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Mitochondrial DNA Diversity and Phylogeographic Patterns Among South African Cape Fur Seals, *Arctocephalus pusillus pusillus*

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ABSTRACT

Cape fur seals (*Arctocephalus pusillus pusillus*) are important apex predators and indicators of ecological health. Historically, their populations were severely reduced by the activities of sealers and guano collectors but has since increased due to legislation controlling, then banning these activities. This study aimed to assess the genetic diversity and population structure of Cape fur seals in Southern Africa's cool (Benguela) and warm (Agulhas) temperate regions. Cape fur seal genetic material ($n = 263$) was collected along the Agulhas Bank and analysed using mitochondrial cytochrome b and D-loop gene markers. Estimates of genetic parameters showed that the south and west populations of Cape fur seals had high levels of haplotype diversity and low levels of nucleotide diversity. Assessment of genetic structure indicated that there was no obvious phylogenetic pattern between haplotypes. Both markers denoted the absence of population differentiation ($F_{ST} < 0$) and the presence of high genetic flow with multiple migrants between colonies. Lack of genetic distinction between localities and high genetic diversity identified here may be attributed to a recent population expansion after the last glacial maximum. Although populations are currently stable, future monitoring of populations is advocated.

1 | Introduction

Arctocephalus pusillus (von Schreber and Wagner 1775) is the largest fur seal and consists of two geographically distinct subspecies: *A.p. doriferus* (Australian fur seal) (Jones 1923) and *A.p. pusillus* (Cape fur seal) (von Schreber and Wagner 1775). It is thought that the Indian Ocean acts as the main dispersal barrier between the subspecies, especially as they are mostly confined to continental shelves for feeding. It is hypothesized that the Australian fur seal arose from migrating Cape fur seals during the last glacial maximum (LGM) (Malan et al. 2022). During this period, environmental changes resulted in lower sea levels (Clark and Mix 2002). This led to the emergence of previously submerged supplementary habitats around the sub-Antarctic islands, facilitating the movement of the seals to Australia. Once the LGM was over, rising sea levels submerged the supplementary habitats, causing a distribution barrier between the subspecies.

The Cape fur seal is the only pinniped that is endemic to the African continent and is distributed along the southern African coastline from southern Angola (Atlantic Ocean) to the south-east coast of South Africa (Indian Ocean) (Kirkman et al. 2011). Approximately 60% of the population occurs in Namibia

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(Kirkman et al. 2013; Wickens et al. 1991). Currently, there are more than 2 million Cape fur seals (Butterworth et al. 1995), and the species is listed as Least Concern (LC) on the International Union for Conservation of Nature (IUCN) Red List assessments (Goldsworthy 2015). Historically, Cape fur seal breeding colonies were restricted to islands and offshore rocky outcrops as mainland areas were avoided due to the presence of terrestrial predators (Butterworth et al. 1995). However, sealing activities on island rookeries, which took place between the 17th and 19th centuries, severely reduced Cape fur seal numbers to below 100,000 individuals. During this time, extirpation of seal breeding colonies occurred at approximately 23 islands and induced a population bottleneck. Legislation controlling sealing (David 1987) contributed to populations doubling between 1970 and 1990 (Kirkman et al. 2007), but re-colonization of some of their former island breeding colonies did not occur due to the activities of guano collectors. However, new breeding colonies were established on isolated mainland locations such as Kleinsee in South Africa and Atlas Bay in Namibia. These areas were suitable for mainland breeding colonies due to few terrestrial predators and low human occupancy as a result of access-restricted mining zones, national parks and an absence of farming (Rand 1972). Additionally, there was a considerable increase in the number of breeding colonies during this time. Presently, there are 41 Cape fur seal breeding colonies located on the Agulhas ecoregion ($n = 3$) and Benguela current system ($n = 38$) (on the Southwest Cape, Namaqua, Namib and Angolan ecoregions) on rocky islands or mainland outcrops (Kirkman et al. 2013).

The two largest breeding colonies in South Africa, Kleinsee and Seal Island (False Bay) are, in the cool Namaqua and Southwest Cape ecoregions, producing 80,897 and 18,339 pups, respectively, in 2003 (Kirkman et al. 2007). Areas on the Atlantic seaboard support higher numbers of Cape fur seals because of the highly productive Benguela Current (Bakun et al. 2015; Fréon et al. 2009), islands that are free from terrestrial predators (David 1987) and prevailing winds that provide a cool environment for breeding (De Villiers and Roux 1992). However, decreases in abundance and shifts in the distribution of preferred prey species such as sardines *Sardinops sagax* and anchovies *Engraulus encrasicolus* due to overfishing and environmental changes (Boyer and Hampton 2001; Coetzee et al. 2008; Gammelsrød et al. 1998; Roy et al. 2007; Van der Lingen et al. 2006) have resulted in a redistribution of Cape fur seals north towards Angola and south towards South Africa (Kirkman et al. 2013). Of potentially nine historical Cape fur seal haul-out sites east of Cape Agulhas (Stewardson 1999), only three remain today: Seal Island (Mossel Bay), Robberg and Black Rocks (Kirkman et al. 2013) (Figure 1). Pup production in the Agulhas Ecoregion remains low, with fewer than 1000 pups born annually in the mid-2000s at each of Black Rocks and Seal Island (Kirkman et al. 2011) and fewer than 100 annually at Robberg (Huisamen et al. 2011). Robberg is a mainland colony that was hunted to extinction but was

