Isotopic and genetic evidence for site fidelity to feeding grounds in southern right whales (*Eubalaena australis*)

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ABSTRACT

Ocean warming will certainly affect the migratory patterns of many marine species, but specific changes can be predicted only where behavioural mechanisms guiding migration are understood. Southern right whales show maternally inherited site fidelity to near-shore winter nursery grounds, but exactly where they go to feed in summer remains mysterious. They consume huge quantities of copepods and krill, and their reproductive rates respond to fluctuations in krill abundance linked to El Niño Southern Oscillation (ENSO). Here we show that genetic and isotopic data, analysed together, indicate maternally directed site fidelity to diverse summer feeding grounds for female right whales calving at Península Valdés, Argentina. Isotopic values from 131 skin samples span a broad range (-23.1 to -17.2‰ $\delta^{13}C$, 6.0 to 13.8‰ $\delta^{15}N$) and are more similar than expected among individuals sharing the same mitochondrial haplotype. This pattern indicates that calves learn summer feeding locations from their mothers, and that the time scale of culturally inherited site fidelity to feeding grounds is at least several generations. Such conservatism would be expected to limit the exploration of new feeding opportunities, and might explain why this population shows increased rates of reproductive failure in years following sea surface temperature anomalies off South Georgia, the richest known feeding ground for baleen whales in the South Atlantic.

KEYWORDS: CULTURALLY INHERITED SITE FIDELITY; FEEDING GROUNDS; STABLE ISOTOPES; MITOCHONDRIAL DNA; GENETIC STRUCTURE; SOUTHERN RIGHT WHALES.

INTRODUCTION

Might an animal population fail to use all of its available food resources because cultural traditions direct its foraging to a subset of the suitable locations? Southern right whales (*Eubalaena australis*) had six known feeding grounds in the South Atlantic, based on the locations of catches recorded by 19th and 20th century whalers (IWC, 2001). Today, the only known feeding ground used in the western South Atlantic is South Georgia (Moore *et al., 1999*; IWC, 2001), despite the species' sustained recovery from near extinction in the early 20th century to a population that probably exceeds 19,000 in 2008 [by extrapolation from population size and growth rate estimates for all Southern Ocean breeding grounds in 1990 (IWC, 2001)]. Right whales make long annual migrations between mid-latitude coastal winter nursery grounds, and mostly high-latitude offshore summer feeding grounds (IWC, 2001). If calves learn these routes from their mothers and then follow them faithfully for life, matrilines will continue to use the same feeding grounds for many generations, despite the availability of better foraging opportunities elsewhere. Here we combine genetic and stable-isotopic analyses of the population calving at Península Valdés, Argentina, to show that such cultural conservatism may help to explain why southern right whales, though recovering numerically, are apparently being slow to return to many parts of their historic range throughout the Southern Hemisphere.

In baleen whales, site fidelity is maternally transmitted with calves learning the location of nursery and feeding grounds during their first annual migration (Hoelzel, 1998). Over many generations, maternally directed site fidelity can result in genetic differentiation among seasonal subpopulations (Hoelzel, 1998). In the most intensely

studied species, humpback whales [*Megaptera novaeangliae*, (Palsboll *et al., 199*7; Baker *et al., 199*8*a,b*)] and North Atlantic right whales [*E. glacialis*, (Schaeff *et al., 199*3; Malik *et al., 199*9)], genetic differentiation of mitochondrial DNA (mtDNA) markers has been found among feeding grounds and among nursery grounds (the latter only in humpback whales in the North Pacific and Southern Hemisphere), consistent with female directed fidelity. Southern right whales show site fidelity to nursery grounds off the coasts of South America, South Africa, Australia and New Zealand (IWC, 2001). Patenaude *et al.* (2007) detected mtDNA differentiation among these four nursery grounds and between feeding grounds off South Georgia and off southwestern Australia; however, within ocean basins, mtDNA haplotypes collected from the feeding grounds were shared with both nursery grounds (e.g. haplotypes from South Georgia were shared with Península Valdés and South Africa). Thus, Patenaude *et al.* (2007) confirmed southern right whale site fidelity to nursery grounds and suggested that whales from different breeding populations within an ocean basin mix in common feeding grounds. However, the difficulty of obtaining samples representing the whales' entire feeding range has prevented a thorough intra-oceanic feeding ground comparison. Despite genetic evidence linking southern right whale nursery grounds to common feeding grounds, the population genetic structure (if any) on the feeding grounds remains unknown.

