotype network. For the *cytb* network, within-group structure did not reflect any clear geographic pattern. The Indo-Pacific group showed a high-frequency haplotype shared by individuals from multiple localities and other lower-frequency haplotypes found in one to three different localities. The Atlantic-Mediterranean group revealed three haplotypes shared between different localities and six single-sequence haplotypes coming from the Atlantic or western North Atlantic. Samples from the eastern North Atlantic and Mediterranean showed one to three haplotypes for each locality, always clustering with other sequences from the Atlantic, and with no private haplotypes (Figure 2b). Similarly, no clear within-group geographic pattern could be observed in the CR network, and samples from Mediterranean and eastern North Atlantic clustered in four haplotypes, all shared with other localities apart from a haplotype only observed in France (Figure S1).

The phylogenetic reconstructions based on unique haplotypes (Figures 3, 4) were overall concordant with previous works, resolving two main phylogenetic clades corresponding to *K. breviceps* and *K. sima* (Chivers et al. 2005; Nishida et al. 2023; Plön et al. 2023). Regarding *K. breviceps*, both *cytb* and CR phylogenetic trees showed no clear clustering based on the geographic provenance of the samples, with samples from the eastern North Atlantic, indicated in red, being scattered over the trees (Figures 3, 4). The existence of two well-defined phylogenetic clades in *K. sima* was also supported when including

the sequences generated in this work, with one group composed of samples from the Indo-Pacific and the other composed of samples from the Atlantic and Mediterranean (Figures 3, 4). *Kogia breviceps* showed moderately low intra-specific genetic distances (0.9% ± 0.3% for *cytb* and 2.2% ± 0.5% for CR), whereas values were higher for *K. sima*, being 3.4% ± 0.7% for *cytb* and 4.7% ± 0.7% for CR (Table 3). On the other hand, genetic divergence between Atlantic and Indo-Pacific populations of *K. sima* were high for both markers (e.g., *cytb* Nei's $d_A = 0.065 \pm 0.018$, CR Nei's $d_A = 0.069 \pm 0.016$) and for CR they were comparable or even higher than the divergence between *K. breviceps* and *K. sima* as a whole (e.g., CR Nei's $d_A = 0.047 \pm 0.012$) (Table 3).