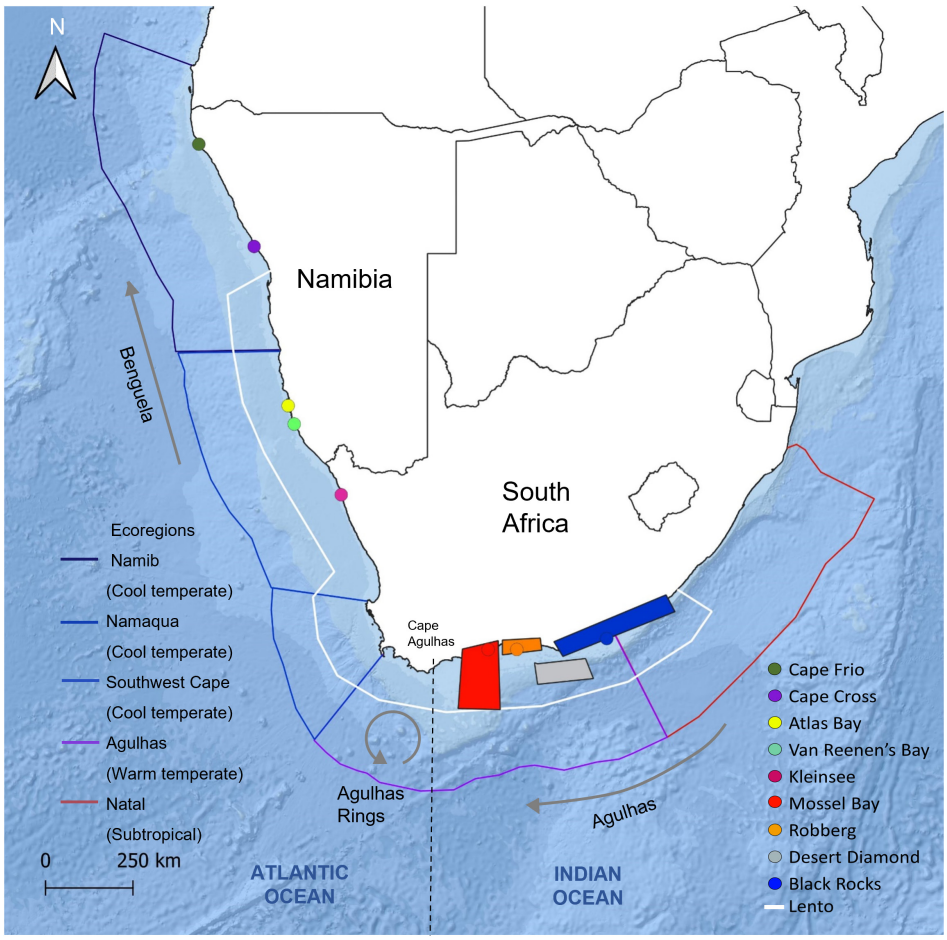


FIGURE 1 | Map of Southern Africa showing the two main currents, ecoregions and samples areas of this study.

recolonized in 1971 (Huisamen et al. 2011). Due to the terrestrial area, current growth in pup production will likely lead to a considerably larger colony.

Cape fur seals are subject to a number of threats. Their distribution is currently impacted by changes in prey abundance and distribution (Kirkman et al. 2013). They have also been subject to recent mortality events (Roux 1998; Seakamela et al. 2021). In addition, their ecosystem is characterized by high levels of temporal variability and is considered particularly vulnerable to climatic shifts (Blamey et al. 2015; Santos et al. 2012). Cape fur seals are subject to direct impacts from fisheries, such as entanglement and direct killing (David and Wickens 2003; Wickens et al. 1991). Furthermore, this species, like other pinnipeds, is vulnerable to diseases, with rabies being recorded recently (Van Helden 2024). Although high pathogenicity avian influenza has yet to be described in Cape fur seals, it has been noted in sympatric species of seabirds (Abolnik et al. 2024) and has resulted in high mortality of other species of pinnipeds (Alava et al. 2024; Campagna et al. 2024).

Despite these threats, only three studies have investigated the genetic structure and diversity of southern African Cape fur seal populations. Molecular genetic studies are needed to clarify the diversity and connectivity levels among seal breeding colonies throughout their distribution range as well as to infer the level of recovery after a population bottleneck. Lento et al. (1997) studied the phylogenetics and geographic variations of fur seals (17 Cape fur seals of unknown origin) in the southern hemisphere using a single mitochondrial DNA (mtDNA) marker (cytochrome b [cytb]). Although population structure was not studied, the authors identified moderate haplotype diversity (0.73) and high DNA sequence divergence between Cape fur seal individuals (average divergence = 0.37%), suggesting geographic structure (Lento et al. 1997). Matthee et al. (2006) studied Cape fur seal pups from five breeding colonies (Cape Frio, Cape Cross, Atlas Bay, van Reenen's Bay and Kleinsee) in their western range and one breeding site on the southern coast (Black Rocks). They identified 57 different haplotypes of the mtDNA hypervariable region 1 (D-loop), high haplotype diversity (0.975) and low nucleotide diversity (0.011) using 106 samples. Nucleotide and haplotype diversity values were similar within and between colonies, and no significant population structure was found. Malan et al. (2022), using microsatellites, showed the possibility of two clusters within the species that were, however, not geographically structured.

