Genetic Variation of Southern Hemisphere Fur Seals (*Arctocephalus* spp.): Investigation of Population Structure and Species Identity

G. M. Lento, M. Haddon, G. K. Chambers, and C. S. Baker

We have examined phylogenetic and geographic patterns of variation in the mitochondrial cytochrome *b* gene of Southern Hemisphere fur seals (*Arctocephalus* spp.). Our survey of 106 individuals from four putative species reveals three distinct patterns of variation reflecting ancient, recent historic, and contemporary gene flow. For the combined samples of Subantarctic (*Arctocephalus tropicalis*) and Antarctic (*Arctocephalus gazella*) fur seals, we find low levels of sequence diversity and reciprocal paraphyly of haplotypes (where representative haplotypes of a species are found to occur infrequently in another species and vice versa). For the Australian and Cape fur seal subspecies (*Arctocephalus pusillus doriferus* and *A. p. pusillus*, respectively), we find low levels of sequence diversity but significant differences in the regional distribution of haplotypes that are consistent with, but not conclusive of, the current subspecies definition based on nonmolecular data. For the New Zealand fur seal (*Arctocephalus forsteri*), we find high levels of average sequence diversity because of the survival of two divergent lineages of mitochondrial haplotypes with differences approaching that found in interspecific comparisons of other mammals. The two divergent clades are distributed sympatrically in some regions, but the overall geographic structure of the variation is significant across the range of this species. These new molecular data are inconsistent with current taxonomic definitions of species within the Southern Hemisphere fur seals and argue for reevaluation of these "species" definitions. For management purposes, the definition of evolutionarily significant units (Ryder 1986) and genetic management units (Moritz 1994) in relation to these species may also be evaluated in light of this molecular genetic information.

Fur seals are marine representatives of the mammalian order Carnivora. They are aquatic feeders but maintain coastal rookeries and haul-outs for mating and pupping. Fur seals exhibit a noncooperative breeding scheme in which territorial males maintain harems of adult females. Behavioral studies report considerable fidelity to natal rookery (philopatry) in females and moderate philopatry in males (Riedman 1990; Mattlin RH, personal communication). Nonbreeding adolescents of both sexes are not present on the rookeries during the breeding period and remain vagrant in ocean ranges with currently unknown boundaries. Though fur seals do not exhibit regular seasonal migration, they are capable of dispersal over large distances (Riedman 1990). Current taxonomy recognizes eight species of fur seal based primarily on their geographic ranges, and secondarily on overlapping morphometric characters and behavioral traits, including vocalization, where their ranges coincide (Repenning et al. 1971). All pinnipeds, fur seals and sea lions (*Otariinae*), walruses (*Odobenidae*), and true seals (*Phocidae*) were subject to severe exploitation during the seal harvests of the early 1800s. Many populations were exterminated and most species were markedly reduced by this hunting. For example, in the New Zealand region, one sealing gang alone reported a take of over 60,000 New Zealand fur seal skins from Antipodes Island; during one season prior to 1815, over 100,000 New Zealand fur seal skins were reported taken from Macquarie Island (Mattlin 1987). Populations of New Zealand fur seals at both islands were exterminated by 1820 (Shaughnessy and Fletcher 1987). Today the estimated population of New Zealand fur seals at Antipodes Island is 1,100 individuals (Mattlin 1987) and 1,200 individuals at Macquarie Island (Shaughnessy and Fletcher 1987). The current estimated number of New Zealand fur seals across their entire range is 66,000 individuals (Mattlin 1987; Shaughnessy and Fletcher 1987).

The pinnipeds have consistently been found to exhibit low levels of genetic polymorphism. For example, no mitochondrial cytochrome *b* sequence variation was found among 40 California sea lions (*Zalophus californicus californicus*; Maldonado et al. 1995). Low genetic variability is also reported for regions of the nuclear ge-