Leaper *et al.* (2006) recently showed that the reproductive success of southern right whales breeding at Península Valdés, Argentina is affected by sea surface temperature (SST) anomalies off South Georgia. High-SST anomalies at South Georgia have been correlated with periods of low krill abundance (Trathan *et al., 200*3). Although southern right whale populations are recovering well from their former exploitation, reproductive failures resulting from food stress are cause for concern (Leaper *et al., 2006*). The correlation between breeding failures, SST anomalies and low krill abundance also suggests that a large proportion of whales that use the Península Valdés nursery ground may feed near South Georgia, which is only one of six major historic right whale feeding grounds in the South Atlantic (IWC, 2001). Furthermore, whaling records show that southern right whales killed south of 50ºS had stomachs filled with krill, north of 40ºS filled with copepods and between these latitudes stomachs were filled with a mix of krill and copepods (Tormosov *et al., 199*8). The exact number and location of current feeding grounds, and the proportion of whales associated with each has not been documented (IWC, 2001). Understanding a species' migratory connections and genetic structure is critical to understanding the impact that fluctuations in food availability may have on it. If the species shows site fidelity to feeding areas, then the effects of changes in food abundance in a particular feeding ground might not be spread throughout the whole breeding population, but focused instead on particular genetic lineages.

Intrinsic markers such as stable isotopes and genetic variability have been used with varying degrees of success to study migratory biology (Webster *et al., 200*2; Rubenstein and Hobson, 2004). Stable carbon and nitrogen isotope ratios in animal tissues are good indicators of food sources and have been used to study animal movements in a broad range of species including butterflies, birds, fish and mammals (Hobson, 1999; Rubenstein and Hobson, 2004). $\delta^{13}C$ (a measure of heavy to light stable carbon isotope ratio) declines with latitude in marine plankton (Rau *et al., 19*82; Hobson, 1999; Kelly, 2000; Rubenstein and Hobson, 2004). This relationship provides the basis for inferring geographic origins of marine predators. Population-specific genetic markers have been widely used to study animal movements, particularly bird migration (Bensch and Hasselquist, 1999; Wennerberg, 2001). However, few studies have combined genetic and isotopic markers to study animal migration (Clegg *et al., 200*3; Kelly *et al., 200*5). Here we describe the population genetic structure of southern right whales on their feeding grounds by combining genetic and stable-isotopic analyses of skin samples collected from live whales at Península Valdés, Argentina. Each skin sample provides the maternal lineage of the whale and information on its feeding location several months before sampling. We used stable carbon and nitrogen isotopes (proxies for feeding locations) and mtDNA haplotypes to show that individuals from a given maternal lineage tend to have similar isotopic values, apparently as a consequence of using the same culturally inherited feeding ground.

MATERIALS AND METHODS

Fieldwork and sample collection

Skin samples were collected by biopsy darting adult female southern right whales on the nursery ground off Península Valdés (42º 30' S, 64º 10' W), Argentina. Sample collection took place over four consecutive years (2003 –, 2006) at the time of peak whale abundance [September and October, (Payne, 1986)]. Whales sampled in, 2003 and, 2006 correspond to the same calving cohort (Payne, 1986). Adult females were recognized by the presence of

an accompanying calf. To avoid including resampled whales, individuals were photographed for later identification based on callosity patterns (Payne et al., 1983). Each skin sample was divided into two subsamples in the field. One subsample was dried in preparation for stable carbon and nitrogen isotope analysis and the other was preserved in saturated NaCl with 20% DMSO to be used for genetic analysis (Amos and Hoelzel, 1991). Samples were frozen on return to the laboratory at the University of Utah.

Stable carbon and nitrogen isotope analysis

Dried samples were ground to a fine powder and lipid extracted following Todd *et al.* (1997). Approximately 1mg of material per sample was analysed in a Carlo Erba 1108 elemental analyser coupled to a Thermo Finnigan Delta S Isotope Ratio Mass Spectrometer at the Stable Isotope Ratio Facility for Environmental Research (SIRFER) at the University of Utah. Isotope ratios are expressed as $\delta^{13}C$ or $\delta^{15}N$ (‰) = $[(R_{sample}/R_{standard}) - 1] \times 100$, where R is the $^{13}C/^{12}C$ or $^{15}N/^{14}N$ for $\delta^{13}C$ or $\delta^{15}N$, respectively. Standards were referenced to Pee Dee Belemnite for carbon and to atmospheric air for nitrogen. The reproducibility of these measurements was 0.2‰ for both $\delta^{13}C$ and $\delta^{15}N$ after repeated analyses of an internal laboratory standard (yeast).