Consequently, the genetic diversity and population structure of Cape fur seals inhabiting the South West Cape and Agulhas ecoregions are unknown. These colonies are among the most isolated for the species (Kirkman et al. 2013), which may impact connectivity. They also have not recovered completely following uncontrolled sealing, and estimates of their abundance in recent decades indicate that it is possibly one twentieth of original levels (Kirkman et al. 2013; Stewardson 1999). In addition, the impacts of fisheries on Cape fur seals in this ecoregion are thought to be considerably higher than those in the Benguela. However, recent changes in the distribution of prey (Coetzee et al. 2008; Roy et al. 2007) and the rapid growth of the colony at Robberg (Huisamen et al. 2011) may have impacted these colonies. Due to these unknowns and the small population size of the Agulhas colonies, it is important to monitor the genetic diversity and abundance of these Cape fur seal populations. Here, we aimed to assess genetic diversity and population structure of Cape fur seal subpopulations in the Agulhas ecoregion, with comparative data from the Benguela current system, using two mitochondrial markers: cytb and D-loop.

2 | Methods

2.1 | Sampling and Dataset

As part of a systematic stranding response programme, the Port Elizabeth Museum at Bayworld collected 180 dead stranded Cape fur seals between 1 January 2004 and 16 December 2022 on the southern coast of South Africa (Figure 1). Carcasses were morphologically identified as Cape fur seals based on colour patterns, tooth and skull shape. Samples were collected either in the field or from carcasses that had been stored frozen. After collection, samples were stored in 95% ethanol at −20°C. The sample area was divided into three regions—Mossel Bay, Robberg and Black Rocks from west to east—based on the location of the stranded seals and their proximity to a breeding colony. Samples collected at sea aboard a fishing trawler (Desert Diamond) were grouped together under the vessel name because they could not be reliably assigned to a locality. For cytb, 16 additional sequences (U18448.1-U18448.9, U18449.1, U18451.2 and U18452.1-U18455.1) from Lento et al. (1997) were downloaded from National Centre for Biotechnology Information (NCBI) and included, although they could not be assigned to specific colonies. For the D-loop dataset, 69 sequences (DQ176872—DQ176941) from Matthee et al. (originating from Cape Frio, Cape Cross, Atlas Bay, van Reenen's Bay and Kleinsee, which are all colonies on the west coast of Southern Africa) were also downloaded.

2.2 | DNA Extraction and Amplification

DNA was extracted from a piece of tissue of approximately 3 × 2 mm in size using a Quick-DNA Kit (Zymo Research, California, USA) following the manufacturer's instructions. Two regions of interest on the mitochondrion were amplified (cytb and D-loop) using the cytb primers (L14841, 5′-AAA AAG CTT CCA TCC AAC ATC TCA GCA TGA TGA AA-3′, H15149 5′-AAA CTG CAG CCC CTC AGA ATG ATA TTT GTC CTC A-3′ to generate a product of 307 bp) and the D-loop primers (L15926 5′-TCA AAG CTT ACA CCA GTC TTG TAA ACC-3′ [Kocher et al. 1989] and a redesigned D-loop reverse HN16450 5′-CCC GAA AAC AGA ACT AGA TA-3′, this study, to generate a product of 543 bp).

The reaction mixes for cytb and D-loop were composed of 1× Taq Mastermix Red (Ampliqon, Denmark), 10 pmol of the forward and reverse primer each, 0.3–0.7 ng of template DNA, and water for a total reaction volume of 12 μL. The reaction conditions for cytb were: initial denaturation at 95°C for 5 min, followed by 35 cycles of denaturation at 95°C for 30 s; annealing at 52°C for 30 s; extension at 72°C for 30 s, before a final extension step at 72°C for 2 min. The reaction conditions for D-loop were initial denaturation at 95°C for 5 min; then 35 cycles of denaturation at 95°C

for 30 s, annealing at 55°C for 30 s, extension at 72°C for 1 min and a final extension step at 72°C for 5 min.

The Exo/SAP-IT system (Thermo Fischer Scientific, USA) was used to purify the amplified product, per manufacturer's protocol, before Sanger Sequencing using the BigDye terminator v3.1 cycle sequencing kit (Applied Biosystems, USA) protocol. Excess dye and ddNTPs were removed using the BigDye XTerminator Purification kit (Applied Biosystems, USA) following the recommended protocol. The reactions were loaded on a 3500 Genetic Analyser (Applied Biosystems, USA). Although both forward and reverse sequences were generated using cytb1 and cytb2, only forward sequences could be produced using D-loop forward likely due to a hairpin structure in this gene.

3 | Data Analysis

Sequences were analysed, trimmed using an error probability limit value of >0.05 and assembled using Geneious v10.2.6 (Biomatters, New Zealand) (Kearse et al. 2012). Consensus sequences were produced using pairwise sequencing alignment of forward and reverse reads for cytb and two forward direction reads for D-loop. Species identity was verified using the basic local alignment tool (BLAST). Consensus sequences were aligned in AliView v.1.28 (Department of Systematic Biology, Uppsala University, Sweden) (Larsson 2014) using MUSCLE alignment and trimmed to 289 bp (cytb) and 364 bp (D-loop).

3.1 | Genetic Diversity and Phylogenetic Analyses

DNASp 6 v 6.12.03 (Rozas et al. 2017) was used to determine genetic diversity parameters including the number of haplotypes (h), haplotype diversity (H_d), the number of segregating sites (s) and nucleotide diversity (π) (Nei 1987). A mismatch distribution was calculated using DNASp v. 6.12.03 for a population with a constant size (Rozas et al. 2017). The F_{ST}, which ranges from 0 to 1, was calculated to verify the level of genetic difference in the population due to genetic structure. A haplotype network was created using the Templeton, Crandall and Sing method (TCS) (Clement et al. 2004) in PopART (Population Analysis with Reticulate Trees) (Leigh and Bryant 2015). Rarefaction analysis was done using the R package vegan 2.6-4 (Oksanen et al. 2013) and graphed using the ggplot2 package (Wickham 2006).