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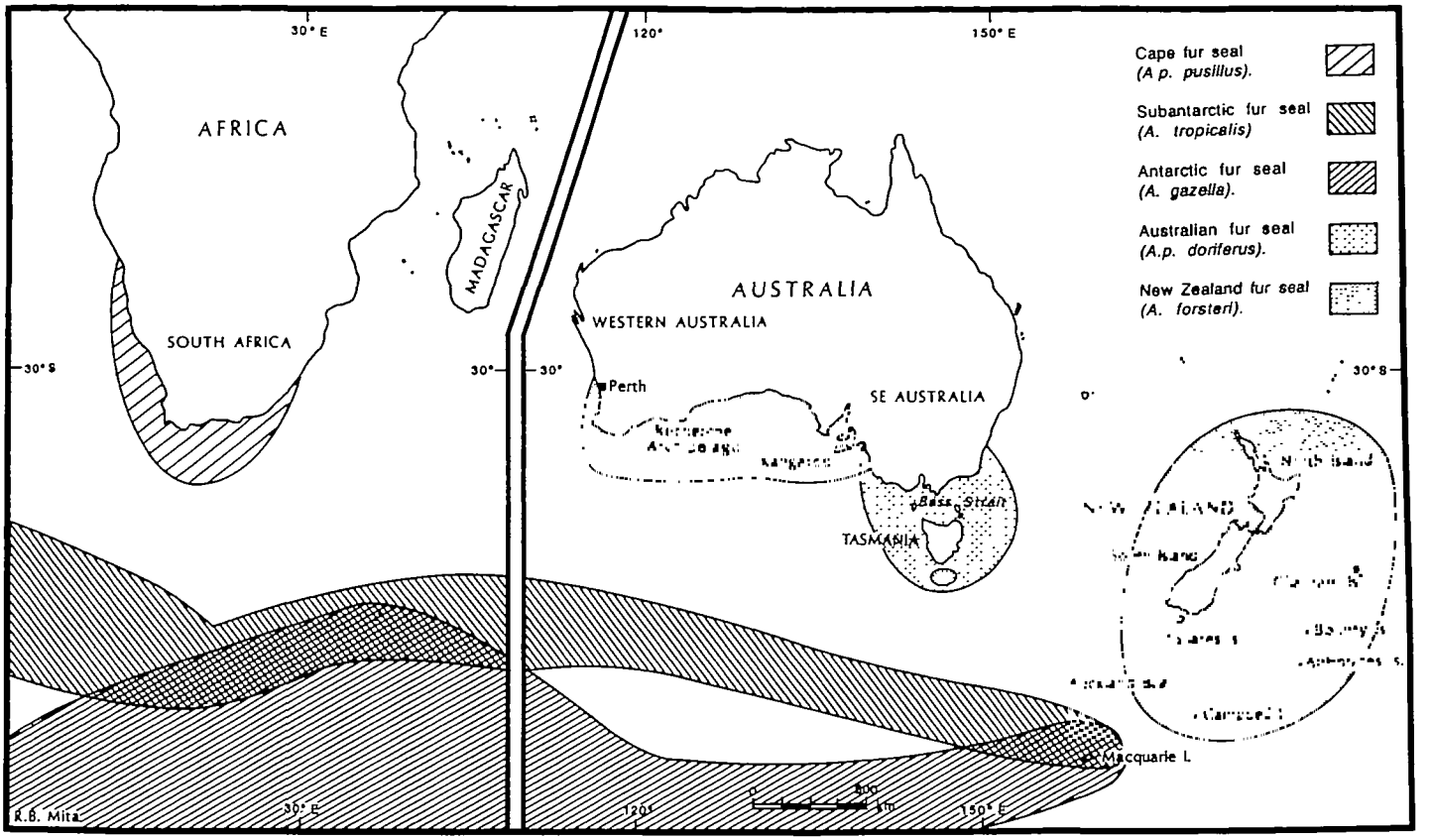

Figure 1. Ranges of the Southern Hemisphere fur seals used in this study [adapted from Croxall and Gentry (1987)]. The stippled and cross-hatched ranges indicate the area in which breeding rookeries for each species are found.

nome of pinnipeds (Slade 1992; Slade et al. 1994). Slade (1992) also measured relative rates of nucleotide substitution among several pinniped and terrestrial carnivore species. Assuming the fossil record is correct (Wayne et al. 1988; Wayne and O'Brien 1987), Slade (1992) proposed that pinnipeds exhibit rates of nucleotides substitution slower than those for any other species included in that study.

In contrast with this low variability in pinnipeds, a study of cytochrome *b* sequence variation among New Zealand fur seals (*Arctocephalus forsteri*) revealed a relatively high level of haplotype divergence (Lento et al. 1994). In the present study we have extended our survey to include cytochrome *b* sequences from four congeneric species of Southern Hemisphere fur seals to compare their genetic variation and population structure and to test the generality of our observation in the New Zealand fur seal. We evaluated mitochondrial DNA (mtDNA) diversity within each species or subspecies and compared the resulting gene trees to the current species trees to verify or challenge current taxonomic classifications.

We found three distinct phylogeographic patterns of mitochondrial cytochrome *b* haplotypes among these related species. These results have implications for defining both evolutionarily significant units (ESUs; Ryder 1986) and genetic management units (MUs; Mortiz 1994) among Southern Hemisphere fur seals.

