Journal of Heredity 2007:98(2):147–157
doi:10.1093/jhered/esm005
Advance Access publication April 8, 2007

Mitochondrial DNA Diversity and Population Structure among Southern Right Whales (*Eubalaena australis*)

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Abstract

The population structure and mitochondrial (mt) DNA diversity of southern right whales (*Eubalaena australis*) are described from 146 individuals sampled on 4 winter calving grounds (Argentina, South Africa, Western Australia, and the New Zealand sub-Antarctic) and 2 summer feeding grounds (South Georgia and south of Western Australia). Based on a consensus region of 275 base pairs of the mtDNA control region, 37 variable sites defined 37 unique haplotypes, of which only one was shared between regional samples of the Indo-Pacific and South Atlantic Oceans. Phylogenetic reconstruction of the southern right whale haplotypes revealed 2 distinct clades that differed significantly in frequencies between oceans. An analysis of molecular variance confirmed significant overall differentiation among the 4 calving grounds at both the haplotype and the nucleotype levels ($F_{ST} = 0.159$; $\Phi_{ST} = 0.238$; $P < 0.001$). Haplotype diversity was significantly lower in the Indo-Pacific ($h = 0.701 \pm 0.037$) compared with the South Atlantic ($h = 0.948 \pm 0.013$), despite a longer history of exploitation and larger catches in the South Atlantic. In fact, the haplotype diversity in the Indo-Pacific basin was similar to that of the North Atlantic right whale that currently numbers about 300 animals. Multidimensional scaling of genetic differentiation suggests that gene flow occurred primarily between adjacent calving grounds within an ocean basin, with mixing of lineages from different calving grounds occurring on feeding grounds.

Southern right whales (*Eubalaena australis*) were once widely distributed across the 3 ocean basins in the southern hemisphere: the South Atlantic, the Indian Ocean, and the South Pacific (Townsend 1935). Extensive coastal- and vessel-based whaling reduced their numbers to near extinction during the 19th century (Dawbin 1986; Du Pasquier 1986). During the period from late 1700s to early 1900s, an estimated 48 000 whales were taken in the South Atlantic, 37 200 in the South Pacific, and about 12 500 animals in the Indian Ocean (Dawbin 1986; Du Pasquier 1986; Best 1987). The pre-exploitation population size is estimated to have been between 55 000 and 70 000 throughout the southern hemisphere (IWC 2001), although this estimate is likely to be low given the incomplete catch history and a possible female-biased ratio in the catches (IWC 2001; Baker and Clapham 2004).

Southern right whales occur in coastal waters for calving in winter months and tend to migrate offshore to feeding grounds during summer months. Migration patterns between winter calving and summer feeding grounds may be north–south (e.g., Australian calving ground to Southern Ocean and Antarctic Ocean feeding grounds, Bannister et al. 1997, 1999) as well as east–west movements (e.g., South Africa calving ground to Gough Island feeding grounds, Best et al. 1993). The International Whaling Commission has identified a number of calving grounds based on the distribution of current or historical sightings and catches (IWC 2001). Of the 11 winter calving grounds identified, 5 are showing signs of recovery: South Africa, Australia, Argentina, Brazil, and sub-Antarctic New Zealand (IWC 2001; Patenaude and Baker 2001; Groch et al. 2005).

Table 1. Sampling locations of southern right whales used in this study and reference to previous reports or publications, with the length of the mtDNA control region fragment used in each study

Region (year of collection)	*n* samples	Sequence length (bp)	Reference or source
Calving grounds			
Argentina (1994–1996)	20	294	Portway (1998)
Argentina (1988–1989)	10[a]	500	Malik et al. (2000)
South Africa (1995)	21	294	Portway (1998)
South Africa (1995, 1996)	20	275	This study
Western Australia (1995)	20	289	Baker et al. (1999)
New Zealand sub-Antarctic (1995)	20	289	Baker et al. (1999)
New Zealand sub-Antarctic (1996)	22	275	This study
Feeding grounds			
South Georgia (2001)	8	294	Portway (1998)
Southwestern Australia (1995)	5	289	Baker et al. (1999)
Total	146	275	

[a] Ten haplotypes, no frequency information reported.

Right whales in the southern hemisphere are isolated with regard to mitochondrial (mt) DNA gene flow from right whales in the North Pacific and the North Atlantic, as evidenced by a pattern of reciprocal monophyly and a small number of fixed substitutions between oceans and hemispheres (Rosenbaum et al. 2000). The genetic differentiation, although shallow, is consistent with 3 phylogenetic species now recognized by the International Whaling Commission as the North Pacific right whale (*Eubalaena japonica*), the North Atlantic right whale (*Eubalaena glacialis*), and the southern right whale (Rosenbaum et al. 2000).

Genetic differences between regional populations and "stocks" of southern right whale have been investigated previously by Baker et al. (1999) for 2 calving grounds (New Zealand sub-Antarctic and southwestern Australia) and 1 feeding ground (lat 40° to 43° south of Western Australia) in the Indo-Pacific, and by Portway (1998) for 2 calving grounds (Argentina and South Africa) and 1 feeding ground (South Georgia) in the South Atlantic. Both studies reported differences in frequencies of mtDNA haplotypes between calving grounds, suggesting that female gene flow within ocean basins has been limited by maternal fidelity to migratory destinations.

Here, we combine the mtDNA control region sequences of animals sampled on 4 calving grounds and 2 feeding grounds from the 2 previous studies (Portway 1998; Baker et al. 1999) with additional sequences from both ocean basins in order to assess the overall diversity, population structure, and phylogenetic relationship of maternal lineages of southern right whales. We compare the levels of mtDNA diversity between ocean basins, given the longer history of exploitation and larger catches in the South Atlantic, and compare the population subdivision between ocean basins to that within ocean basins, given the limited east–west dispersal presumed from the north–south migration pattern.

Materials and Methods

Sample Collection, mtDNA Sequences, and Sex Identification

The mtDNA control-region sequences used in this study include published and unpublished sources as summarized in Table 1. Data from the Indo-Pacific included published sequences from the calving grounds of sub-Antarctic New Zealand (NZ, $n = 20$) and the southern coast of Western Australia (SWA, $n = 20$) and from the feeding grounds south of Western Australia (SWAF, $n = 5$; Table 1, Figure 1). Data from the South Atlantic included unpublished sequences from the calving grounds of South Africa (SA, $n = 21$) and Argentina (AR, $n = 20$) and from the feeding grounds of South Georgia (SGF, $n = 8$).