Phylogenetic trees were generated using unique haplotype sequences for each gene fragment using BEAST (Bayesian evolutionary analysis by sampling trees) v. 1.10.4 (Drummond and Rambaut 2007). The run files were generated in BEAUTi (Bayesian Evolutionary Analysis Utility) v. 1.10.4, and the closest taxonomic relative, the Subantarctic fur seal (*Arctocephalus tropicalis*, sample from this study, from a specimen accessioned to the Port Elizabeth Museum at Bayworld) was used for calibration of the molecular clock based on published data from the split of the species (1.17 mya) (Lopes et al. 2021; Yonezawa et al. 2009). In addition, one haplotype from the conspecific Australian fur seal was also included as this is a recent divergence. The HKY model was determined to be the best fit substitution model by MEGA11 (Tamura et al. 2021). A strict clock with a Coalescent: Bayesian Skyline tree type was used. A chain length of 10 million generations was used and set to echo every 1000 trees. Using TreeAnnotator v. 1.10.4, the burnin was set to 20%. Trees were viewed and formatted using FigTree v1.4.4 (Letunic and Bork 2024).

3.2 | Population Structure

A pairwise F_{ST} comparison and a global test of differentiation were done in Arlequin v 3.5.2.2. (Excoffier and Lischer 2010) to evaluate population differentiation using a matrix to test for significant differences. A global test of differentiation is based on an exact non-parametric procedure using a Markov chain method. The partitioning of genetic structure among populations was determined through the analysis of molecular variance (AMOVA) also using Arlequin (Excoffier and Lischer 2010) as described in Excoffier et al. (1992), and a total of eight localities were included (Black Rocks, Robberg, Mossel Bay, Kleinsee, van Reenen's Bay, Atlas Bay, Cape Cross and Cape Frio). The Desert Diamond dataset was not included in the AMOVA because the specimens were collected while foraging offshore and could not be traced to a specific colony. The Lento et al. (1997) dataset was removed due to the sample localities being unknown. For cytb, two Agulhas subgroups were analysed: Mossel Bay and Robberg were treated as one subgroup, whereas Black Rocks was treated as a separate subgroup. For the D-loop region, two AMOVA were done. For the first, colonies were grouped into two groups based on whether they were situated on the south or west coast. The three south coast colonies included Mossel Bay, Robberg and Black Rocks, whereas the five west coast colonies were Kleinsee, van Reenen's Bay, Atlas Bay, Cape Cross and Cape Frio. For the second AMOVA, colonies were split into three groups: Those on the west coast split into one group, and the colonies on the south coast were split into two groups, as done for cytb. It was found that the first AMOVA gave the most significant results. To further assess genetic diversity in the Cape fur seal population, migration rates (M) between colonies were calculated using population pairwise genetic distances calculated in Arlequin v 3.5.2.2 for a haploid population using the method described in Raymond and Rousset (1995) and Slatkin (1991).

4 | Results

4.1 | Genetic Diversity

A total of 178 samples were sequenced for mitochondrial cytb. Sequences generated were approximately 176–377 bp and were trimmed to a consensus of 289 bp. The sequences contained 19 variable sites (6.6%), consisting of nine parsimony-informative sites, 10 singletons and no indel (insertion and deletion) sites. Overall haplotype diversity (H_d), including 16 published sequences from Lento et al. (U18448.1-U18448.9, U18449.1, U18451.2 and U18452.1-U18455.1), was 0.58 with a nucleotide diversity of 0.0027. Haplotype diversities of the cytb region for the three southern colonies of Cape fur seal ranged between 0.44 and 0.64 (Table 1) with the maximum occurring in Robberg Ledges ($H_d = 0.64$) and the minimum in Mossel Bay ($H_d = 0.44$).

D-loop was successfully amplified for 139 samples. The sequences generated ranged from 395 to 722 bp before being

TABLE 1 | Genetic parameters in each locality for cytb (in parenthesis south coast only) and D-loop. Number of samples (n), number of haplotypes (N_h), number of private haplotypes (N_{PH}), haplotype diversity (H_d), nucleotide diversity (pi, π), number of segregating sites (s), average number of nucleotide differences (k) and Tajima's D statistic.

Colony	Sub-group	*N*	N_h	N_{PH}	H_d	π	s	k	Tajima's D
Benguela									
Cape Frio	West	11	11	6	1	0.01207	18	4.309	−1.55
Cape Cross	West	9	9	1	1	0.01152	13	4.111	−0.67
Atlas Bay	West	10	10	1	1	0.01326	17	4.733	−1.05
Van Reenen's Bay	West	10	9	3	0.978	0.00865	11	3.089	−0.92
Kleinsee	West	30	22	8	0.975	0.01086	26	3.841	−1.52
Overall	West	70	44	19	0.979	0.01136	37	4.067	
Agulhas									
Mossel Bay	South	8 (11)	8 (2)	0 (0)	1 (0.436)	0.0094 (0.0015)	13 (1)	4.428 (0.436)	−1.00 (0.67)
Robberg	South	29 (40)	21 (9)	3 (3)	0.978 (0.635)	0.0092 (0.0030)	25 (6)	4.320 (0.866)	−1.55 (−1.32)
Black Rocks	South	90 (107)	38 (13)	13 (5)	0.966 (0.585)	0.0115 (0.0026)	36 (8)	4.101 (0.750)	−1.32 (−1.39)
Overall	South	127 (157)	44 (16)	16 (8)	0.965 (0.584)	0.0108 (0.0026)	38 (9)	3.862 (0.754)	(−1.69)
Total	**All**	**209 (157)**	**65 (16)**	**35 (8)**	**0.966 (0.584)**	**0.0106 (0.0026)**	**48 (9)**	**3.800 (0.754)**	**−1.60 (−1.69)**