Materials and Methods

We collected a total of 106 samples from the four described fur seal species throughout the Southern Hemisphere (Figure 1 and Figure 2, column 3). Skin samples from 106 fur seal pups were clipped from the tip of a digit on a hind flipper. Total cellular DNA was extracted, amplified, and sequenced as described in Lento et al. (1994). Cytochrome *b* sequence data were read manually from autoradiographs and aligned by comparing the translated sequences to the published amino acid sequence of harbor seal cytochrome *b* (Árnason and Johnsson 1992) and to cytochrome *b* sequences from several other vertebrate species (Irwin et al. 1991).

We surveyed 25 Australian fur seals (*A. pusillus doriferus*) and 17 Cape fur seals (*A. p. pusillus*). The Australian fur seal samples represent about 95% of their breeding range, whereas the Cape fur seal samples were collected from only two localities representing an unknown, but likely only moderate, proportion of their breeding range. The Australian and Cape fur seals are currently classified as subspecies based on geographic range and minor differences in skull morphometrics (Repenning et al. 1971; King 1968). We also surveyed 56 New Zealand fur seals from 15 localities representing about 95% of their breeding range. The total New Zealand fur seal population forms a group that is morphologically and ecologically consistent with a single species definition. Due to limited accessibility of Subantarctic (*A. tropicalis*) and Antarctic fur seals (*A. gazella*), we were able to obtain samples of only four individuals from each species. All eight samples were taken from Macquarie Island, an Australian subantarctic island approximately 1000 km southwest of New Zealand and 1200 km southeast of Tasmania. Macquarie Island is one of two localities where the breeding ranges of these two species overlap (Figure 1). The Subantarctic and Antarctic fur seals are currently described as separate species

H'type class*	Haplo-type	(Total)	No. of individuals per h'type	Variable positions 1111111111122222222222222223333333333 1112235678800244567899011233344445788911122234456 0294760051558447152958439824703599627125847992810	Changes relative to haplotype NZA
	NZA		14	ACATAAATTTGCCGCATTATACCATCATTGCTCACCTCCACGTTACCCA	-
	NZB		3	.....T.....	1
I	NZG	(41)	1	.....C..A.....C.....	3
	NZH		1	.....C.....C.....C.....	3
	NZC		4	.....G.....	1
	NZD		9	.....C.....C.....	2
	NZE		1	C...G..C.C....TT.C.....G...C.....C.TG..AC.....	14
II	NZF		6	....G..C.C....TT.C.....C.....TG..A.....	12
	NZI		2	....G..C.C....TT.C.....G...C.....C.TG..AC.....	13
	†AntA		2	.T.C.G.C.C...A.T.....TT.A.G.....TA..T.TAAC.....	18
	AntB	(4)	1	.T.C.G.C.C...A.T..G..TT.A.G.....TA..T.TAAC.....	19
	‡AntC		1	.T.C.G.C.C...A.T.C...TT.A.G.....TA..T.TAAC.....	19
	†SubA		2	.T.C.G.C.C...A.T.....TT.A.G.....TA..T.TAAC.....	18
	SubB	(4)	1	.T.C.G.C.C...A.T.....TT.AT.....TA..T.TAAC.....	18
	‡SubC		1	.T.C.G.C.C...A.T.C...TT.A.G.....TA..T.TAAC.....	19
	§AusA		23	.TG.G..CCC.T.A.TCC.....G..CCAT.T.....T.AAGC.TTTG	26
	AusB	(25)	1	.TG.G.TCCC.T.A.TCC.....G..CCAT.T.....T.AAGC.TTTG	27
	AusC		1	.TG.G..CCC.TTA.TCC.....G..CCAT.T.....T.AAGC.TTTG	27
	CapeA		9	.TG.G..CCC.T.A.TCC.....G..CCAT.T.....T.AAGC.TT.G	25
	CapeB		1	.TG.G..CCC.T.A.TCC.C....G..CCAT.T.....T.AAGC.TT.G	26
	CapeC		1	.TG.G..CCC.T.A.TCC.....G..CCATCT.....T.AAGC.TT.G	26
	§CapeD		2	.TG.G..CCC.T.A.TCC.....G..CCAT.T.....T.AAGC.TTTG	26
	CapeE	(17)	1	.TG.G..CCC.T.A.TCC.....G...CAT.T.....TGAAGC.TTTG	25
	CapeF		1	.TG.G..CCC.T.A.TCC.....G...CAT.T.....T.AAGC.TT.G	24
	CapeG		1	.TG.G..CCC.T.A.TCC.....G..CCAT.T.....T.AAGCGTTTG	26
	CapeH		1	.TG.G..CC..T.A.TCC.....G..CCAT.T.....T.AAGC.TTTG	25

Figure 2. Summary alignment of variable positions of cytochrome *b* mtDNA sequence haplotypes. Position zero is set at the first nucleotide of the open reading frame (start codon ATG). Full sequences for each haplotype have been deposited to GenBank with accession numbers U12837, U12839, U12841, U18533–U18538, and U18448–U18464. The single and double daggers indicate pairs of identical haplotypes. The § indicates common haplotypes.

based on coat color differences in the pups and a notable difference in the weaning times of pups (12–14 weeks in the Subantarctic fur seal and 8–9 months in the Antarctic fur seal; Shaughnessy and Fletcher 1987).