Additional nucleotide sequence data were obtained for 275 bp of the 5′ end of the control region from skin tissue samples collected by biopsy sampling in the New Zealand sub-Antarctic Auckland Islands ($n = 22$) and in South Africa ($n = 20$), as described in Baker et al. (1999) and Portway (1998), respectively. For these samples, total DNA was extracted using standard methods (Sambrook et al. 1989) and the mtDNA control region was amplified by the polymerase chain reaction (PCR) with the primers' light-strand tPro-whale (5′-TCACCCAAAGCTGRARTTCTA-3′) and heavy-strand Dlp-5 (5′-CCATCGWGATGTCTTATTTAAGRGGAA-3′) as reported in Baker et al. (1999). PCR fragments from the South African samples were initially amplified at the American University, Washington DC, and subsequently reamplified at Auckland University, New Zealand. Amplified fragments were purified using a Concert™ rapid PCR purification system (Life Technologies, Rockville, MD), cycle sequenced using PE Big Dye chemistry and visualized on an Applied Biosystems 377A or 3130 automated sequencing system. Unique haplotypes were sequenced in both directions to confirm identity. Sequences were aligned in Sequencher 3.0 (Gene Codes Corp, Ann Arbor, MI).

Combining these sequences with the previous sequences from Baker et al. (1999) and Portway (1998) resulted in a 275-bp consensus region for a total of 136 samples representing 6 sampling locations (Table 1, Figure 1). These include 4 calving grounds: NZ ($n = 42$), SWA ($n = 20$), AR ($n = 20$), and SA ($n = 41$) and 2 feeding grounds: SWAF ($n = 5$) and SGF (2 = 8). An additional 10 haplotypes from AR were reconstructed from Malik et al. (2000) (Table 1). Because no frequency information was available for these sequences, they were only included in the phylogenetic reconstruction. The consensus region starts at the end of the tPro-RNA gene where position

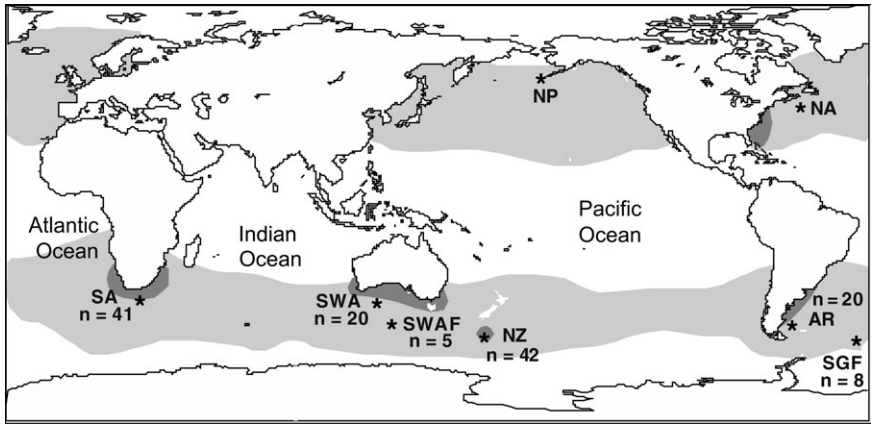

Figure 1. Historical worldwide distribution of right whales (light gray) and sampling locations, including calving grounds (dark gray) off South Africa (SA), Argentina (AR), New Zealand (NZ), Southwest Australia (SWA), and feeding grounds near South Georgia (SGF) and south of Western Australia (SWAF) (n = sample size). Grounds of the Northern Hemisphere include Western North Atlantic (NA) and Eastern North Pacific (NP).

1 corresponds to the same position in Baker et al. (1999). Alignment of sequences was unambiguous because there were no insertions or deletions. To allow easy reference to previous publications and reports, haplotypes were coded by a 3-letter abbreviation of the first author to report the haplotype, followed by the alphabetical or numerical code used in original publications (e.g., BakHapA from Baker et al. 1999)

The sex of the NZ samples was identified by the *Taq*I restriction digest of an amplified ZFX/Y gene (Palsbøll et al. 1992) and the sex of the SA samples was identified by multiplex amplification with 3 ZFX/Y primers (Bérubé and Palsbøll 1996).

Phylogenetic Reconstruction

The phylogenetic relationship of maternal lineages of southern right whales was reconstructed with the program PAUP* 4.0d60 (Swofford 2000) using all available published or reconstructed mtDNA sequences. MtDNA sequence haplotypes from the North Atlantic (Malik et al. 2000) and the North Pacific right whales (Rosenbaum et al. 1997; Rosenbaum et al. 2000) were included to represent the worldwide diversity of right whales. The sequence for the out-group species, the bowhead whale (*Balaena mysticetus*), was obtained from Baker and Palumbi (1994; Genbank no. L35609). Optimal trees were constructed by heuristic search using maximum parsimony (MP), neighbor-joining (NJ), and maximum likelihood (ML). Based on a likelihood ratio test (Goldman 1993), the preferred model of evolution was HKY85 with variable rates among sites (HKY + G).

Population Demography

Two tests were performed to investigate past expansion or contraction in the southern right whale populations: Tajima's *D*-test of selective neutrality (Tajima 1989) and the mismatch distribution (Rogers and Harpending 1992). Tajima's D was calculated in the computer program ARLEQUIN version 2.000 (Schneider et al. 2000), and the significance of the D statistic was tested by simulating a distribution (1000 replicates) of D values under the null hypothesis of population stability (Schneider et al. 2000). In populations that have remained stable in size over time, Tajima's D-statistic is expected to be close to zero. Mismatch distributions were calculated using ARLEQUIN version 2.000, and the shape of the observed distribution was tested against the expected distribution under population expansion using the sum of squared deviations. The distribution is usually multimodal in samples drawn from populations at demographic equilibrium, whereas populations which have gone through a recent demographic expansion are expected to be unimodal (Slatkin and Hudson 1991; Rogers and Harpending 1992).