trimmed to 364 bp to accommodate the length of the sequences downloaded from GenBank. The sequences contained 48 variable sites (13.2%), consisting of 35 parsimony-informative sites, 13 singletons and six indels. Overall haplotype diversity, including 69 published sequences (DQ176872-DQ176941), was high ($H_d = 0.97$) with a nucleotide diversity of 0.0106. Analysis conducted per region (west and south) identified similar diversity estimates for west ($H_d = 0.99$, $\pi = 0.0110$) and south ($H_d = 0.98$, $\pi = 0.0100$), respectively (Table 1). In the west, haplotype diversity was high, with multiple localities having a haplotype diversity of 1 (Cape Frio, Cape Cross and Atlas Bay). In the south, haplotype diversity ranged from 0.97 (Black rocks) to 1 (Mossel Bay). The three south coast colonies (127 samples) had a high haplotype diversity of 0.97 with a nucleotide diversity of 0.0108. The five west coast colonies (70 samples) had 44 haplotypes with a high haplotype diversity of 0.98 and nucleotide diversity of 0.0113 (Table 1).

Tajima's D values and Fu's F statistics were negative for both cytb (−1.69 and −1.52) and D-loop (−1.60 and −1.72) but not significant ($p > 0.05$). The mismatch distribution using a model of constant population size (Figure 2c) showed a unimodal graph for both genes (skewed for cytb). A low raggedness index for both genes (cytb: 0.0992, D-loop: 0.0193) was observed.

4.2 | Population Differentiation and Structure

Both the cytb and D-loop haplotype networks suggest a recent population expansion (Figure 2b,c). The most common haplotype was present in all colonies in both genes. The cytb network has a star-shaped phylogeny, and the most common haplotype accounted for 62% ($n = 120$) of samples, with the second most common haplotype accounting for 21% of samples ($n = 41$); both were present in all colonies (Table S1). The eight private haplotypes were found among two colonies ($n = 5$ for Black Rocks and $n = 3$ for Robberg). Rarefaction analysis showed that Robberg and Black Rocks were not sampled to completion, but Mossel Bay was (Figure S1) as Mossel Bay was the only sampling site that had reached an asymptote, despite having the fewest samples. The haplotype network for D-loop had haplotypes that were shared between all colonies, suggesting incomplete lineage sorting, as the haplotypes have not coalesced into a common ancestral haplotype. Three haplotypes were shared widely, accounting for 17.2% ($n = 36$) of the samples. Of 35 private haplotypes, 19 were found in the west coast (Benguela) colonies, and 16 were found in the south coast (Agulhas) colonies. Of the eight colonies that were included in this study, seven had private haplotypes (Table 1). Rarefaction analysis showed that none of the colonies were completely sampled, as none had reached an asymptote (Figure S1).

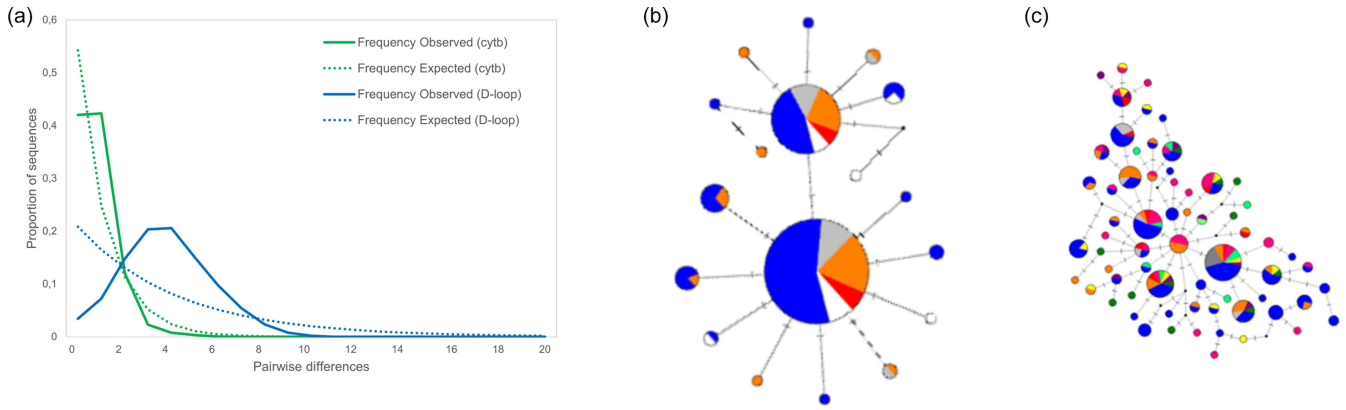


FIGURE 2 | Haplotype network of (a) cytb and (b) D-loop. For each haplotype network, colours correspond to the colony of origin and the size of the circle indicate the number of individuals with that haplotype. (c) Pairwise difference comparison of the populations for each of the two genes.