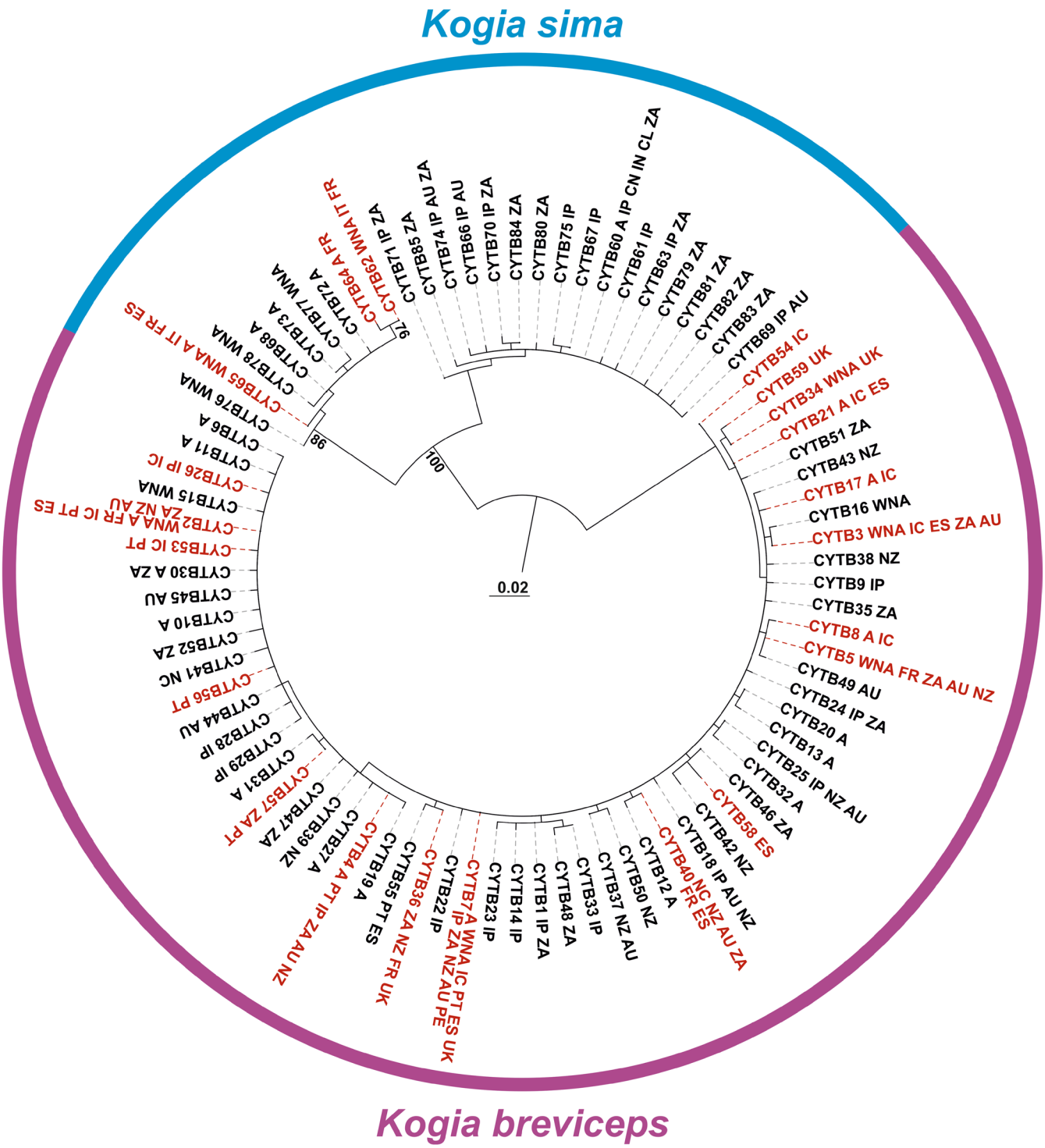

FIGURE 3 | Maximum likelihood phylogenetic hypothesis of Kogia species based on 302 bp of the cytb gene. Haplotype names refer to Table S1 and Table S2 and haplotypes obtained in this work are highlighted in red. Numbers at nodes indicate bootstrap values, shown only when ≥ 75. Acronyms following haplotype names indicate the geographic provenance of the samples. A: Atlantic, AU: Australia, CL: Chile, CN: China, ES: Spain, FR: France, IC: Canary Islands, IN: India, IP: Indo-Pacific, IT: Italy, NC: New Caledonia, NZ: New Zealand, PE: Peru, PT: Portugal, UK: Scotland, WNA: Western North Atlantic, ZA: South Africa.

4 | Discussion

Our genetic evidence from the eastern North Atlantic aligns with and extends the global phylogeographic patterns previously reported for *Kogia* species. *K. breviceps* showed absent or weak geographic structure across the sampled localities, with several haplotypes shared among distant regions or even between ocean basins, suggesting substantial historical connectivity and/or a large effective population size, as hypothesized by earlier studies (Chivers et al. 2005; Plön et al. 2023). However, some analyses have identified weak but significant structure in some regions. In the western North Atlantic, for example, Viricel (2012) found slight mitochondrial differentiation among the Gulf of Mexico, Mid-Atlantic Bight, and