Genetic Diversity and Differentiation

mtDNA diversity for each calving ground and each ocean basin was estimated at both the haplotype (h) and nucleotide (π) levels according to Nei (1987) using the computer program ARLEQUIN version 2.000 (Schneider et al. 2000). Differences in levels of diversity were tested using a t-test (Nei 1987).

Geographic differentiation was evaluated between all calving and feeding grounds as well as by oceanic basin, using the analysis of molecular variance (AMOVA; Excoffier et al. 1992) and a modified exact test (Raymond and Rousset 1995) as implemented in the computer program ARLEQUIN version 2.000 (Schneider et al. 2000). For the analysis of ocean basins, samples from NZ, SWA, and SWAF were considered to represent the Indo-Pacific basin and samples from AR, SA, and SGF to represent the South Atlantic basin. Whereas the SWA, SGF, and SWAF samples were collected in a single year, the NZ samples comprised biopsies collected in 2 years (1995, $n = 20$; 1996, $n = 22$), the AR were collected in 3 years (1994, $n = 8$; 1995, $n = 8$; 1996, $n = 4$), and the SA samples were collected in 2 years (1995, $n = 35$; 1996, $n = 6$). Because

Table 2. Variable sites observed in 275 bp consensus region of mtDNA control region of southern right whales used in this studies. Position 1 corresponds to position 1 in Baker et al. (1999) and to position 13 of haplotype SHeaV (GenBank AF275361) in Rosenbaum et al. (2000)

	Haplotype	Synonyms	7	33	58	59	60	64	65	66	67	68	69	76	77	81	84	85	92	93	111	114	124	144	187	209	225	227	232	236	239	246	248	255	265	266	267	271	273
Clade "A"	BakHapA		A	A	A	T	C	T	A	A	T	T	C	G	T	C	T	G	G	G	T	T	C	C	T	T	T	A	G	A	A	C	T	A	A	C	C	T	T
	BakHapA+		G	G	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
	BakHapB		.	.	.	.	.	.	.	.	C	C	T	.	.	.	.	A	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
	PorHap6		.	.	.	.	.	.	.	.	C	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
	PorHap1		.	.	.	.	.	.	.	.	.	C	.	.	.	.	.	.	.	.	.	.	.	T	.	C	.	.	.	.	.	.	.	.	.	.	.	.	.	.
	PorHap2	MalHapD	.	.	.	.	.	.	.	.	.	C	.	.	.	.	.	.	.	.	.	.	.	.	.	C	.	.	.	.	.	.	.	.	.	.	.	.	.	.
	PorHap3		.	.	.	.	.	.	.	.	.	C	.	.	.	.	.	.	.	.	C	.	.	.	.	C	.	.	.	.	.	.	.	.	.	.	.	.	.	.
	PorHap4		.	.	.	.	.	.	.	.	.	C	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
	PorHap5		.	.	.	.	.	.	.	.	C	C	.	.	.	.	.	A	.	.	.	.	.	.	.	C	.	.	.	.	.	.	.	.	.	.	.	.	.	.
	PorHap7		.	.	.	.	.	.	.	.	C	C	.	.	.	.	.	A	.	.	.	.	.	T	.	C	.	.	.	.	.	.	.	.	.	.	.	.	.	.
	Porhap8		.	.	.	T	.	.	.	.	.	C	.	.	.	.	.	A	.	.	.	.	.	.	.	C	.	.	.	.	.	.	.	.	.	.	.	.	.	.
	PorHap9		.	.	.	T	.	.	.	.	.	C	.	.	.	.	.	.	.	.	.	.	.	.	.	C	.	.	.	.	.	.	C	.	.	.	.	.	.	.
	PorHap10		.	.	.	T	.	.	.	C	C	C	.	.	.	.	.	A	.	.	.	.	.	.	.	C	.	.	.	G	.	.	.	.	.	.	.	.	.	.
	PorHap11		.	.	.	T	.	.	.	C	C	C	.	.	.	.	.	A	.	.	.	.	.	.	.	C	.	.	.	.	.	.	.	.	.	.	.	.	.	.
	MalHapA		.	.	.	.	.	.	G	C	C	C	.	.	.	.	.	A	.	.	.	.	.	T	.	C	.	.	.	.	.	.	.	.	.	.	.	.	.	.
	MalHapB		.	.	.	.	.	.	.	C	C	C	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
	PorHap24	MalHapE	.	.	.	T	.	.	.	.	.	C	.	.	.	.	.	.	.	.	.	.	.	.	.	C	.	.	.	.	.	.	.	.	.	.	.	.	.	.
	PorHap26	MalHapC	.	.	.	.	.	.	.	.	C	C	.	.	.	.	.	.	.	.	.	.	.	.	.	C	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Clade "W"	BakHapC		.	.	.	.	.	.	.	.	.	.	.	.	C	.	C	.	.	.	.	.	T	.	C	C	.	G	A	.	G	T	.	.	.	.	.	.	.	.
	BakHapD		.	.	.	T	.	.	.	C	.	.	A	C	.	C	.	.	.	.	.	.	T	.	C	C	.	.	A	.	G	.	.	.	.	.	T	.	.
	BakHapF		.	.	.	T	.	.	.	.	.	.	.	C	.	C	A	A	.	.	.	.	T	.	C	C	.	G	A	.	G	T	.	.	.	.	.	.	C
	PorHap12		.	.	C	.	.	.	.	.	C	.	A	C	.	C	.	.	.	.	.	.	T	.	.	C	.	G	A	.	G	.	.	.	.	.	T	.	.
	PorHap13		.	.	.	.	.	.	.	.	C	.	.	C	.	C	.	.	.	.	.	.	T	.	C	C	.	G	A	.	G	.	.	.	G	.	T	.	.
	BakhapE	MalHapGPorHap20	.	.	.	T	.	.	.	.	.	.	.	C	.	C	A	.	.	.	.	.	T	.	C	C	.	G	A	.	G	.	.	.	.	.	.	.	.
	PorHap14	MalHapH	.	.	.	.	.	.	.	.	.	.	.	C	.	C	A	.	.	.	.	.	T	.	C	C	.	G	A	.	G	T	.	.	.	.	T	.	.
	PorHap15		.	.	.	.	.	.	.	.	C	.	.	.	.	.	A	.	.	.	C	T	.	C	C	.	G	A	.	G	.	C	.	.	T	T	.	C
	PorHap16		.	.	.	.	.	.	.	.	.	.	.	C	.	.	A	.	.	.	.	T	.	C	C	.	G	A	.	G	T	.	.	.	.	T	.	.
	PorHap17		.	.	.	.	.	.	.	.	C	.	.	.	.	.	A	.	.	.	.	T	.	C	C	C	G	A	.	G	T	.	.	.	.	.	.	.
	PorHap18	MalHapJ	.	.	.	.	.	.	.	.	C	.	.	A	C	.	C	.	.	.	.	T	.	C	C	.	.	A	.	G	.	.	.	.	.	T	.	.
	PorHap19		.	.	.	.	.	.	.	.	C	.	.	.	.	.	C	.	.	.	C	T	.	C	C	.	G	A	.	G	.	.	.	.	T	T	.	C
	PorHap21		.	.	.	T	.	.	.	C	.	.	.	C	T	C	A	A	.	.	.	T	.	C	C	.	G	A	.	G	T	.	G	.	.	.	.	C
	PorHap22	MalHapI	.	.	G	.	T	C	G	.	C	.	.	.	.	C	A	.	A	.	.	T	.	C	C	.	G	A	.	G	.	.	.	.	.	.	.	.
	PorHap23		.	.	.	T	.	.	.	.	C	.	.	.	.	C	A	.	A	.	.	T	.	C	C	.	G	A	.	G	.	.	.	.	.	.	.	.
	PorHap25		.	.	.	.	.	.	.	.	.	.	.	C	.	.	A	.	.	.	.	T	.	C	C	.	G	A	.	G	.	.	.	G	.	T	C	.
	PatHap27		.	.	.	.	.	.	.	.	.	C	.	.	.	.	.	.	.	.	C	T	.	C	C	.	G	A	.	G	.	.	.	.	T	T	.	C
	PatHap28		.	.	.	.	.	.	.	.	.	C	.	.	.	C	A	.	.	.	C	T	.	.	C	.	G	A	.	G	.	.	.	.	T	T	.	.
	MalHapF		.	.	.	.	.	.	.	.	.	C	.	.	.	.	A	.	.	.	C	T	.	C	C	.	G	A	.	G	.	.	.	.	T	T	.	C