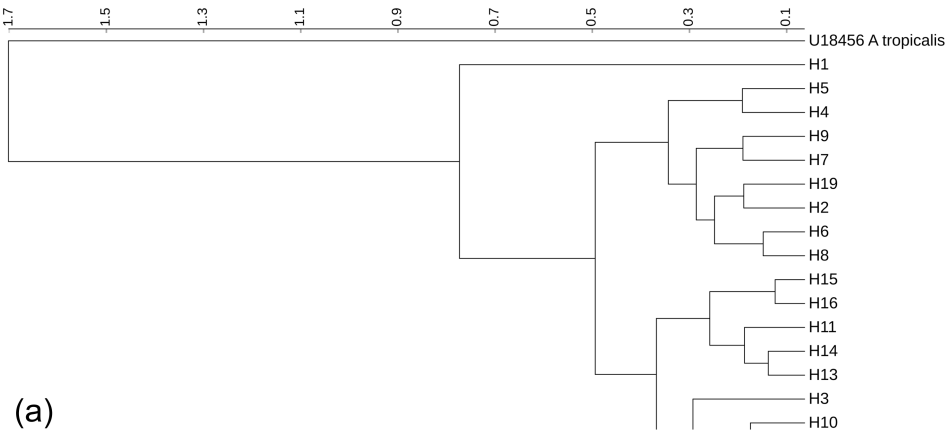


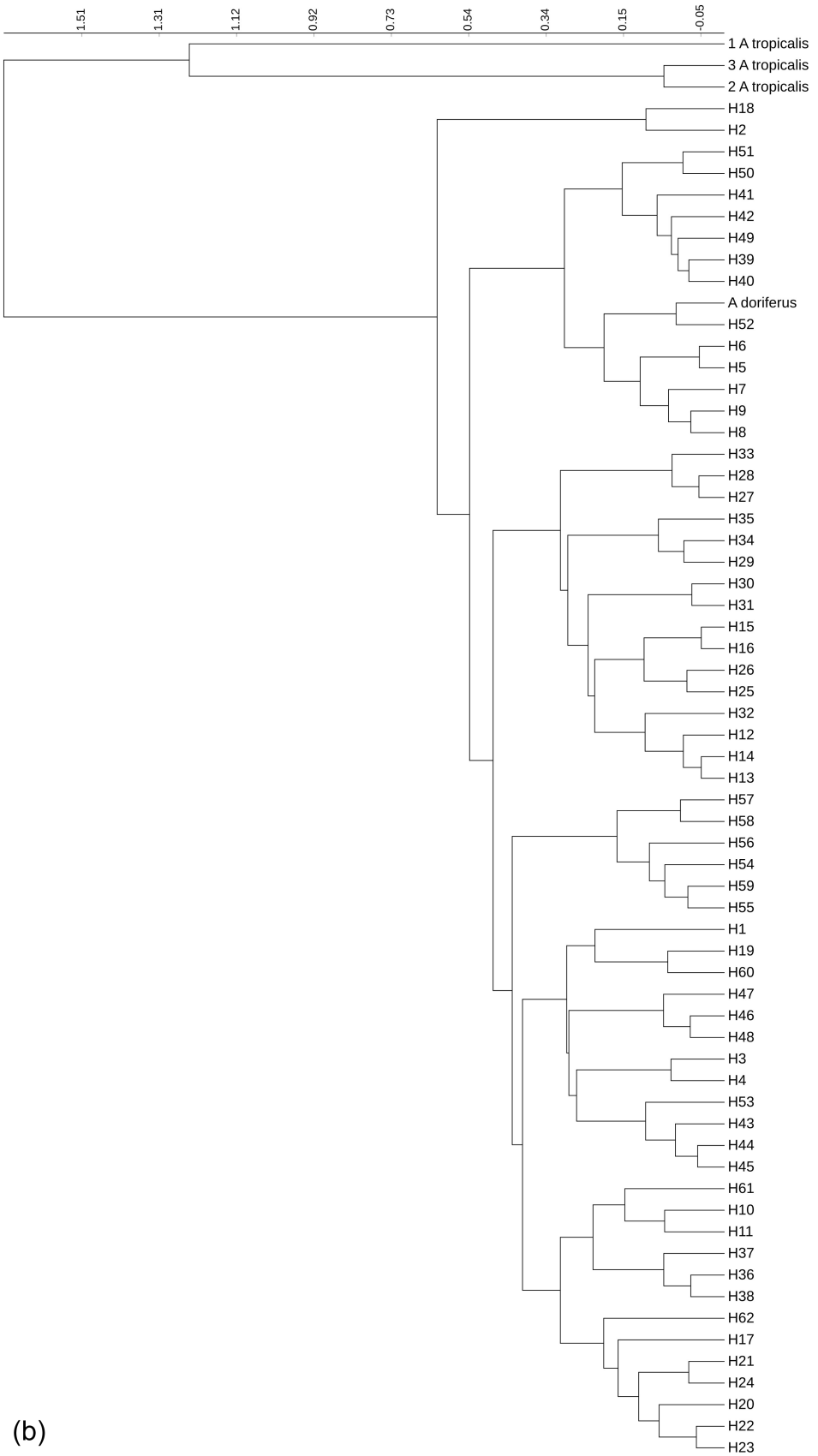
FIGURE 3 | Time tree of (a) cytb and (b) D-loop using the subantarctic fur seal (*Arctocephalus tropicalis*) as an outgroup.

The phylogenetic trees for cytb and D-loop (Figure 3) displayed no correspondence between the topology and geographical origin of the samples, indicating a lack of geographic sub-structure. The Australian fur seal closely grouped within the haplotypes of the Cape fur seals, further confirming the close relation between these subspecies based on these two mitochondrial DNA markers.