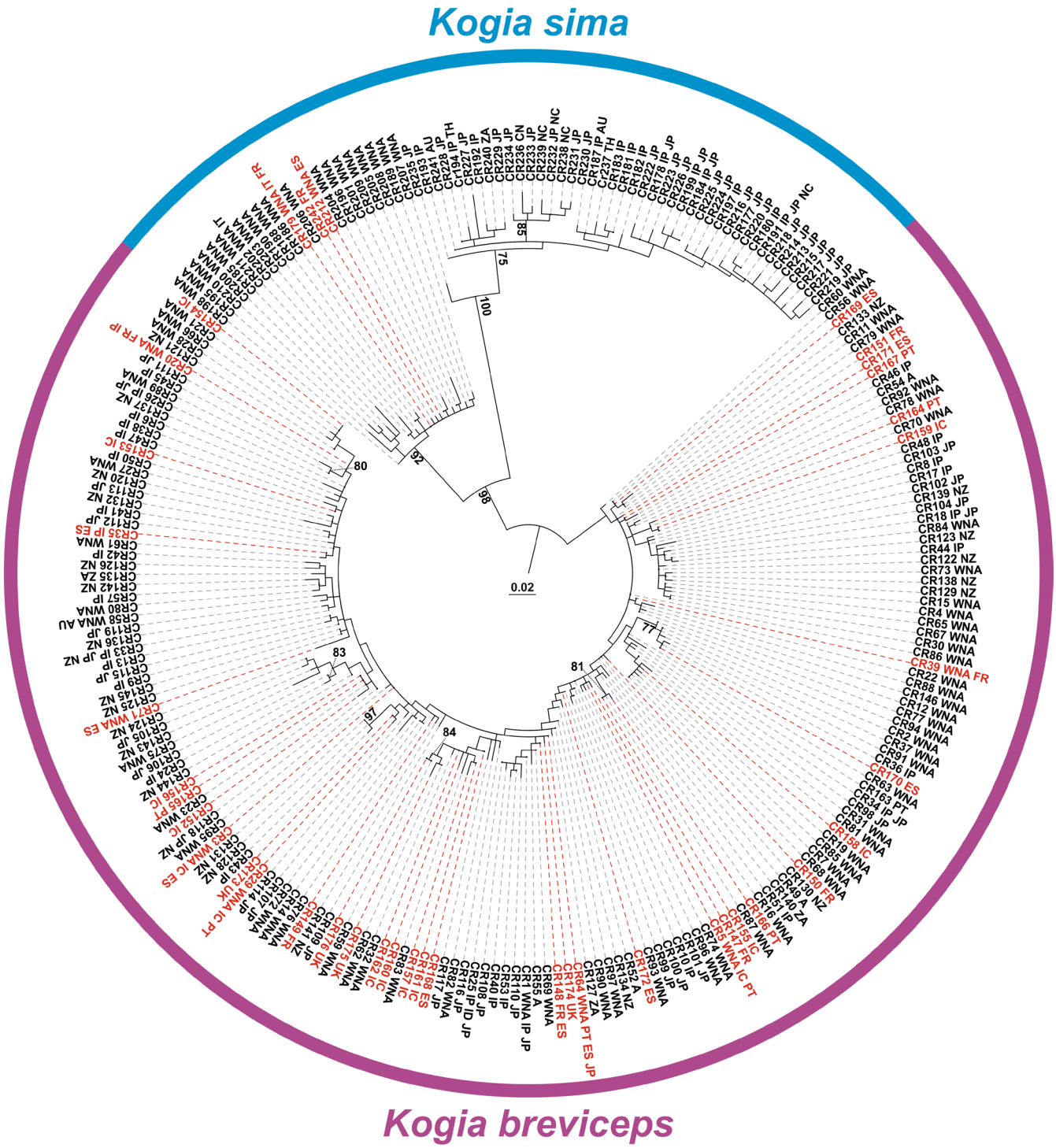

FIGURE 4 | Maximum likelihood phylogenetic hypothesis of Kogia species based on 361 bp of the mitochondrial CR. Haplotype names refer to Table S1 and Table S2 and haplotypes obtained in this work are highlighted in red. Numbers at nodes indicate bootstrap values, shown only when ≥ 75. Acronyms following haplotype names indicate the geographic provenance of the samples. A: Atlantic, AU: Australia, CN: China, ES: Spain, FR: France, IC: Canary Islands, ID: Indonesia, IP: Indo-Pacific, IT: Italy, JP: Japan, NC: New Caledonia, NZ: New Zealand, PT: Portugal, TH: Thailand, UK: Scotland, WNA: Western North Atlantic, ZA: South Africa.

TABLE 3 | Summary of mean genetic divergence (Kimura 2-parameter distances, %) ± standard deviation within and between *Kogia* species and populations, with Nei's d_A indicated between brackets.

	K. breviceps	*K. sima*
(a) *cytb* genetic distances		
K. breviceps (184)	0.9 ± 0.3	
K. sima (65)	13.7 ± 2.3 (0.116 ± 0.023)	3.4 ± 0.7
	K. sima (Indo-Pacific)	*K. sima* (Atlantic)
K. sima Indo-Pacific (46)	0.5 ± 0.1	
K. sima Atlantic (19)	7.5 ± 1.8 (0.065 ± 0.018)	1.5 ± 0.3
(b) CR genetic distances		
K. breviceps (224)	2.2 ± 0.5	
K. sima (93)	8.1 ± 1.2 (0.047 ± 0.012)	4.7 ± 0.7
	K. sima (Indo-Pacific)	*K. sima* (Atlantic)
K. sima Indo-Pacific (61)	1.7 ± 0.3	
K. sima Atlantic (32)	8.3 ± 1.6 (0.069 ± 0.016)	1.1 ± 0.3

Note: Values are shown for (a) *cytb* and (b) CR datasets. Sample sizes for each group are indicated in the first column between brackets. The analysis for *K. sima* was conducted under two frameworks: including all individuals as a single taxon and partitioning them into Indo-Pacific and Atlantic operational units.

South Atlantic Bight, whereas microsatellite data suggested a slightly different pattern of regional connectivity. Our CR AMOVA detected a small but significant overall structure, despite the lack of obvious phylogeographic clustering, indicating at most a weak ocean-scale differentiation. Similarly, pairwise Φ_{ST} and F_{ST} values between Atlantic and Indo-Pacific localities were generally low and rarely significant, with significant comparisons restricted to a few isolated cases. Accordingly, eastern North Atlantic samples did not form a distinct regional lineage and showed no consistent separation from western North Atlantic or Indo-Pacific samples, with only a few low but significant Φ_{ST} and F_{ST} values. Together, these results indicate that *K. breviceps* is likely well connected at the ocean-basin scale but may still show some regional structure that cannot be fully resolved with mitochondrial DNA alone. Additional genetic markers and a more balanced sampling across localities are therefore required to clarify the global phylogeography of the species and to provide further insights into possible sex-biased dispersal or regional differences in effective population size.