Haplotype prefix refers to the author of the initial description: BakHap, published in Baker et al. (1999); PorHap. published in Portway (1998); MalHap, published in Malik et al. (2000); and PatHap, unpublished by Patenaude. BakHapA corresponds to haplotype SheaV (GenBank AF275361) in Rosenbaum et al. (2000).

between-year sampling heterogeneity within grounds has been reported for some species (e.g., humpback whales; Baker et al. 1994, fin whales; Daníelsdóttir et al. 1991), the NZ, AR, and SA samples were tested for differences between years.

Analyses were conducted using molecular distances between haplotypes, $\Phi_{ST,}$ and by conventional F_{ST} using haplotype frequencies, that is, Wright's F_{ST} statistics (Wright 1951). The statistical significance of F_{ST} and Φ_{ST} indices was tested using a matrix permutation procedure (1000 simulations). To correct for multiple comparisons, we applied the sequential Bonferroni correction with a global significance level of 0.05 (Holm 1979; Rice 1989).

Spatial patterns of interrelationships between sampling locations and ocean basins were described by multidimensional scaling (MDS) of Φ_{ST} and F_{ST} values using the computer package STATISTICA version 5.1 (Statsoft 1997). MDS is an ordination procedure that depicts complex relationships among statistical properties of samples, such as their genetic relationships (Lessa 1990). The appearance of clusters and other kinds of structures, including geometrical shapes, axes, or basic lattice designs, is an effective way to interpret MDS plots (Degerman 1972). The degree of correspondence between the distances among samples implied by MDS and the genetic distance matrix input is measured inversely by a stress function. Stress values range from 0 to 1 where 0 means that the MDS map perfectly reproduces the input data.

Results

MtDNA Sequences

The nucleotide sequences of the mtDNA control region for 146 right whale samples provided a 275-bp consensus region with 37 variable sites, all of which were transitions (Table 2). No insertions or deletions were observed. The 37 polymorphic sites defined 37 unique haplotypes (Table 2), including 2 previously unreported haplotypes (PatHap27 and PatHap28) found among the 42 newly sequenced samples.

No haplotype was shared by all 4 calving grounds and only one haplotype (BakHapE) was shared between ocean basins (Figure 2). The 3 haplotypes from the Indo-Pacific feeding ground (SWAF) were found in NZ and 1 SWAF haplotype was found in SWA (BakHapA). All haplotypes from the South Atlantic feeding ground (SGF) were shared with either SA (n = 2) or AR (n = 3) or with both AR and SA (n = 2). No southern hemisphere haplotypes were shared