Genetic analysis

DNA was extracted using standard protocols for cetacean skin described in Amos and Hoelzel (1991). 630 base pairs of the mitochondrial control region were amplified by polymerase chain reaction (PCR) using primers AB6617 and H00034 (Malik *et al., 199*9). The purified PCR product was then directly sequenced in both directions either at the DNA Sequencing Core Facility at the University of Utah Health Science Center or at the High-Throughput Genomics Unit, University of Washington. Sequences were assembled using Sequencher 4.5 software (Gene Codes Corp.). Haplotype (h) and nucleotide (π) diversity (Nei, 1987) were estimated using Arlequin 2.0 (Schneider *et al.,, 200*0). The degree of differentiation among years was estimated by AMOVA (Excoffier *et al., 199*2) as implemented in Arlequin 2.0.

Statistical analysis

The $\delta^{13}C$ and $\delta^{15}N$ distributions were significantly non-normal (Shapiro-Wilk W test: $N = 131$; $p < 0.001$; Fig. 1). Non-parametric statistics (Kruskal-Wallis analysis of variance by ranks and Dunn's Multiple Comparison test) were used to test for differences of isotopic values among years and among haplotypes (Dunn, 1964; Sokal and Rohlf, 1981). α was set at 5% for all tests, which were conducted in R (R Development Core Team, 2005) and JMP (SAS Institute Inc., 2005).

Under the null hypothesis (no site fidelity to feeding grounds) it is expected that whales from the same matriline (same haplotype) will have isotopic values as different from each other as whales from different matrilines. We used the unsigned magnitudes of the isotope-ratio differences between whales as a metric referred to as pair-wise difference. We calculated this pair-wise difference for each possible combination and then separated these values into two groups: a group were both members of the pair had the same haplotype (difference within haplotype) and a group were members had different haplotypes (difference between haplotype). Under the hypothesis of site fidelity we predicted that the mean pair-wise difference within haplotypes (ΔWH) would be smaller than that between haplotypes (ΔBH). Because each sample appears in many pair-wise comparisons, the assumption of independence for a two-way comparison (e.g. t-test of ΔWH versus ΔBH) is violated (Sokal and Rohlf, 1981). Consequently, we used a randomisation test, based on 1000 permutations of the haplotypes and stable isotope values to assess the probability of obtaining the observed difference (D) between ΔWH and ΔBH under the null hypothesis. In each of the 1000 iterations, the stable isotope values of the samples were randomly assigned to the haplotypes; in each year only the haplotypes and isotopic values obtained for that particular year were used. The mean pair-wise differences within (ΔWH) and between haplotypes (ΔBH), and their arithmetic difference ($D = \Delta WH - \Delta BH$) were then calculated. The significance level for the randomisation test was the proportion of randomly generated values of D that were smaller than or equal to the observed D value from the original dataset (Manly, 1997).

RESULTS

Stable carbon and nitrogen isotopes

Skin samples collected in September and October from 131 adult female southern right whales from 2003 to 2006 show a wide range of stable carbon and nitrogen isotope values (Table 1, Fig. 1), with $\delta^{13}C$ ranging from -23.1 to -17.2‰ (mean = -20.8‰, SD = 1.3‰) and $\delta^{15}N$ ranging from 6.0 to 13.8‰ (mean = 8.0‰, SD = 1.9‰). $\delta^{13}C$ values differ among years (Kruskal-Wallis $\chi 2 = 13.4$; $p = 0.004$), with values in, 2006 (median = -20.2‰) being significantly higher than those in, 2004 and, 2005 (median = -21.4 and -21.4‰ respectively; Dunn's Multiple Comparison tests; $p < 0.05$ for both comparisons). $\delta^{15}N$ values also differ among years (Kruskal-Wallis $\chi 2 = 8.2$; $p = 0.041$), with values in, 2006 (median = 7.8‰) being higher than those in, 2005 (median = 7.1‰; Dunn's Multiple Comparison test; $p < 0.05$).