To quantify the geographic structure of maternal lineages, we calculated the *H* statistics of Hudson et al. (Hudson et al. 1992). Like Wright's *F* statistic (Wright 1951), Nei's *G* statistic (Nei 1987), and Excoffier's Φ statistic (Excoffier et al. 1992), the *H* statistics reflect the proportion of sequence variation that is explained by the observed geographic distribution of haplotypes. The H_i values in each analysis are measures of haplotype diversity in each composite region, *i*. (where *i* = NZ, Aus, Aus', and Cape; for abbreviations, see notes to Table 2). A significant H_i value means that the observed distribution of haplotypes is unlikely to be the result of a random distribution of haplotypes among the sampling locations surveyed. H_S is a measure of haplotype diversity in the whole population considering population subdivision (i.e., a weighted average of all H_i, values). H_T is a measure of the whole population haplotype diversity disregarding population subdivision. H_{ST} is then a measure of the effect of population structure on haplotype diversity. These quantitative statistics are based on qualitative differences in haplotype frequencies: no weighting is made for the magnitude of sequence divergence. Hudson et al. (1992) have shown that haplotype statistics have the same power as *F* and *G* statistics for quantitative analysis of population structure. Haplotype statistics are a complex measurement as they indicate not only an amount of diversity, but also how evenly distributed that diversity is among the sampling locations.

Hudson et al. (1992) also present a further quantitative statistic, *K*, that accounts for the amount of sequence divergence between haplotypes in determining population structure. To examine the sequence diversity at this higher level of resolution, we have calculated the corresponding *K* statistics for the New Zealand fur seal and Australian/Cape fur seal populations using the program Permtest (provided by R. R. Hudson, University of California, Irvine, California).

Separate phylogenetic analyses of the Australian/Cape fur seals and the New Zealand fur seals were performed to examine migration events. Using sequences from each species, a branch-and-bound search for the most parsimonious tree was conducted using the PAUP program (Swofford 1993). The optimal neighbor-joining tree for each species was found using the PHYLIP software package (Felsenstein 1991). The four optimal trees from both methods were subjected separately to bootstrap analysis with 1,000 replicates. The topology of the consensus trees from both parsimony and neighbor-joining analyses for each species were identical and are supported by comparable bootstrap values, respectively.

Results and Discussion

Population structure was first examined by mapping the frequency distributions of mitochondrial cytochrome *b* haplotypes found among the New Zealand fur seal and the Australian and cape fur seals. Haplotypes were grouped for some of the statistical tests based on the locality of their highest concentration and, in the case of the New Zealand haplotypes, on sequence similarity.

Figure 2 is a summary of cytochrome *b* sequence variability observed in the four fur seal species surveyed. The absence of stop codons and frame shifts, the general conservation of inferred cytochrome *b* amino acid sequence and protein secondary structure, and a ratio of substitutions between first, second, and third codon positions that is comparable to previously

Table 1. Comparison of average percent sequence differences within and between Southern Hemisphere fur seal species

Species		Avg. difference (%)	Range (%)
Within species			
A. forsteri			
Type I clade	(New Zealand fur seal)	0.85	0.28–1.11
Type II clade	(New Zealand fur seal)	0.74	0.28–0.83
	Between types	3.40	2.22–4.20
A. pusillus			
pusillus	(Australian fur seal)	0.62	0.28–1.11
doriferus	(Cape fur seal)	0.37	0.28–0.55
	Between *Apu* subspecies	0.47	0.28–1.11
A. tropicalis	(Subantarctic fur seal)	0.55	0.28–0.83
A. gazella	(Antarctic fur seal)	0.37	0.28–0.55
	Between *A trop* and *A. gaz*	0.37	0.00–0.83
Between species			
A. forsteri type I	*Apu*	6.95	5.54–7.76
A. forsteri type II	*Apu*	6.71	6.09–7.48
A. forsteri type I	*A. trop/A gaz*	5.31	4.99–5.54
A. forsteri type II	*A. trop/A. gaz*	5 28	4.71–5.82
Apu	*A. trop/A gaz*	6 90	6.09–7.48

reported ratios (Árnason et al. 1993; Árnason and Johnsson 1992) indicate that the sequences are aligned unambiguously and are not nuclear homologs of cytochrome *b* (Irwin et al. 1991; Lento et al. 1994). In each species we found a number of haplotypes. Table 1 shows the average percent sequence differences between the haplotypes within and between each species. The data in Figure 2 and Table 1 provide insights into comparative population structure in the five species or subspecies of Southern Hemisphere fur seals. Examination of this structure revealed three distinct and unexpected patterns of mtDNA variation.