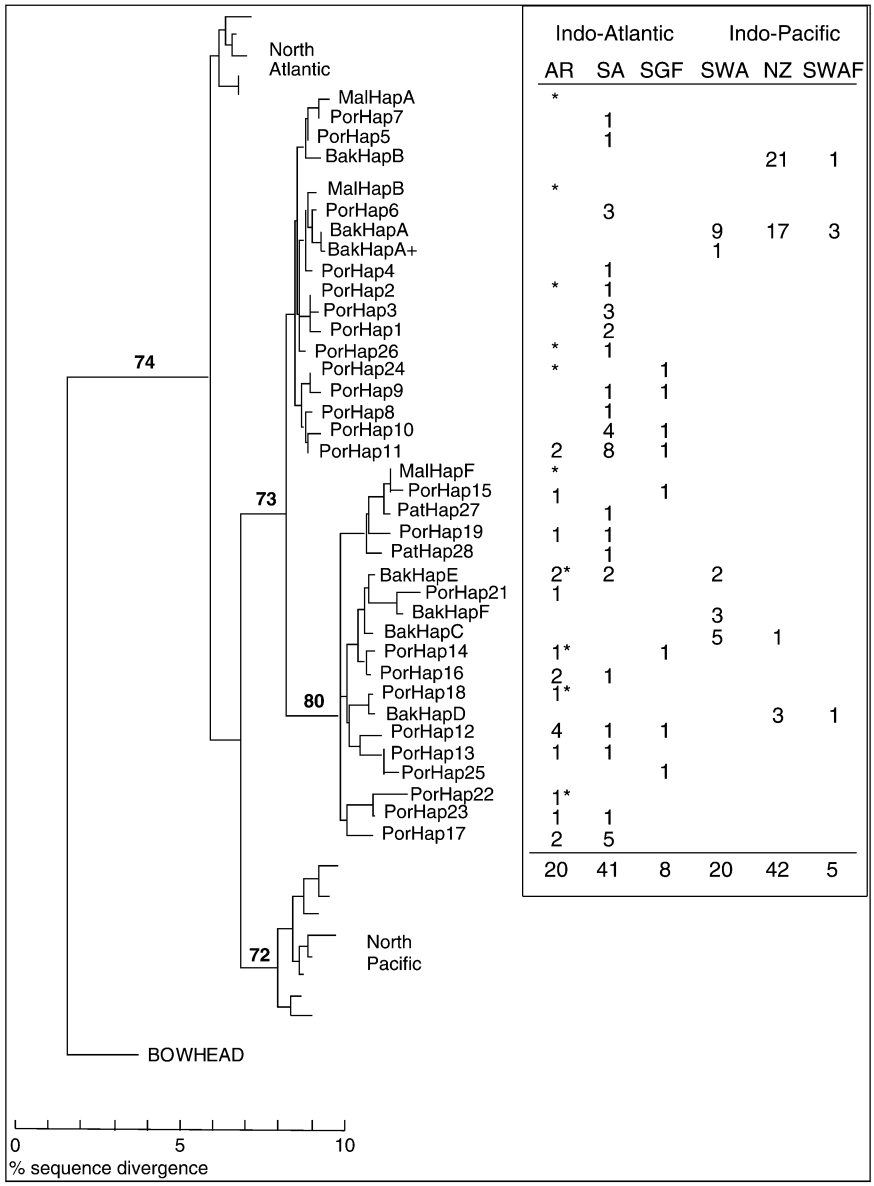

Figure 2. Phylogenetic reconstruction among mtDNA haplotypes from southern right whales in South Africa (SA), Argentina (AR), New Zealand sub-Antarctic (NZ), and Southwest Australia (SWA) calving grounds and the South Georgia (SGF) and Southwest (SWAF) Australia feeding grounds. Codes adjacent to branches represent haplotype designations. The tree is rooted with a sequence from the bowhead whale. Frequencies for each area are adjacent to each haplotype. * denotes cases when a haplotype obtained from Malik et al. (2000) was included without frequency information.

with the North Atlantic or North Pacific samples, consistent with previous reports (Rosenbaum et al. 2000).

Phylogenetic Reconstruction

Phylogenetic reconstruction of the southern hemisphere sequences using ML showed 2 divergent clades (Figure 2), referred to previously as the "A" and "W" clades (Baker et al. 1999). Reconstructions using MP or NJ had similar topologies [MP tree length 116, consistency index (CI) 0.552, retention index (RI) 0.821; NJ tree length 119, C.I. 0.538, R.I. 0.810]. The 2 clades were supported by 73% and 80% bootstrap values (NJ 1000 simulations), with 3 fixed nucleotide differences between haplotypes of the 2 clades (Table 1). As reported in Rosenbaum et al. (2000), the North Atlantic samples were basal to the North Pacific and southern hemisphere samples, when the tree was rooted with a bowhead whale as the out-group.

The A and W clades were found in both ocean basins (Figure 2) but differed in haplotype frequencies at the regional ($\chi^2 = 40.0$, df = 3, $P < 0.001$) and oceanic level ($\chi^2 = 13.3$, df = 1, $P < 0.001$). The A clade was most

Table 3. Comparative levels of mtDNA variation in southern right whales by region and ocean basin. Comparison based on sequences (275 bp) in southern right whales (this study) and northern right whales

Region	*n* samples	*n* haplotypes	Haplotype diversity *h* (±SD)	Nucleotide diversity π (%) (±SD)
Eubalaena australis				
Argentina (AR)	20	13[a]	0.947 ± 0.032	2.82 ± 1.53
South Africa (SA)	41	21	0.937 ± 0.022	2.43 ± 1.30
South Georgia feeding (SGF)	8	8	1.000 ± 0.063	3.27 ± 1.92
South Atlantic basin	69	28	0.948 ± 0.013	2.90 ± 1.51
Western Australia (WA)	20	5	0.737 ± 0.072	2.41 ± 1.32
New Zealand (NZ)	42	4	0.595 ± 0.042	1.37 ± 0.78
SW Australia feeding (SWAF)	5	3	0.700 ± 0.218	2.11 ± 1.42
Indo-Pacific basin	67	7	0.701 ± 0.037	2.03 ± 1.09
Total	136	34	0.914 ± 0.014	2.71 ± 1.41
Eubalaena glacialis				
Western North Atlantic	269[b]	5	0.698 ± 0.016	0.60 ± 0.30
Eubalaena japonica				
North Pacific	5[c]	2	0.600 ± 0.129	1.89 ± 1.22

[a] Does not include 6 haplotypes from Malik et al. (2000) for which frequency information is unavailable.

[b] Includes 89 samples for which mtDNA haplotype was inferred by maternal offspring relationships, likely to introduce a negative bias (Malik et al. 2000).

[c] Includes 5 samples collected from live whales in 1997, of which 3 were later found to be replicates (Rosenbaum et al. 2000; Leduc et al. 2001).

common in NZ (90%, $n = 38$), whereas the SWA samples were divided equally between clades. Most AR samples (90%, $n = 18$) were found in the W clade, whereas a higher proportion of SA samples were found in Clade A (65%, $n = 26$). Overall, the South Atlantic samples were equally distributed between clades, whereas about 78% of samples from the Indo-Pacific were found in clade A.