The results of the AMOVA among colonies and subgroups were not significant ($p < 0.05$) for all cytb subgroup comparisons. However, the F_{ST} and F_{CT} values for this dataset were negative, indicating greater variation within defined subgroups and colonies than among them. High migration rates between colonies suggest high levels of gene flow among Cape fur seal colonies (Figures S1a–S1c). For the D-loop dataset, the AMOVA was significant ($p < 0.05$) for comparisons between two subgroups [West coast colonies on the Benguela (Cape Frio, Cape Cross, Atlas Bay, van Reenen's Bay and Kleinsee) versus South coast colonies on the Agulhas (Mossel Bay, Robberg and Black Rocks)]. However, a negative F_{ST} value indicated a higher variation among individuals in colonies within subgroups. This was supported by the statistically significant ($p < 0.05$) positive F_{CT} value, which indicates high genetic variation within colonies (Table 2 and Figures S2b and S2).

5 | Discussion

Here, for the first time, we assessed the genetic diversity of Cape fur seals in their southern distribution in the Agulhas ecoregion in South Africa, in addition to their genetic structure throughout their distribution range (west and south). Moderate haplotype diversity ($H_d = 0.44–0.64$) with low nucleotide diversity ($\pi = 0.003$) was observed for cytb, whereas high haplotype diversity ($H_d = 0.98–0.99$) and low nucleotide diversity ($\pi = 0.010–0.011$) were detected in the D-loop gene. Non-significant negative Tajima's D and Fu's F statistics indicate a population that is evolving neutrally. Diversity estimates identified here are similar to patterns observed in other fur seal species, including the New Zealand fur seal (*Arctocephalus forsteri*) (cytb: $H_d = 0.25–0.77$, $\pi = 0.001–0.011$, $n = 33$), the South American fur seal (*Arctocephalus australis*) (D-loop: $H_d = 0.88$, $\pi = 0.011$, $n = 36$) and the Australian fur seal (*A.p. doriferus*) (D-loop: $H_d = 0.71–0.91$, $\pi = 0.005–0.012$) (Malan et al. 2022). Following a historical population bottleneck due to overexploitation, Cape fur seal populations in South Africa and along the west coast of southern Africa have shown significant expansion and growth since the 1970s (Butterworth et al. 1995). Thus, despite the population bottleneck, it is unlikely that these sealing events have affected genetic diversity. Similarly, several seal species worldwide have



(b)

FIGURE 3 | (Continued)

TABLE 2 | AMOVA results showing gene flow between colonies for D-loop and in brackets cytb for two subgroups. Significant values are indicated with an asterisk.

Source of variation	Sum of squares	Variance components	Percentage of variation	Fixation indices	*p*
Among groups	2.62 (2.62)	0.02 (0.02)	0.80 (0.99)	0.01471 (−0.02)	1.00 (0.12)
Among colonies within groups	3.22 (8.62)	−0.03 (−0.03)	−1.46 (−1.49)	−0.01 (−0.01)	0.98 (0.99)
Within colonies	292.68 (369.48)	2.00 (2.00)	100.66 (100.50)	0.01 (0.01)	0.03* (0.93)
Total	**299.35 (380.72)**	**1.95 (1.95)**			

experienced population declines due to exploitation, followed by rapid population expansion due to legislation against seal harvesting. In addition, population resilience has been aided by their generalist foraging behaviour. An extreme example of this is the Antarctic fur seal, which was hunted to near extinction. It has since recovered to an estimated population high of 3.5 million individuals at its largest breeding colony in 2009, though the species has experienced a subsequent decline in abundance (Forcada et al. 2023). The Australian fur seal population size has doubled between 1960 and 2002 (Kirkwood et al. 2005), and New Zealand fur seals have an overall population that is increasing (Chilvers 2023) despite some breeding colonies decreasing due to bycatch mortality (Abraham and Berkenbusch 2017).

Here, recent population expansion in Cape fur seals was supported by the difference between the expected and observed pairwise distance graphs. In addition, like other seal species, the cytb haplotype network of Cape fur seal displayed a star-shaped phylogeny. A star-shaped phylogeny, as seen in the cytb haplotype network, and incomplete lineage sorting, as seen in the D-loop haplotype network, are indicative of recent rapid population expansion. There were also several unique haplotypes on the edges of the distribution range of the Cape fur seal, namely, Black Rocks and Cape Frio. Unique haplotypes are more likely to be observed on the edges of an organism's distribution range as the environmental conditions are at the limits of the organism's adaptation and could be an indication of some population structure and isolation (Eckert et al. 2008).

In general, genetic structure in pinnipeds can be shaped by several factors, including geographic barriers (Bickham et al. 1998), climatic events (De Oliveira et al. 2009; Goldsworthy et al. 2000), sex-biased dispersal and philopatry (Giardino et al. 2016), as well as anthropogenic activities. The evidence for geographic barriers shaping genetic structure in pinnipeds is clearly evidenced by the subspeciation of Cape and Australia fur seals. Further, coastal waters in southern Africa are characterized by complex oceanographic processes that can influence the connectivity of marine populations (Bryan-Brown et al. 2017). Lett et al. (2024) have identified seven corridors and eight barriers to marine connectivity in southern Africa using data from biophysical modelling and ecological and molecular studies (Lett et al. 2024). The Cape Agulhas barrier occurs between southern and western Cape fur seal populations and can constitute a physical barrier to connectivity as two different upwelling regimes occur on either side (Chang et al. 2009). Several species have demonstrated genetic structure due to this barrier, including the abalone *Haliotis midae* (Evans et al. 2004; Van der Merwe 2009), the klipfish *Clinus cottoides* (von der Heyden et al. 2008) and the coastal shark *Mustelus mustelus* (Maduna et al. 2016). Furthermore, Cape Agulhas has been suggested to be responsible for speciation in a number of genera of dolphins via the so-called South African Species Gate (Perrin 2007). However, other species such as goby *Caffrogobius caffer* (Neethling et al. 2008) and the silver kob *Argyrosomus inodorus* (Mirimin et al. 2016) do not show genetic differentiation. Four eastern areas (Natal pulse, Wild coast, Waterfall bluff and KwaZulu Natal bight) have been identified as potential barriers to species movement due to differences in temperature, hydrodynamics and/or complex and unpredictable hydrographic features (Lett et al. 2024). These barriers are unlikely to affect Cape fur seals as they inhabit both coastal and marine environments. These barriers also affect prey distribution; however, as Cape fur seals are generalist predators that feed on a mix of pelagic and benthic species (Connan et al. 2014), it is unlikely that changes in prey species will pose a barrier to their own movements. However, it should be noted that seals forage at areas of increased abundance of fish stocks (Botha et al. 2023).