Subantarctic and Antarctic Fur Seals: No Fixed Genetic Differences

We found three haplotypes within each of these two species differing by an average of 0.55% and 0.37%, respectively. The haplotypes from each species differ from each other by 0.00–0.83% (Table 1). The Subantarctic and Antarctic fur seal individuals examined share two of the four unique haplotypes found among them. Consequently the species identity of six of the eight samples is indeterminable (Figure 2). The four haplotypes are reciprocally paraphyletic (i.e., representative haplotypes of each species are found to occur among the other species). This is clearly inconsistent with a separate species distinction under the phylogenetic species definition.

One explanation for this finding is extensive hybridization between Subantarctic and Antarctic fur seals. These samples came from one of two areas where the breeding ranges of the two species overlap (Figure 1). Cross-mating behavior at Macquarie Island has been frequently observed (Shaughnessy P and Goldsworthy S, personal communication). However, assuming this interpretation is correct, one would predict that there should be deep divergence between some haplotypes representing the original distinct species. Such divergence was not evident in these data. The average percent sequence divergence is shallow compared to the New Zealand fur seal and similar to the Australian and Cape fur seals (only 0.55% for the two species combined; Table 1). This does not rule out extensive hybridization, but hybridization would not be phylogenetically consistent with these results unless the mtDNA of one species has completely replaced the mtDNA of the other in this zone of overlap. The data suggest that these two species share a recent common ancestor if we accept that the two species are hybridizing.

Australian and Cape Fur Seals: Low Sequence Diversity, High Geographic Structure

Among the 17 Australian fur seals we found three haplotypes differing from each other by an average sequence divergence of 0.37% (Table 1). Among the 25 cape fur seals, we found eight haplotypes differing from each other by an average of 0.62% (Table 1). The Australian and Cape fur seal subspecies differed by an average of 0.47% and shared one common haplotype (Table 1 and Figure 2).

The haplotype statistics for the Australian and Cape fur seals are shown in Table 2. Haplotype diversity is significantly lower in the Australian fur seal relative to the Cape fur seal as indicated by the H_i values (0.1567 and 0.7279, respectively). This is not surprising since 23 of the 25 individuals surveyed share a single haplotype and the two remaining individuals have unique haplotypes. The high H_{Cape} value reflects the occurrence of seven unique haplotypes (plus one shared haplotype) with similar frequencies within the Cape fur seal population. The H_{Cape} value does not differ significantly ($P = .9158$) from a random assortment of individuals among the eight haplotypes. Pairwise comparisons of the two regions using a randomized chi-square test (Roff and Bentzen 1989) are in agreement with the H statistics (results not shown).

The phylogenetic reconstruction suggests that the most parsimonious explanation for the observed distributions of haplotypes is that the Australian population is the result of a single, recent historical founder from the Cape fur seal followed by the accumulation of a few small mutations in some members of this lineage (Figure 2). The Cape and Australian fur seal populations are of phylogenetically "shallow," but geographically structured, divergence (Figure 3A).

Overall this survey of mitochondrial cytochrome *b* sequence variation is consistent with the subspecies definition currently held for the Cape and Australian populations based on nonmolecular data. However, we raise the question whether such paraphyly is necessarily a basis for a subspecies definition. Further, we do not find similar consistency between analogous molecular surveys and current species definitions for either the New Zealand fur seal or the Subantarctic and Antarctic fur seals.

New Zealand Fur Seals: High Sequence Diversity, High Geographic Structure

Among the 56 New Zealand fur seals, we found two deeply divergent clades of mitochondrial lineages. The average percent sequence divergence between clades is 3.4%, which is an order of magnitude larger than that found in either the Australian/Cape species or the Subantarctic/Antarctic "species" (Table 1). The maximum sequence divergence (4.2%) approaches an approximate threshold of divergence found for comparisons between closely related mammalian species using cytochrome *b* (5.0%; Irwin et al. 1991, Smith and Patton 1991). Pairwise comparisons of the average percent sequence difference