Genetic Diversity

Haplotype diversity in the calving grounds ranged from 0.595 (±0.042) to 0.947 (±0.032) and was not significantly different between calving grounds within each ocean basin (Table 3; AR vs. SA $t_{\sqrt{59}} = 0.45$, $P = 0.8$; NZ vs. SWA $t_{\sqrt{60}} = 0.73$, $P = 0.09$). However, haplotype diversity in the Indo-Pacific basin was significantly lower than that in the Indo-Atlantic basin ($t_{\sqrt{134}} = 5.50$, $P < 0.001$). In fact, the haplotype diversity of the Indo-Pacific basin was similar to that of the critically endangered North Atlantic right whale population ($t_{\sqrt{334}} = 0.70$, $P = 0.5$), whereas the haplotype diversity of the Indo-Atlantic basin was significantly higher than that of the North Atlantic population ($t_{\sqrt{336}} = 12.1$, $P < 0.001$).

Nucleotide diversity ranged from 1.37% (±0.78) to 3.27% (±1.92) but was not significantly different for any comparisons between calving grounds ($P > 0.1$ for all), between ocean basins ($t_{\sqrt{134}} = 0.42$, $P = 0.6$), or between ocean basins and the North Atlantic population (Indo-Pacific vs. NA $t_{\sqrt{334}} = 1.3$, $P = 0.1$; Indo-Atlantic vs. NA $t_{\sqrt{336}} = 1.5$, $P = 0.07$).

Population Demography

Values of Tajima's D for both ocean basins were not significantly different from zero (Indo-Pacific $d = 1.01$, $P = 0.87$; South Atlantic $d = 0.52$, $P = 0.77$). Mismatch distributions revealed significant differences between ocean basins. The shape of the mismatch distribution for South Atlantic basin was weakly bimodal with the highest peak located at the right side of the graph but did not differ significantly from the expected unimodal distribution of a population that has undergone expansion [sum of squard differences (SSD) = 0.014,

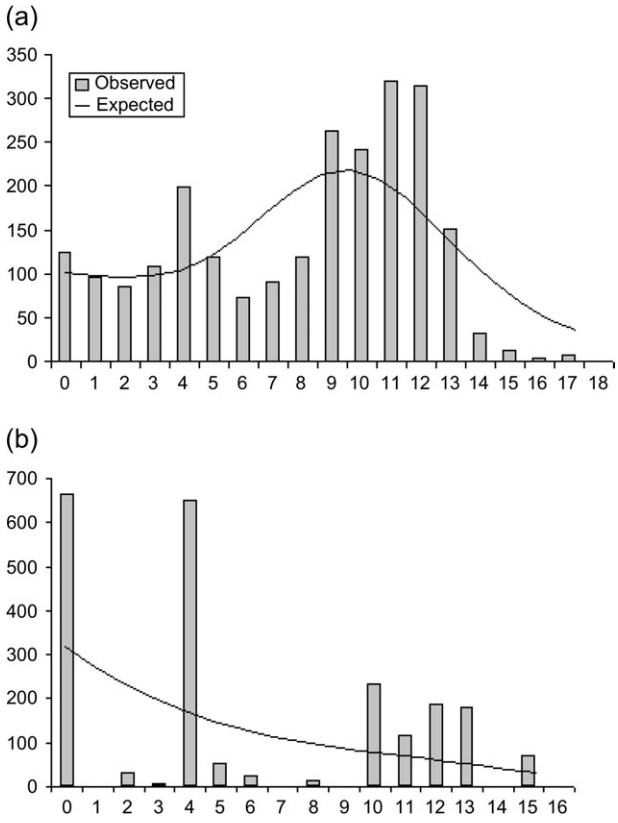

Figure 3. Mismatch distribution between haplotypes from (**a**) South Atlantic and (**b**) Indo-Pacific. The histograms represent the observed mismatch distribution from segregating sites of the aligned sequences. The solid line represents the expected mismatch distribution of a stationary population.

Table 4. Haplotype frequency for individual southern right whales of known sex

	South Atlantic				Indo-Pacific			
	AR		SA		SWA		NZ	
Haplotype	M	F	M	F	M	F	M	F
PorHap1			1	1				
PorHap2			1					
PorHap3			2	1				
PorHap4			1					
PorHap5				1				
PorHap6			2	1				
PorHap7				1				
PorHap8				1				
PorHap9				1				
PorHap10			3	1				
PorHap11	1	1	4	3				
PorHap12	2		1					
PorHap13				1				
PorHap14		1						
PorHap15	1							
PorHap16		2	1					
PorHap17		2		3				
PorHap18		1						
PorHap19		1	1					
PorHap21	1							
PorHap22	1							
PatHap27			1					
PatHap28			1					
BakHapA					2	6	9	8
BakHapA+					1			
BakHapB							9	12
BakHapC					2	2		1
BakHapD							1	2
BakHapE	1	1	1	1	2			
BakHapF					3			
Total	7	9	20	16	10	8	19	23

$P = 0.14$]. The Indo-Pacific basin was multimodal, with the highest peak skewed to the left of the graph (Figure 3) and differed significantly from the expected unimodal distribution of a population that has undergone expansion (SSD = 0.12, $P = 0.008$).

Within-Population Heterogeneity

The AMOVA revealed significant differentiation between NZ samples for the 2 study years (1995 and 1996) when based on the Φ_{ST} statistic ($\Phi_{ST} = 0.105$, $P = 0.001$) but not when based on the F_{ST} statistic ($F_{ST} = 0.002$, $P = 0.30$) or for the exact test ($P = 0.117$). However, a recent analysis of a larger sample from NZ across 4 years (1995, 1996, 1997, and 1998) did not find significant heterogeneity among years (Carroll 2006), and considering the annual samples as separate populations when comparing with other calving or feeding grounds did not affect the significance of the AMOVA results (data not shown). Consequently, both samples were pooled for further analysis. There were no significant yearly differences for the SA or AR samples for either AMOVA statistics or the exact test ($P \geq 0.4$ for all).

Sex was identified for most of the samples from the calving grounds ($n = 112$ of 123; Table 4). There was no evidence of differences in nucleotide (Φ_{ST}) or haplotype (F_{ST}) differentiation by sex within AR, SA, or NZ ($P > 0.1$ for all comparisons). Sex was identified for most of the samples from the calving grounds ($n = 112$ of 123; Table 4). The modified exact test showed no significant differences in haplotype frequencies between sexes within calving grounds except for WA, where differences approached significance ($P = 0.06$).