Conversely, the newly obtained data corroborate the presence of two distinct phylogenetic clades in *K. sima*. The population genetics, phylogenetic, and divergence analyses provide a strong argument that these Atlantic and Indo-Pacific lineages may represent distinct species as first discussed by Chivers et al. (2005). The fact that CR divergence between these lineages is comparable or greater than the interspecific divergence to *K. breviceps* provides a powerful argument for recognizing them as distinct species, a taxonomic revision with significant implications for conservation. However, whether this represents a clear phylogeographic break between two species or geographically distinct populations remains uncertain. Specimens from the same locality in South Africa (St Helena Bay) have been found in both genetic groups (Plön et al. 2023), complicating the picture. This ambiguity could be due to post-mortem drift, as marine carcasses may drift for days before stranding (Deslias et al. 2024), biasing geographic reconstructions. Therefore, a broader sampling strategy, including samples from living animals, analyses of nuclear markers, and thorough morphological examinations (Rosel et al. 2017), is required to conclusively resolve the population structure and taxonomic status within *K. sima*. Additionally, ecological tracers, such as trophic ecology or exposure to chemical contaminants, are useful markers for clarifying the potential differentiation between populations (e.g., Méndez-Fernandez et al. 2020) and their integration with genetic data could clarify the presence of different populations or species within *K. sima*. Ecological tracers may also provide useful information about the conservation status of the inferred *Kogia* species and populations, for instance in terms of exposure to toxic contaminants at the spatial and temporal scales (e.g., Romero et al. 2017; Méndez-Fernandez et al. 2022). All this information is fundamental for the transfer of knowledge to other stakeholders, including, among the others, conservation managers as well as the general public, and to eventually inform effective conservation strategies at the species, subspecies or population level (Taylor et al. 2017).

A fundamental caveat is that all observed geographic patterns are based on stranded animals. Interpreting stranding localities as proxies for species presence requires caution. Detection rates vary with coastline accessibility, human density, and observer effort (Ponti et al. 2025), and only a fraction of at-sea mortalities reach the shore (Cook et al. 2021; da Cunha Ramos et al. 2022). Therefore, while strandings are an invaluable data source, they must be used carefully when inferring population estimates and true geographic distributions. Considering these limitations, the stranding patterns for the two species are variable, with many examples of higher frequencies for *K. breviceps* (e.g., O'Brien 2008; Plön 2023) but also the opposite situation (e.g.,

Moura et al. 2016; Dulau et al. 2024). These variations may reflect differences in the ecological preferences of the two species, as well as in the population size, but further global and local assessments are needed to shed light on the ecology and demography of *Kogia* species.

This study provides the first comprehensive genetic data for *Kogia* species from multiple eastern North Atlantic countries, significantly expanding knowledge in a previously understudied region. We identified numerous haplotypes, including private ones for continental Spain, Portugal, and Scotland. Our results confirm the contrasting phylogeographic patterns: large-scale mtDNA homogeneity in *K. breviceps* versus a profound, possibly species-level divergence between Atlantic and Indo-Pacific lineages of *K. sima*, with no further geographic structure within each group.

Overall, these findings improve the resolution of the population genetics for these elusive cetaceans. In the specific case of Kogiidae, the relatively high levels of genetic diversity revealed here and in previous studies suggest that these species may not have experienced severe recent genetic erosion, and the observed patterns provide cautiously optimistic indications of healthy populations, albeit poorly observed. However, mitochondrial DNA diversity alone cannot be taken as direct evidence of demographic health, since the mtDNA is a single, maternally-inherited locus, possibly subjected to introgression and non-neutrality and, therefore, may not accurately reflect the evolutionary history of the group (Ballard and Whitlock 2004; Rosel et al. 2017). Therefore, additional data are strongly needed to assess the health of the group at both the species and population levels.

This work establishes a critical baseline for conservation, particularly for data-deficient populations in European waters. Future research must prioritize increased sampling, the use of nuclear markers to test the proposed cryptic speciation in *K. sima* and to verify the panmixia in *K. breviceps*, and the integration of data from living animals to mitigate the biases inherent to stranding records.

Author Contributions

Davide Maggioni: conceptualization, methodology, data curation, investigation, formal analysis, resources, writing – original draft, writing – review and editing. **Graziella Pupillo:** conceptualization, data curation, investigation, formal analysis, writing – original draft, writing – review and editing. **Alessia Rota:** data curation, writing – review and editing. **Fausto Ramazzotti:** data curation, investigation, writing – review and editing. **Vidal Martín:** investigation, resources, writing – review and editing. **Francesca Fusar Poli:** investigation, resources, writing – review and editing. **Charlotte Dumortier:** investigation, resources, writing – review and editing. **Paula Méndez-Fernandez:** investigation, resources, writing – review and editing. **Andreia Torres-Pereira:** investigation, resources, writing – review and editing. **Sara Sá:** investigation, resources, writing – review and editing. **Mariel T. I. ten Doeschate:** investigation, resources, writing – review and editing. **Andrew C. Brownlow:** investigation, resources, writing – review and editing. **Pablo Covelo:** investigation, resources, writing – review and editing. **Alfredo López:** investigation, resources, writing – review and editing. **Andrea Galimberti:** investigation, funding acquisition, resources, writing – review and editing. **Elena Valsecchi:** conceptualization, data curation, investigation, funding acquisition, supervision, resources, writing – original draft, writing – review and editing.