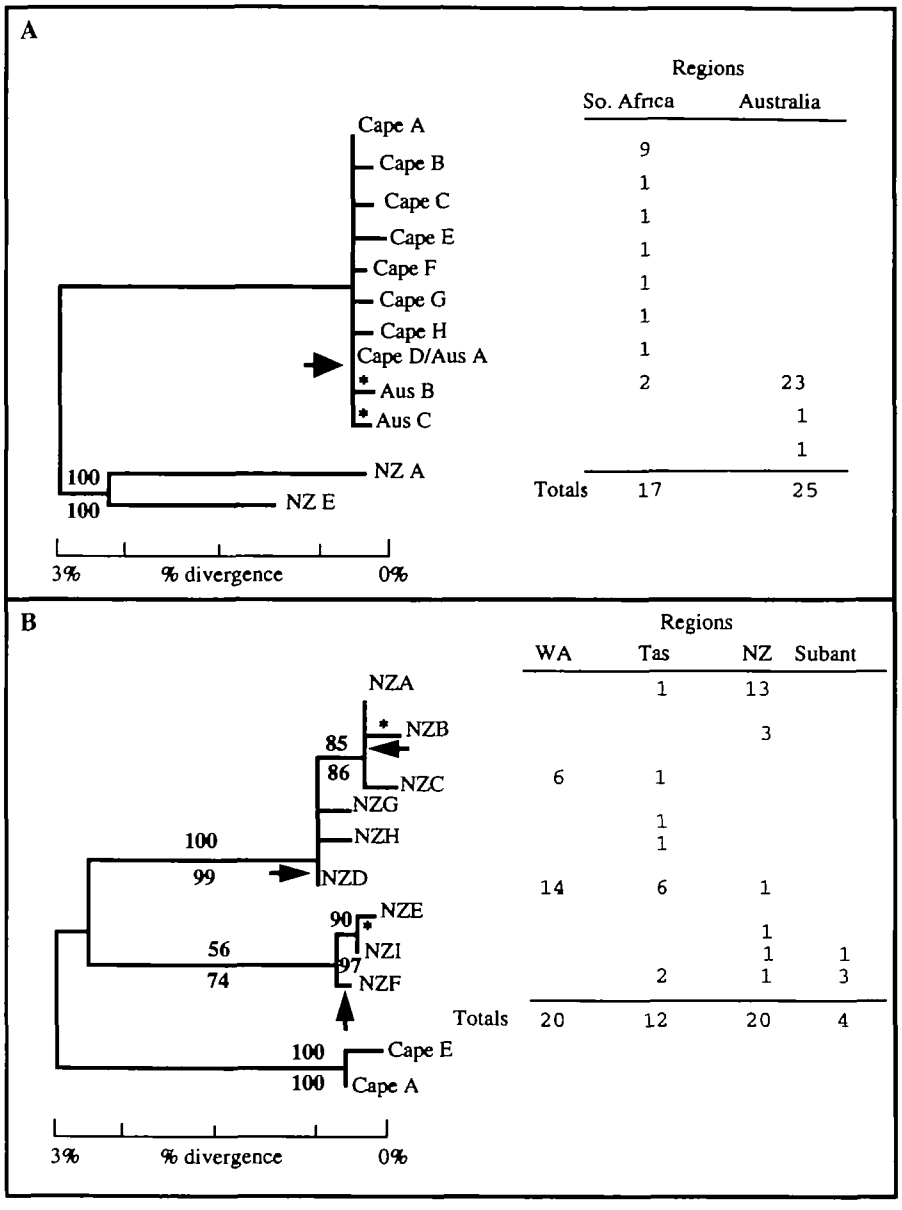

Figure 3. (A) Unrooted parsimony tree of Australian and Cape fur seal haplotypes using New Zealand fur seal haplotypes as outgroups (steps = 42; CI = 0.88). Taxa are labeled as in Figure 2. The neighbor-joining tree has the same topology and the terminal branch lengths are: 0.000 to Cape A and D and Aus A; 0.001 to Cape F; 0.002 to Cape H and Aus B and C; 0.003 to Cape B, C, and G; 0.004 to Cape E; 0.023 to NZA; 0.015 to NZE; and 0.046 for the single internal branch. Values above branches are percent bootstrap values for 1,000 parsimony replicates; those below the branches are the corresponding values for 1,000 neighbor-joining replicates. Arrows indicate migration events. Asterisks indicate hypothesized local mutation events. The geographic distribution of haplotypes has been juxtaposed next to the phylogenetic tree to suggest explanation of the migration and mutation events necessary to account for all haplotypes. None of the haplotypes are fixed, indicating that the variability is not dependent on physical distance between locations of individuals with these haplotypes. (B) The corresponding phylogenetic tree for New Zealand fur seal (*A. forsteri*) haplotypes using Cape fur seal haplotypes as outgroups (steps = 39, CI = 0.91). Again the neighbor-joining tree has the same topology and the terminal branch lengths are 0.000 to NZA, D, and I; 0.001 to NZF; 0.003 to NZB, C, G, H, and E; 0.002 to Cape A; and 0.007 to Cape E. Internal branch lengths are: 0.46 to the outgroups; 0.004 to NZE, F, and I and a further 0.008 to NZE and I; 0.018 to the remaining taxa; and 0.005 to NZA, B, and C. All other notes and symbols are as in (A).

between species for these fur seals are shown in Table 1. These new data support the findings of our earlier study of genetic variation in New Zealand fur seal (Lento et al. 1994).