Population Differentiation

The 4 calving grounds showed significant overall differentiation at both the nucleotide and the haplotype level (overall $\Phi_{ST} = 0.238$, $P < 0.001$, overall $F_{ST} = 0.159$, $P < 0.001$; Table 5). Pairwise comparisons between calving grounds were all significant for Φ_{ST} values using the sequential Bonferroni correction ($P < 0.05$). Using the same correction methods, all F_{ST} comparisons between calving grounds were significant except for the AR and SA samples ($F_{ST} = 0.009$). The Bonferroni correction is conservative and the differences between these 2 grounds may have biological significance. The exact test of differentiation based on haplotype frequencies also showed significant differences for all comparisons except AR and SA ($P = 0.18$).

Table 5. Measures of pairwise population differentiation for southern right whales from 4 calving grounds (AR, Argentina; SA, South Africa; SWA, Southwest Australia; NZ, sub-Antarctic New Zealand) and 2 feeding grounds (SGF, South Georgia Feeding; SWAF, SW Australia Feeding). Genetic differentiation and significance levels are presented for F_{ST} (above diagonal) and Φ_{ST} statistics (below diagonal)

	AR	SA	SGF	SWA	NZ	SWAF
AR		0.009	0.030	0.147***	0.249***	0.145***
SA	0.221***		0.002	0.152***	0.235***	0.150**
SGF	0.065	0.009		0.149**	0.255***	0.134
SWA	0.165**	0.156**	0.121		0.188**	0.067
NZ	0.500***	0.205***	0.344***	0.312***		0.008
SWAF	0.299***	0.081	0.100	0.067	−0.002	

***$P < 0.001$; **$P < 0.01$; based on sequential Bonferroni corrections.

There was no significant genetic differentiation at either the nucleotide or the haplotype level between feeding grounds and calving grounds within oceanic regions (SGF vs. SA and AR; SWAF vs. SWA and NZ; $P > 0.05$ for both statistics). However, statistical power was low because of the small sample sizes for the feeding grounds.

The MDS plots of the F_{ST} and Φ_{ST} values illustrate the relative genetic distance between all calving and feeding grounds (Figure 4). A two-dimensional plot of the Φ_{ST} statistic shows 2 curves, parallel to each other, joining calving and feeding grounds within ocean basins (AR-SGF-SA and SWA-SWAF-NZ) on the horizontal axis. In both cases, the feeding ground is found intermediate (and equidistant) to each calving ground within the same ocean basin. The low stress value (0.015) indicates a good fit of the data. The two-dimensional plotting of the F_{ST} statistic shows a tight linear aggregate with the feeding grounds intermediate to the calving grounds for the South Atlantic basin and a loose grouping with the feeding ground intermediate but much more closely associated to NZ and SWA for the Indo-Pacific basin (stress value = 0.004).

Discussion

Phylogeny and Historical Demography

The geographic distribution and phylogeny of southern right whale mtDNA are characterized by pronounced gaps between 2 divergent clades that are distributed widely but that differ significantly in frequency between the South Atlantic and Indo-Pacific Oceans. Such a phylogeographic pattern (type II) can reflect zones of secondary admixture between formerly allopatric populations or species (Avise et al. 1987; Avise 2000), as suspected in a number of species (Wayne et al. 1990; Quinn 1992; Arctender et al. 1996; Lento et al. 1997). Alternatively, a type II phylogeographic pattern could arise by random lineage sorting in a species with a large evolutionary effective population size and high gene flow (Avise 2000).

Tajima's *D*-test suggested that the southern right whale sequence diversity within ocean basin conformed to the neutral model of population at equilibrium (or equilibrium in the past). Although simulations indicate that Tajima's *D*-test is generally powerful against the alternative hypothesis of population subdivision, the test can detect population subdivision

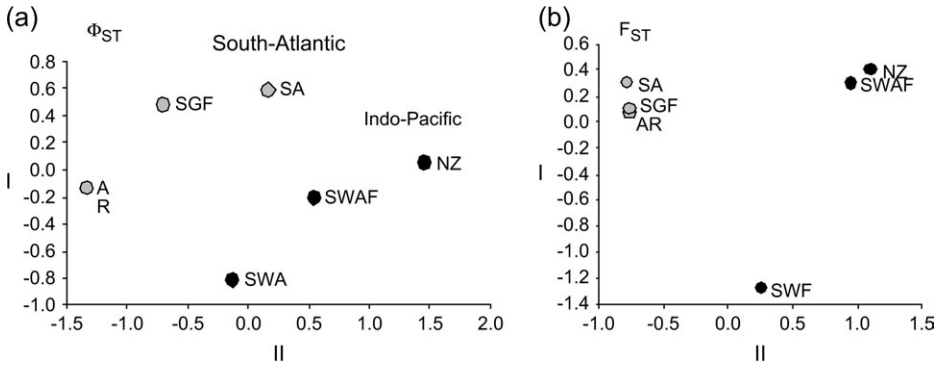

Figure 4. MDS plot of 2 measures of genetic differentiation among southern right whale samples plotted in 2 dimensions. Localities include calving grounds in South Africa (SA), Argentina (AR), New Zealand sub-Antarctic (NZ), Southwest Australia (SWA), and feeding grounds near South Georgia (SGF) and Southwest Australia (SWAF). (**a**) Sequence-based genetic differentiation (Φ_{ST}) among localities (stress = 0.0148), (**b**) haplotype-based genetic differentiation (F_{ST}) among localities (stress = 0.004).

only when it has persisted for a very long time (Simonsen et al. 1995). Consequently, evolutionarily recent population subdivision between ocean basins, such as those observed for the A and W clades, would be undetected. In contrast to Tajima's D, the mismatch distributions for the South Atlantic and the Indo-Pacific Oceans do not suggest populations at equilibrium. The mismatch distribution of the South Atlantic Ocean was similar to the expected unimodal distributions for a population that has experienced past expansion. However, the mismatch distribution for the Indo-Pacific Ocean was shifted strongly to the left, as a result of a few common and closely related haplotypes, with a secondary peak to the right, as a result of relatively rare haplotypes. Such a distribution is consistent with a loss of intermediate haplotypes and a recent increase in a small number of surviving haplotypes as a result of 19th-century whaling and slow recovery during the latter decades of the 20th century (see below). Further analyses of multiple genetic markers are needed to reconstruct historical demography, on an evolutionary and ecological timescale, with greater confidence.