MtDNA sequence data

Sequence analysis of a 630 base pair region of the mitochondrial control region revealed 49 polymorphic sites defining 31 unique sequences or haplotypes (Table 2). The haplotypes are not equally represented in the sample; six haplotypes account for 53% of the sample while ten occur only once (singletons, Table 2). Levels of haplotype and nucleotide diversity are similar across all four years (overall haplotype diversity $h = 0.94$ and nucleotide diversity $\pi = 1.6\%$, Table 2). A modest but almost significant differentiation is detected by AMOVA among years at the haplotype level (overall Fst = 0.01; $p = 0.06$), and a similarly slight differentiation is significant at the nucleotide level (overall Φst = 0.01; $p = 0.02$).

Table 1. Mean (SD), range and median $\delta^{13}C$ and $\delta^{15}N$ of southern right whale skin samples by year of collection and for all years combined. Non-significant differences (Dunn's Multiple Comparisons test; $p < 0.05$) between years are indicated by the same letter next to the medians. N is sample size.

Year	Statistic	$\delta^{13}C$ (‰)	$\delta^{15}N$ (‰)
All years	Mean ± SD	-20.8 ± 1.3	8.0 ± 1.9
(N = 131)	Range	-23.1 to -17.2	6.0 to 13.8
	Median	-21.1	7.3
2003	Mean ± SD	-20.9 ± 1.0	7.7 ± 1.5
(N = 12)	Range	-22.3 to -19.2	6.7 to 12.3
	Median	-21.1 [a, b]	7.2 [a, b]
2004	Mean ± SD	-21.1 ± 1.3	8.0 ± 1.8
(N = 39)	Range	-23.1 to -17.9	6.1 to 13.7
	Median	-21.4 [a]	7.3 [a, b]
2005	Mean ± SD	-21.1 ± 1.3	7.8 ± 1.9
(N = 49)	Range	-23.0 to -18.3	6.0 to 13.5
	Median	-21.4 [a]	7.1 [a]
2006	Mean ± SD	-20.1 ± 1.3	8.7 ± 2.2
(N = 31)	Range	-22.0 to -17.2	6.4 to 13.8
	Median	-20.2 [b]	7.8 [b]

Figure 1 Scatter plot and histograms of stable carbon and nitrogen isotope values for 131 adult female southern right whales sampled at Península Valdés, Argentina from, 2003 to, 2006. $\delta^{13}C$ and $\delta^{15}N$ values are not normally distributed (Shapiro-Wilk W test; $p < 0.001$ for both distributions).

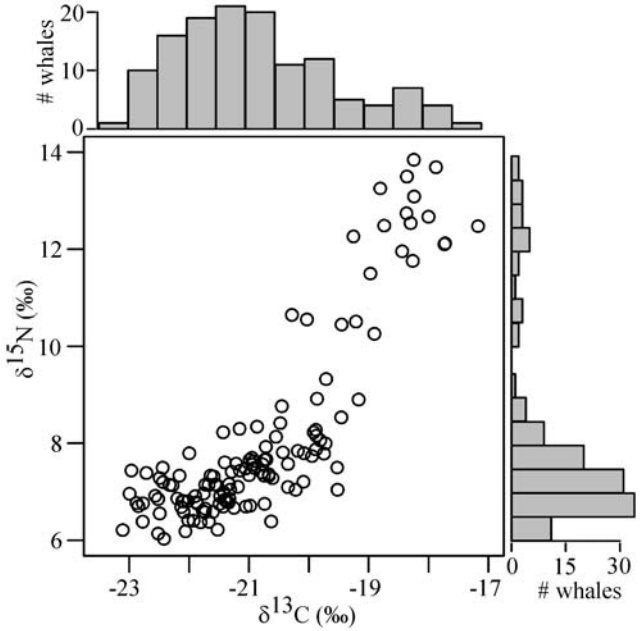

Table 2. Frequency of mtDNA haplotypes and diversity indices by year of collection and for all samples combined. Singletons (Singl.) are haplotypes observed in only one whale. Haplotype (h) and nucleotide diversity (π) indices were indistinguishable across years. N is sample size.