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Conflicts of Interest

The authors declare no conflicts of interest.

Data Availability Statement

The data that support the findings of this study are openly available in GenBank at https://www.ncbi.nlm.nih.gov/, reference number PX692166-PX692267.

References

Baird, R. W. 2005. "Sightings of Dwarf (*Kogia sima*) and Pygmy (*K. breviceps*) Sperm Whales From the Main Hawaiian Islands." *Pacific Science* 59, no. 3: 461–466. https://doi.org/10.1353/psc.2005.0031.

Baird, R. W., S. D. Mahaffy, and J. K. Lerma. 2022. "Site Fidelity, Spatial Use, and Behavior of Dwarf Sperm Whales in Hawaiian Waters: Using Small-Boat Surveys, Photo-Identification, and Unmanned Aerial Systems to Study a Difficult-To-Study Species." *Marine Mammal Science* 38, no. 1: 326–348. https://doi.org/10.1111/mms.12861.

Ballard, J. W. O., and M. C. Whitlock. 2004. "The Incomplete Natural History of Mitochondria." *Molecular Ecology* 13, no. 4: 729–744. https://doi.org/10.1046/j.1365-294X.2003.02063.x.

Baumgartner, M. F., K. D. Mullin, L. N. May, and T. D. Leming. 2001. "Cetacean Habitats in the Northern Gulf of Mexico." *Fishery Bulletin* 99, no. 2: 219–239. https://doi.org/10.1016/S0967-0637(01)00035-8.

Benak, D., P. Carter, J. Ebr, et al. 2025. "Sighting of a Large Group of Pygmy Sperm Whales (*Kogia breviceps*) and a Recent Record of a Dwarf Sperm Whale (*K. sima*) in the Azores." *Journal of the Marine Biological Association of the United Kingdom* 105: e129. https://doi.org/10.1017/S0025315425100830.

Berrow, S. D., and E. Rogan. 1997. "Review of Cetaceans Stranded on the Irish Coast, 1901–95." *Mammal Review* 27, no. 1: 51–75. https://doi.org/10.1111/j.1365-2907.1997.tb00372.x.

Best, P. B. 2007. *Whales and Dolphins of the Southern African Subregion*. Cambridge University Press.

Chivers, S. J., R. G. LeDuc, K. M. Robertson, N. B. Barros, and A. E. Dizon. 2005. "Genetic Variation of *Kogia* spp. With Preliminary Evidence for Two Species of *Kogia sima*." *Marine Mammal Science* 21, no. 4: 619–634. https://doi.org/10.1111/j.1748-7692.2005.tb01255.x.

Cook, M., J. L. Reneker, R. W. Nero, B. A. Stacy, D. S. Hanisko, and Z. Wang. 2021. "Use of Drift Studies to Understand Seasonal Variability in Sea Turtle Stranding Patterns in Mississippi." *Frontiers in Marine Science* 8: 659536. https://doi.org/10.3389/fmars.2021.659536.

Covelo, P., and A. López. 2021. "First Record of Dwarf Sperm Whale (*Kogia sima*) in the North of Spain." *Galemys* 33, no. 1: 64–68. https://doi.org/10.7325/Galemys.2021.N8.

da Cunha Ramos, H. G., A. C. Colosio, M. C. C. Marcondes, et al. 2022. "Carcass Non-Recovery Rate of Franciscana Dolphin (*Pontoporia blainvillei*), Calibrated With a Drift Mark-Recapture Study at FMA Ia, Brazil." *Latin American Journal of Aquatic Mammals* 17, no. 2: 93–104. https://doi.org/10.5597/lajam00288.

Darriba, D., D. Posada, A. M. Kozlov, A. Stamatakis, B. Morel, and T. Flouri. 2020. "ModelTest-NG: A New and Scalable Tool for the Selection of DNA and Protein Evolutionary Models." *Molecular Biology and Evolution* 37, no. 1: 291–294. https://doi.org/10.1093/molbev/msz189.

Dávila, C., P. Gauffier, F. T. A. Cruz, P. Verborgh, R. Domingues, and L. Freitas. 2026. "Evidence of Killer Whale Predation on Deep-Diving Cetaceans in Madeira." *Marine Mammal Science* 42, no. 1: e70103. https://doi.org/10.1111/mms.70103.

Deslias, C., P. Daniel, A. López, J. Martínez-Cedeira, V. Ridoux, and H. Peltier. 2024. "Predicting the Drift of Small Cetaceans Stranded Along the Atlantic Coast of the Iberian Peninsula: Parametrization of the MOTHY Drift Model." *PLoS One* 19, no. 12: e0315593. https://doi.org/10.1371/journal.pone.0315593.