Differentiation of Calving Grounds and Genetic Diversity

The near absence of shared haplotypes between the 2 oceans suggests a considerable degree of isolation over evolutionary history, with respect to maternal gene flow. Further, the AMOVA revealed significant differentiation between each of the 4 calving grounds, including relatively large Φ_{ST} values consistent with isolation or low levels of gene flow over an evolutionary timescale (Baker and Medrano-Gonzalez 2002). Although tests considering only haplotype frequencies (F_{ST} and χ^2) were not significant for the SA and AR calving grounds, this could reflect a lack of statistical power given the higher haplotype diversity of these 2 calving grounds (e.g., numerous haplotypes represented by a single individual), rather than a higher level of maternal gene flow.

The levels of haplotype diversity of southern right whales in the Indo-Pacific Ocean were significantly lower than those in the South Atlantic Ocean, despite a longer history of exploitation and larger catches in the South Atlantic (IWC 2001). In fact, the Indo-Pacific has haplotype diversity similar to that of the North Atlantic right whale that currently numbers about 300 animals (IWC 2001). This suggests the influence of one or more of 3 forces, relative to the South Atlantic population: 1) a smaller historical effective population size, 2) a more recent founder event, or 3) a more severe or prolonged bottleneck due to human exploitation. Although population dynamic modeling supports the assumption that the NZ population underwent a severe demographic bottleneck as a result of whaling (Patenaude 2002; Carroll 2006), comparable demographic models are not available to evaluate other calving grounds. Consequently, we cannot exclude the contribution of the 2 longer-term evolutionary influences.

Seasonal Population Structure

Interestingly, haplotypes from the 2 feeding grounds (except one unique to SGF) were present in both adjacent calving grounds within each ocean basin. The MDS analysis of genetic differentiation (F_{ST}) plotted feeding grounds within each ocean basin as intermediate between adjacent calving grounds, suggesting that mixing of wintering ground "stocks" occurs on these feeding grounds. This is in contrast to northern humpback whales in the North Pacific and North Atlantic, where marked segregation of mtDNA types occurs on the feeding grounds rather than on the breeding grounds (Baker and Medrano-Gonzalez 2002). More data on the genetic structure of southern right whale populations on feeding grounds are needed to better understand this seasonal population structure. For the South Atlantic basin these include South Georgia, waters offshore of southern Brazil and Argentina, Shag Rocks, around Tristan da Cunha, between Tristan de Cunha and South Africa, near the Antarctic Peninsula and between 10°W and 30°E south of 50°S (Townsend 1935; Ohsumi and Kasamatsu 1986; Stone and Hammer 1988; Tormosov et al. 1998; Moore et al. 1999). The feeding grounds in the South Pacific/Indian Ocean are less well known but might include waters between the subtropical and Antarctic convergence (45°S–55°S), waters south of Australia (41°S–44°S), in the southeastern Indian Ocean between 61°S and 65°S, and off the Chatham Rise east of New Zealand (Townsend 1935; Ohsumi and Kasamatsu 1986; Bannister et al. 1997; Tormosov et al. 1998).

Maternal Gene Flow and the Impact of Whaling

Maternal site fidelity has been suggested as a mechanism of isolation responsible for population genetic structure in several migratory species, including marine turtles (Bowen et al. 1992) and whales (Hoelzel 1994; Baker and Palumbi 1995). Although maternal site fidelity in southern right whales seems to be the norm based on photographic records of naturally marked individuals (Payne 1986; Best 1990), there are also documented cases of female interchange between calving grounds. For example, 2 reproductive females photographed in Argentina were sighted in subsequent years with calves on a Brazilian calving ground some 2050 km to the north. Another female accompanied by a second whale was observed off Gough Island and sighted in South Africa 5 years later (Best et al. 1993). Two reproductive females accompanied by calves were first photographed at the Head of the Bight, South Australia (in 1990 and in 1994), and sighted on the NZ sub-Antarctic calving ground in subsequent years (Anonymous 2002).

Although difference between ocean basins seem to be the result of long-term isolation, it is interesting to consider the potential impact of exploitation on enhancing differentiation between calving grounds within oceans, as well as on loss of diversity within calving grounds. Standard logistic population models suggest that, following 19th-century shore-based and "Yankee" whaling, right whales throughout the southern hemisphere could have been reduced to as few as 60 mature females (IWC 2001), and individual calving grounds, such as NZ, reduced to as few as 7–26 mature females (Patenaude 2002). Such a decline is likely to have reduced the number of existing lineages on each calving ground independently (i.e., increase random lineage extinction) and limited the

number of permanent female migrants between calving grounds. Together, these effects would have contributed to the observed differentiation of adjacent calving grounds today. Now as these populations begin to recover in abundance, even moderate levels of permanent female migrants could partly restore haplotype diversity and reduce differentiation between calving grounds. If so, continued protection of these populations offers the opportunity to document the natural genetic restoration, as well as ecological restoration, of southern right whales (Baker and Clapham 2004).

Acknowledgments

This research was supported by grants to N.J.P. and C.S.B. from the Whale and Dolphin Conservation Society and to C.S.B. from the US Department of State (Program for Cooperative US/NZ Antarctic Research), the Auckland University Research Council, the New Zealand Marsden Fund and the New Zealand Department of Conservation. C.M.S. acknowledges the support of American University and the Pittsburgh Zoo (Pittsburgh Zoo Conservation Fund). J.L.B. acknowledges the Scott Foundation, C. Burton, R. Holst, P. Spurr, H. Kato, and H. Koichi. P.B.B. acknowledges Earthwatch Institute, National Research Foundation (South Africa), D. Reeb, D. Kemp, V. Calder, and R. Hughes. We thank E. Carroll and D. Steel for technical review and F. Pichler, S. Lavery, A. Rodrigo, and 4 anonymous reviewers for their comments on this manuscript.

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