The haplotype statistics for the New Zealand fur seals are shown in Table 2. These calculations were made for the two composite regions only (see Table 2 notes). The H_t values for each composite region both show notable variability within each region (0.6812 and 0.6089, for New Zealand and Australia, respectively). The H_S and H_T values are also large (0.6399 and 0.7909, respectively), indicating that there is high diversity in the population as a whole (high H_T value) and within population subdivisions (high H_S value). In contrast the H_{ST} value is small (0.1910), indicating that while there is considerable diversity within each region, there is little movement between regions that would lead to greater uniformity of this diversity across the whole population. In addition, results from analysis of geographic structure using the randomized chi square and AMOVA (Excoffier et al. 1992) agree with these H statistics (results not shown) that a considerable proportion of the diversity within this species is attributable to geographic structuring.

Table 2. Statistical analysis of geographic structure and diversity of New Zealand fur seals and Australian and Cape fur seals based on cytochrome *b* DNA sequences

	H statistics	Values	P
Aus/Cape fur seals (2 regions)	$H_{Aus'}$	0.1567	<.0001
	H_{Cape}	0.7279	.9158
	H_S	0.3879	<.0001
	H_{ST}	0.3638	<.0001
	H_T	0.6098	N/A
NZ fur seals (2 regions)	H_{NZ}	0.6812	.014
	H_{Aus}	0.6089	<.0001
	H_S	0.6399	<.0001
	H_{ST}	0.1910	<.0001
	H_T	0.7909	N/A
NZ fur seals (4 regions)	H_{Tas}	0.7576	.3411
	$H_{W/S\ Aus}$	0.5105	<.0005
	H_{WCS}	0.7000	.0818
	H_{EC}	0.6429	.1201
	H_S	0.6365	<.0001
	H_{ST}	0.1952	<.0001
	H_T	0.7909	N/A

Haplotype statistics are calculated as in Hudson et al. For New Zealand fur seals: *Tas* = three Maatsuiyer I rookeries; *W/S Aus* = western Australia plus southern Australia; *WCS* = west coast, New Zealand plus Snares Islands; *EC* = east coast, New Zealand; *NZ* = *WCS* plus *EC*; *Aus* = *W/S Aus* plus *Tas*

For Aus/Cape fur seals: *Aus'* = *A. p. doriferus* individuals sampled in Bass Strait, Australia; *Cape* = *A. p. pusillus* individuals sampled in South Africa. *P* values are based on 10,000 resamplings.

We performed phylogenetic analyses on the nine New Zealand fur seal haplotypes to investigate possible historical explanations for this diversity. Figure 3B shows the optimal tree from parsimony analyses of the New Zealand fur seal haplotypes (neighbor-joining analyses returned the same tree). Two Australian/Cape haplotypes are used as outgroups. From this tree we infer a minimum of three migration events and two subsequent mutation events to explain the relationships among these nine haplotypes. The tree also supports the division between the two apparent clades based on average percent sequence divergence (Table 1).

We suggest four possible interpretations for this finding. First, one of these clades, most likely Type II (Figure 2), which is

present in lower frequency in this sample, could represent a relic matrilineal mtDNA type from a once more abundant and diverse population of haplotypes. Given the range of sequence divergence and the estimated rate of evolution of the mitochondrial cytochrome *b* gene (2% per million years; Irwin et al. 1991), this would require survival over 1–2 million years and persistence through recent population bottlenecks as a result of hunting. This interpretation is not directly testable barring the genetic analysis of suitable subfossil material.

Second, the two divergent clades may be the result of intraspecific variation in evolutionary rates as suggested by Wayne et al. (1990) to account for a similar phylogeographic pattern found in the black-backed jackal in eastern Africa. In contrast to the study of black-backed jackals, however, there is geographic structure apparent in the frequency distribution of the New Zealand fur seal haplotypes in the present study (Table 2). Thus this current pattern of distribution does not favor this interpretation (intraspecific variation in evolutionary rates) over others. Further, our test of relative rates of evolution among haplotypes of all Southern Hemisphere fur seal species in this study (data not shown) does not show significant deviation from equality. However, there are not many comparable studies in the literature with which to compare our values.