Duguy, R. 1966. "Quelques Données Nouvelles sur un Cétacé Rare sur les Côtes d'Europe: Le Cachalot à Tête Courte, *Kogia breviceps* (Blainville, 1838)." *Mammalia* 30: 259–269. https://doi.org/10.1515/mamm.1966.30.2.259.

Duguy, R., and P. Budker. 1972. "Rapport Annuel sur les Cétacés et Pinnipèdes Trouvés sur les Côtes de France I. Année 1971." *Mammalia* 36: 517–520. https://doi.org/10.1515/mamm.1972.36.3.517.

Dulau, V., V. Estrade, A. Bein, et al. 2024. "Records From Visual Surveys, Strandings and eDNA Sampling Reveal the Regular Use of Reunion Waters by Dwarf Sperm Whales." *Advances in Marine Biology* 99: 65–97. https://doi.org/10.1016/bs.amb.2024.08.003.

Dunphy-Daly, M. M., M. R. Heithaus, and D. E. Claridge. 2008. "Temporal Variation in Dwarf Sperm Whale (*Kogia sima*) Habitat Use and Group Size Off Great Abaco Island, Bahamas." *Marine Mammal Science* 24: 171–182. https://doi.org/10.1111/j.1748-7692.2007.00183.x.

Excoffier, L., and H. E. Lischer. 2010. "Arlequin Suite ver 3.5: A New Series of Programs to Perform Population Genetics Analyses Under Linux and Windows." *Molecular Ecology Resources* 10, no. 3: 564–567. https://doi.org/10.1111/j.1755-0998.2010.02847.x.

Fraser, F. C. 1974. *Report on Cetacea Stranded on the British Coasts From 1948 to 1966*. 14th ed. British Museum (Natural History).

Handley, C. O. 1966. "A Synopsis of the Genus Kogia (Pygmy Sperm Whales). Kogia sima—Dwarf Sperm Whale." In *Whales, Dolphins and Porpoises*, edited by K. Norris, 62–69. University of California Press.

Katoh, K., and D. M. Standley. 2013. "MAFFT Multiple Sequence Alignment Software Version 7: Improvements in Performance and Usability." *Molecular Biology and Evolution* 30, no. 4: 772–780. https://doi.org/10.1093/molbev/mst010.

Kimura, M. 1980. "A Simple Method for Estimating Evolutionary Rates of Base Substitutions Through Comparative Studies of Nucleotide Sequences." *Journal of Molecular Evolution* 16, no. 2: 111–120. https://doi.org/10.1007/BF01731581.

Kiszka, J. J., G. Maricato, and M. Caputo. 2024. "Habitat Suitability, Occurrence, and Behavior of Dwarf Sperm Whales (*Kogia sima*) Off St. Vincent and the Grenadines, Eastern Caribbean." *Advances in Marine Biology* 99: 1–19. https://doi.org/10.1016/bs.amb.2024.09.002.

Kocher, T. D., W. K. Thomas, A. Meyer, et al. 1989. "Dynamics of Mitochondrial DNA Evolution in Animals: Amplification and Sequencing With Conserved Primers." *Proceedings of the National Academy of Sciences* 86, no. 16: 6196–6200. https://doi.org/10.1073/pnas.86.16.6196.

Leigh, J. W., D. Bryant, and S. Nakagawa. 2015. "POPART: Full-Feature Software for Haplotype Network Construction." *Methods in Ecology and Evolution* 6, no. 9: 1110–1116. https://doi.org/10.1111/2041-210X.12410.

MacLeod, C. D., N. Hauser, and H. Peckham. 2004. "Diversity, Relative Density and Structure of the Cetacean Community in Summer Months East of Great Abaco, Bahamas." *Journal of the Marine Biological Association of the United Kingdom* 84, no. 2: 469–474. https://doi.org/10.1017/S0025315404009476h.

Maio, N., T. Fioravanti, L. Latini, et al. 2024. "Genetic Characterization, Age and Reproductive Status of Dwarf Sperm Whales (*Kogia sima*) Stranded Along the Italian Coastlines." *Mediterranean Marine Science* 25, no. 2: 374–381. https://doi.org/10.12681/mms.35701.

Maio, N., F. Pollaro, A. Gasparro, et al. 2017. "New Record of Dwarf Sperm Whale *Kogia sima* (Owen, 1866) From the Mediterranean Sea (Cetacea Kogiidae)." *Biodivers Journal* 8, no. 4: 947–950.

Martin, A. P., and S. R. Palumbi. 1993. "Protein Evolution in Different Cellular Environments: Cytochrome b in Sharks and Mammals." *Molecular Biology and Evolution* 10, no. 4: 873–891. https://doi.org/10.1093/oxfordjournals.molbev.a040047.

Martín, V., M. Tejedor, M. Carrillo, et al. 2024. "Strandings and at-Sea Observations Reveal the Canary Archipelago as an Important Habitat for Pygmy and Dwarf Sperm Whales." *Advances in Marine Biology* 99: 21–64. https://doi.org/10.1016/bs.amb.2024.09.003.