In this study, both cytb and D-loop analyses identified an absence of significant geographic structure with high levels of gene flow within and between colonies from the southern and western distribution range, demonstrating that Cape fur seals can traverse the Atlantic and Indian Oceans. Our results thus support findings reported by Matthee et al. (2006) showing a lack of population structure in Cape fur seals in the west. Here, we also suggest that the Cape fur seal forms a single panmictic unit throughout their local range. The lack of significant population structure likely reflects the species high genetic connectivity, high mobility, small distribution area compared to other fur seal species and large foraging areas within their small distribution area, as well as a lack of geographical boundaries, whereby individuals from several different breeding colonies can mix. Geographical structuring of populations may be additionally due to behavioural processes. Records of the movements of tagged seals suggest male and female site philopatry in Cape (Oosthuizen 1991) and Australian fur seals (Oosthuizen 1991; Warneke 1975) that are expected to reduce gene flow between populations. Whereas adult Cape fur seals are thought to show high site fidelity, immature seals may move between colonies (Oosthuizen 1991), a trait that is common among fur seals (Boyd 2002). However, our mtDNA results do not show

any evidence that suggests site philopatry is strong enough to result in any regional substructure, as seen in previous studies by Lancaster et al. (2010) and Matthee et al. (2006). Further, previous studies have demonstrated that 10 or more migrants per generation is sufficient to prevent genetic differentiation due to genetic drift (Mills and Allendorf 1996). Here, the number of migrants varied from 27.63 to infinite, supporting a single panmictic unit due to abundant migration maintaining high genetic diversity. High and significant F_{ST} values were identified between Cape Frio and Black Rocks ($p = 0.044$) as well as Kleinsee and Black Rocks ($p = 0.015$), which may be attributed to genetic structure between samples among colonies. The lack of significant population structure has been reported in other species of fur seals, including the Australian fur seal (Lancaster et al. 2010). These authors attributed the absence of genetic differentiation between populations to the movement patterns of seals (adult females identified with pups at different colonies) and due to the close proximity of colonies facilitating gene flow. In South American fur seals, an absence of genetic structure was observed between populations from the Atlantic Ocean and Guafo Island, whereas populations in Peru were highly divergent (De Oliveira et al. 2009). These authors attributed this finding to the isolation of the Peruvian population during the Late Pleistocene glaciation.

In conclusion, the Cape fur seal population is a single panmictic unit throughout its distribution range despite high levels of site philopatry and populations being separated by different major currents. The severe population bottleneck caused by past hunting activities followed by rapid population recovery has not affected mitochondrial genetic diversity. However, as mitochondrial DNA evolves independently of the nuclear genome, it may not be the best indicator for total genetic diversity (Nabholz et al. 2008). There is also a disparity between Tajima's D and Fu's F statistics, which indicate that the population is not expanding significantly, and other parameters, which show that it is. This study also only used two genes, which are not a representation of the full genetic diversity of an individual. Thus, to elucidate fine-scale genetic structure and a deeper insight into the genetic diversity of the Cape fur seal population, further studies using full genomes are required.

Ethics Statement

Ethical approval for this study was obtained from the University of Pretoria Ethics committee (NAS059/2022); permits for collection of samples were obtained by the Port Elizabeth Museum at Bayworld (RES2022-63), permits to possess samples from listed or threatened species were obtained by Bayworld Museum (29101), and a loan agreement between Bayworld and the author was obtained for use of samples (2022-005).

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/genbank/ accession number [PV920065–PV920202].

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Supporting Information

Additional supporting information can be found online in the Supporting Information section. **Table S1:** Distribution of twenty haplotypes of the cytb gene from three breeding colonies and two unknown localities of the Cape fur seal. **Table S2:** Distribution of 65 haplotypes of the D-loop gene from eight breeding colonies and one unknown locality of the Cape fur seal. **Figure S1a:** Population structure of cytb and D-loop. A schematic indicating the migration rate between colonies for cytb. For simplicity, any connections that were infinite were removed. **Figure S1b:** Population structure of cytb and D-loop. A matrix of pairwise comparisons for the different colonies for cytb. **Figure S1c:** Population structure of cytb and D-loop. A schematic indicating the migration rate beween colonies for D-loop. **Figure S1d:** Population structure of cytb and D-loop. A matrix of pairwise comparisons for the different colonies for D-loop. **Figure S2a:** Rarefaction analysis for cytb. **Figure S2b:** Rarefaction analysis of D-loop. **Figure S2:** Legend for rarefaction analysis.