Third, the two divergent clades may be the result of current or recent historical introgressive hybridization. Direct evidence for this interpretation would be the identification of the "parental" species. One possible parental pair might be the extant "New Zealand fur seal" and a species that no longer exists. Alternatively, the parental species may be the "New Zealand fur seal" and another extant *Arctocephalus* species that is not yet in our catalog of mtDNA types. This latter possibility is attractive because it is testable by surveying the mtDNA of other Southern Hemisphere fur seals; however, this possibility is not supported by our limited survey. None of the mtDNA haplotypes reported here resemble the mtDNA haplotypes of either New Zealand fur seal clade (see Figure 2). Other possible candidates include four other Southern Hemisphere fur seal species that have not yet been tested. These are the Juan Fernandez fur seal (*A. phillippi*), the Galapagos fur seal (*A. galapagoensis*), the South American fur seal (*A. australis*), and the Guadalupe fur seal (*A. townsendi*).

As mtDNA data do not provide conclusive information with respect to the possibility of hybridization, we suggest a fourth interpretation which we believe to be the most conservative and plausible hypothesis given the data provided by this survey. This interpretation is that of a secondary hybrid swarm of contact between two previously diverging populations or "subspecies." One can envision a population substructure before sealing exploitation that consisted of incipient allopatric speciation between the "New Zealand fur seal" ranging from western and southern Australia to the east and west coasts of New Zealand's South Island and a second potential subspecies, which perhaps may be called *A. forsteri snaresensis*, ranging throughout New Zealand's subantarctic islands including the Snares, Campbell, Chatham, Antipodes, and Bounty Islands. Subsequent to the cessation of large-scale sealing in the 1820s and 1830s, it is plausible that there was movement of the postulated divergent *A. f. snaresensis* populations toward recolonizing vacant rookeries on the New Zealand mainland, Tasmania, and Australia, creating a zone of secondary hybrid contact with the remnant "New Zealand fur seal" populations (which perhaps may be called *A. forsteri forsteri*). The so-called Upland seal is a candidate for the putative subspecies that is now lost due to this hybrid swarm [but see Richards (1995) and Shaughnessy and Fletcher (1987) for an alternative identification of the Upland seal].

At the present time, the phylogeographic pattern we find in this survey of mitochondrial cytochrome *b* haplotypes could be a partial reestablishment of the original distribution of haplotypes with considerable admixture in certain areas (e.g., Maatsukyer Island, Tasmania). Tasmania appears to be the coalescent for all nine haplotypes and is the center of diversity. Alternatively, this diversity could be the result of gene flow from the two distinct population centers, western Australia and New Zealand.

Conclusions

Three distinctly different patterns of molecular evolution and population substructure were found among these four congeneric fur seals. One might reasonably expect that congeneric species with comparable biology, ecology, and demographic history would also share similar patterns of molecular evolutionary change and consequent population substructure. Our survey of mitochondrial cytochrome *b* sequence variation reveals interesting contradictions to that expectation. First, the Subantarctic and Antarctic fur seals are reciprocally paraphyletic with low sequence divergence. This pattern is inconsistent with these two taxa being treated as separate species or ESUs, but is consistent with separate MUs (see below). Second, the Australian and Cape fur seal subspecies show highly structured geographic distribution suggestive of a recent historical migration event accompanied by an unexplained low level of sequence divergence. Third, the New Zealand fur seal population supports lineages with deep divergence bordering on species-level distinction. There is also notable geographic structure within this population that is otherwise morphologically and ecologically consistent with a single-species definition.

While this study provides another intriguing example of the common disparity between the molecular and nonmolecular definitions of a species, it provides important novel information on this marine mammal group for definition of ESUs and/or genetic MUs. Moritz (1994) suggests that "ESUs should be reciprocally monophyletic for mtDNA alleles and show significant divergence of allele frequencies at nuclear loci." MtDNA haplotypes (or alleles) do not exhibit the reciprocal monophyly within any of the species surveyed here that is required to define separate ESUs. Further, information on nuclear allele frequencies does not exist for any of these species at the level of comparison undertaken here. However, the reciprocal paraphyly exhibited in the Subantarctic and Antarctic fur seals may indicate a population at an intermediate state between separate species identity and hybridization.

Moritz (1994) also suggests that "MUs are . . . recognized as populations with significant divergence of allele frequencies at nuclear or mitochondrial loci, regardless of the phylogenetic distinctiveness of the alleles." With this theoretical definition of separate genetic MUs, and given the mtDNA haplotypes revealed in this study for the New Zealand fur seal, we make the conservative suggestion that individuals of the type II clade found in the Snares Islands region should be considered a separate MU from the type I individuals inhabiting the rest of the range. Further, given the very small proportion of western and southern Australia haplotypes found in the New Zealand region, it would be rea-

sonable to consider the New Zealand fur seals inhabiting Australian regions as a third MU.

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