Matsuda, A. T., T. F. Matsuishi, F. Noto, M. Amano, Y. Tajima, and T. K. Yamada. 2023. "Notes on Stomach Contents of Pygmy and Dwarf Sperm Whales (*Kogia* spp.) From Around Japan." *Advances in Marine Biology* 96: 1–24. https://doi.org/10.1016/bs.amb.2023.08.001.

McAlpine, D. F. 2009. "Pygmy and Dwarf Sperm Whales." In *Encyclopedia of Marine Mammals*, edited by W. F. Perrin, B. Würsig, and J. G. M. Thewissen, 2nd ed., 936–938. Elsevier Academic Press. https://doi.org/10.1016/B978-0-12-373553-9.00212-1.

Méndez-Fernandez, P., J. Spitz, C. Dars, et al. 2022. "Two Cetacean Species Reveal Different Long-Term Trends for Toxic Trace Elements in European Atlantic French Waters." *Chemosphere* 294: 133676. https://doi.org/10.1016/j.chemosphere.2022.133676.

Méndez-Fernandez, P., S. Taniguchi, M. C. Santos, et al. 2020. "Population Structure of the Atlantic Spotted Dolphin (*Stenella frontalis*) Inferred Through Ecological Markers." *Aquatic Ecology* 54, no. 1: 21–34. https://doi.org/10.1007/s10452-019-09722-3.

Moura, J. F., E. Acevedo-Trejos, D. C. Tavares, et al. 2016. "Stranding Events of *Kogia* Whales Along the Brazilian Coast." *PLoS One* 11, no. 1: e0146108. https://doi.org/10.1371/journal.pone.0146108.

Nishida, S., A. Uchimura, Y. Tajima, and T. K. Yamada. 2023. "Comparative Analysis of the Genetic Structures of *Kogia* spp. Populations in the Western North Pacific." *Advances in Marine Biology* 96: 25–37. https://doi.org/10.1016/bs.amb.2023.08.002.

O'Brien, N. M. 2008. *An Analysis of Dwarf and Pygmy Sperm Whale (Kogia sp.) Stranding Data in the Southeast United States*. Nova Southeastern University.

Penas-Patiño, X. M., and A. Piñeiro-Seage. 1989. *Cetáceos, Focas e Tartarugas das Costas Ibéricas*. Consellería de Pesca (Xunta de Galicia).

Plön, S. 2023. "Pygmy Sperm Whale *Kogia breviceps* (de Blainville, 1838)." In *Handbook of the Mammals of Europe*, edited by K. Hackländer and F. E. Zachos. Springer.

Plön, S., and R. Baird. 2022. "Dwarf Sperm Whale, *Kogia sima* (Owen, 1866)." In *Handbook of the Mammals of Europe*, edited by K. Hackländer and F. E. Zachos. Springer. https://doi.org/10.1007/978-3-319-65038-8_91-1.

Plön, S., P. B. Best, P. Duignan, et al. 2023. "Population Structure of Pygmy (*Kogia breviceps*) and Dwarf (*Kogia sima*) Sperm Whales in the Southern Hemisphere May Reflect Foraging Ecology and Dispersal Patterns." *Advances in Marine Biology* 96: 85–114. https://doi.org/10.1016/bs.amb.2023.09.001.

Ponti, M. J., M. L. Russell, C. Díaz Clark, et al. 2025. "Stranded Marine Mammal Detection by the Public, Trained Responders, and Drones Using Decoy Carcasses." *Marine Mammal Science* 41, no. 1: e13169. https://doi.org/10.1111/mms.13169.

Romero, M. B., P. Polizzi, L. Chiodi, A. Robles, K. Das, and M. Gerpe. 2017. "Metals as Chemical Tracers to Discriminate Ecological Populations of Threatened Franciscana Dolphins (*Pontoporia blainvillei*) From Argentina." *Environmental Science and Pollution Research* 24, no. 4: 3940–3950. https://doi.org/10.1007/s11356-016-7970-9.

Rosel, P. E., A. E. Dizon, and J. E. Heyning. 1994. "Genetic Analysis of Sympatric Morphotypes of Common Dolphins (*Delphinus*)." *Marine Biology* 119, no. 2: 159–167. https://doi.org/10.1007/BF00349552.

Rosel, P. E., B. L. Taylor, B. L. Hancock-Hanser, et al. 2017. "A Review of Molecular Genetic Markers and Analytical Approaches That Have Been Used for Delimiting Marine Mammal Subspecies and Species." *Marine Mammal Science* 33, no. S1: 56–75. https://doi.org/10.1111/mms.12412.

Ross, G. J. B. 1979. "Records of Pygmy and Dwarf Sperm Whales Genus *Kogia* From Southern Africa With Biological Notes and Some Comparisons." *Annals of the Cape Provincial Museums, Natural History* 11: 259–327.

Rozas, J., A. Ferrer-Mata, J. C. Sánchez-DelBarrio, et al. 2017. "DnaSP 6: DNA Sequence Polymorphism Analysis of Large Data Sets." *Molecular Biology and Evolution* 34, no. 12: 3299–3302. https://doi.org/10.1093/molbev/msx248.

Santos, M. B., G. J. Pierce, A. Lopez, R. J. Reid, V. Ridoux, and E. Mente. 2006. "Pygmy Sperm Whales *Kogia breviceps* in the Northeast Atlantic: New Information on Stomach Contents and Strandings." *Marine Mammal Science* 22, no. 3: 600–616. https://doi.org/10.1111/j.1748-7692.2006.00038.x.

Sequeira, M., A. Inácio, and F. Reiner. 1992. *Arrojamentos de Mamíferos Marinhos na Costa Portuguesa Entre 1978 e 1988. Estudos De Biologia e Conservação Da Natureza 7*. Serviço Nacional de Parques, Reservas e Conservação da Natureza.

Sequeira, M., A. Inácio, M. A. Silva, and F. Reiner. 1996. "Estudos de Biologia e Conservação da Natureza 19." In *Arrojamentos de Mamíferos Marinhos na Costa Continental Portuguesa entre 1989–1994*. Serviço Nacional de Parques, Reservas e Conservação da Natureza.

Stamatakis, A. 2014. "RAxML Version 8: A Tool for Phylogenetic Analysis and Post-Analysis of Large Phylogenies." *Bioinformatics* 30, no. 9: 1312–1313. https://doi.org/10.1093/bioinformatics/btu033.

Staudinger, M. D., R. J. McAlarney, W. A. McLellan, and D. Ann Pabst. 2014. "Foraging Ecology and Niche Overlap in Pygmy (*Kogia breviceps*) and Dwarf (*Kogia sima*) Sperm Whales From Waters of the US Mid-Atlantic Coast." *Marine Mammal Science* 30, no. 2: 626–655. https://doi.org/10.1111/mms.12064.

Tamura, K., G. Stecher, and S. Kumar. 2021. "MEGA11: Molecular Evolutionary Genetics Analysis Version 11." *Molecular Biology and Evolution* 38, no. 7: 3022–3027. https://doi.org/10.1093/molbev/msab120.

Taylor, B. L., W. F. Perrin, R. R. Reeves, et al. 2017. "Why We Should Develop Guidelines and Quantitative Standards for Using Genetic Data to Delimit Subspecies for Data-Poor Organisms Like Cetaceans." *Marine Mammal Science* 33, no. S1: 12–26. https://doi.org/10.1111/mms.12413.

Valsecchi, E., A. Rota, G. Pupillo, et al. 2026. "Seeing Through the "Clouds" With Molecular "Eyes". First eDNA-Based Detections of Pygmy Sperm Whale (*Kogia breviceps*) in the Mediterranean Sea." *Mammal Review* 56, no. 1: e70028. https://doi.org/10.1111/mam.70028.

Viricel, A. 2012. *Using Genetics to Assess Population Structure in Three Cetacean Species and to Investigate the Etiology of Cardiomyopathy in Kogia breviceps*. PhD thesis, University of Louisiana at Lafayette.

Wang, M. C., W. A. Walker, K. T. Shao, and L. S. Chou. 2002. "Comparative Analysis of the Diets of Pygmy Sperm Whales and Dwarf Sperm Whales in Taiwanese Waters." *Acta Zoologica Taiwanica* 13, no. 2: 53–62.

Willis, P. M., and R. W. Baird. 1998. "Status of the Dwarf Sperm Whale, *Kogia simus*, With Special Reference to Canada." *Canadian Field-Naturalist* 112, no. 1: 114–125.

Supporting Information

Additional supporting information can be found online in the Supporting Information section. **Figure S1:** Median-joining haplotype network based on CR alignment of (a) *Kogia breviceps* and (b) *Kogia sima* sequences. The size of circles is proportional to the number of sequences carrying that specific haplotype. Perpendicular lines represent the number of substitutions between adjacent haplotypes. Small black circles represent putative missing haplotypes, while colors refer to geographic provenience, as indicated in the legend. **Table S1:** Summary of sequences obtained in the present study, with all the available information on each sample. **Table S2:** Sequences of *Kogia* species mined from GenBank. **Table S3:** Genetic diversity indices of *Kogia* species based on *cytb* and CR datasets for each stranding locality, including number of sequences (n), number of variable sites (Sv), number of haplotypes (H), haplotype diversity (h), and nucleotide diversity (π). **Table S4:** Pairwise Φ_{ST} (a, b) and F_{ST} (c, d) values among sampling localities for *K. breviceps* based on *cytb* and CR datasets. Φ_{ST} and F_{ST} values are reported below the diagonal, while p values are shown above the diagonal. Significant comparisons are indicated in bold ($p < 0.01$). WN: Western North.