	Haplotype																									
	M	F	K	E	J	B	I	A	Q	O	W	P	H	D	C	N	L	X	Y	Z	BB	Singl.	h	(SD)	π (%)	(SD)	N
All	17	12	12	11	9	8	7	6	6	4	4	4	4	3	2	2	2	2	2	2	2	10	0.94	(0.01)	1.6	(0.82)	131
2003	3	3		1	1			1		1	1				1								0.91	(0.06)	1.6	(0.97)	12
2004	3	2	5	4	1	1	6	2	2	1		2	1	1	1	2	1					4	0.95	(0.02)	1.7	(0.88)	39
2005	9	4	6	3	7	2		1	1	1	1	2	2	1				2	2	1	1	3	0.93	(0.02)	1.6	(0.84)	49
2006	2	3	1	3		5	1	2	3	1	2		1	1			1			1	1	3	0.95	(0.02)	1.4	(0.72)	31

Isotopic values of individual haplotypes

Isotopic values are not independent of haplotypes. A statistical analysis of the distribution of haplotypes over the isotopic ranges, considering all four years combined, reveals significant differences among haplotypes for $\delta^{13}C$ (Kruskal-Wallis $\chi 2 = 41.1$; $p = 0.004$) and $\delta^{15}N$ (Kruskal-Wallis $\chi 2 = 34.3$; $p = 0.024$). Fig. 2*a* shows the distribution of haplotypes along the $\delta^{13}C$ range. Some haplotypes tend to be associated with low $\delta^{13}C$ values (e.g. haplotype X); others show average values (e.g. haplotypes N and B); and others are concentrated at high values (e.g. haplotype BB). Some haplotypes are found throughout the isotopic range (e.g. haplotypes K, F and E), and some show variability between years (e.g. haplotype F) and variability within years (e.g. haplotype E in 2004). Fig. 2*b* illustrates the distribution of haplotypes along the $\delta^{15}N$ range and shows a pattern that is comparable to that of $\delta^{13}C$. Again, some haplotypes appear only at low or high values of the distribution (e.g. haplotypes P and BB) while others appear throughout the distribution (e.g. haplotype M and K). For some of the haplotypes with larger ranges in $\delta^{15}N$ there is between year (e.g. haplotype E) and within year variation (e.g. haplotype F in 2003).

Overall, isotopic values are more similar among samples with identical haplotypes than among samples with different haplotypes (Table 3). For $\delta^{13}C$, the mean pair-wise difference in isotope values within haplotypes (ΔWH) is smaller than the mean pair-wise difference between haplotypes (ΔBH) in 2003, 2005, 2006 and all years combined (table 3). The difference between these two means (D) is significant in 2005, 2006 and all years combined (Table 3). For $\delta^{15}N$, ΔWH is smaller than ΔBH in, 2005, 2006 and all years combined, and D is significant in, 2005 and all years combined (Table 3).

DISCUSSION

Southern right whale mitochondrial haplotype diversity is structured with respect to stable carbon and nitrogen isotope values. Individual haplotypes show isotopic values that are more similar than expected, indicating that whales from the same matriline tend to consume isotopically similar food. Some haplotypes show apparently larger ranges and more variation within and between years than others. Haplotypes with broad ranges may represent distinct closely related matrilines that could be distinguished by longer mtDNA sequences (work is currently underway to test this hypothesis). Nitrogen isotope values show larger variation than carbon, possibly because physiological processes and trophic position have a greater effect on $\delta^{15}N$ than on $\delta^{13}C$ (Hobson and Clark, 1992*b*).

For the most part, the isotopic values measured in our study fall within the range previously detected along the length of baleen plates of southern right whales obtained from South Africa [$\delta^{13}C$ range = -26.5 to -16.0‰, $\delta^{15}N$ range = 4.0 to 12.5‰, (Best and Schell, 1996)]. Best and Schell (1996) found that the isotopic values of the baleen plates oscillate in what appear to be annual cycles and suggested that these cycles correspond to the whales' annual migrations between isotopically different areas. The isotope values of the skin samples in our study are somewhat similar, but higher than the mean stable isotope values of seven baleen plates from Península Valdés [$\delta^{13}C$ range of means = -24.6 to -20.8‰, $\delta^{15}N$ range of means = 5.9 to 9.5‰, (Rowntree *et al., 200*1)]. The differences between the values reported in our study and the studies mentioned above may be related to intrinsic differences between tissues (skin vs. baleen), such as tissue-specific isotope fractionation and turnover rate (Kelly, 2000).

Figure 2 $\delta^{13}C$ (*a*) and $\delta^{15}N$ (*b*) values of individual haplotypes. For each haplotype a filled circle represents the mean isotopic value, and the vertical lines (below haplotype means) represent the raw values. Raw isotopic values are organized vertically by year, with, 2003 at the bottom and, 2006 at the top (see haplotype M). Haplotypes are ordered from low (bottom of figure) to high (top) mean $\delta^{13}C$ values. Only haplotypes sampled more than once are presented.

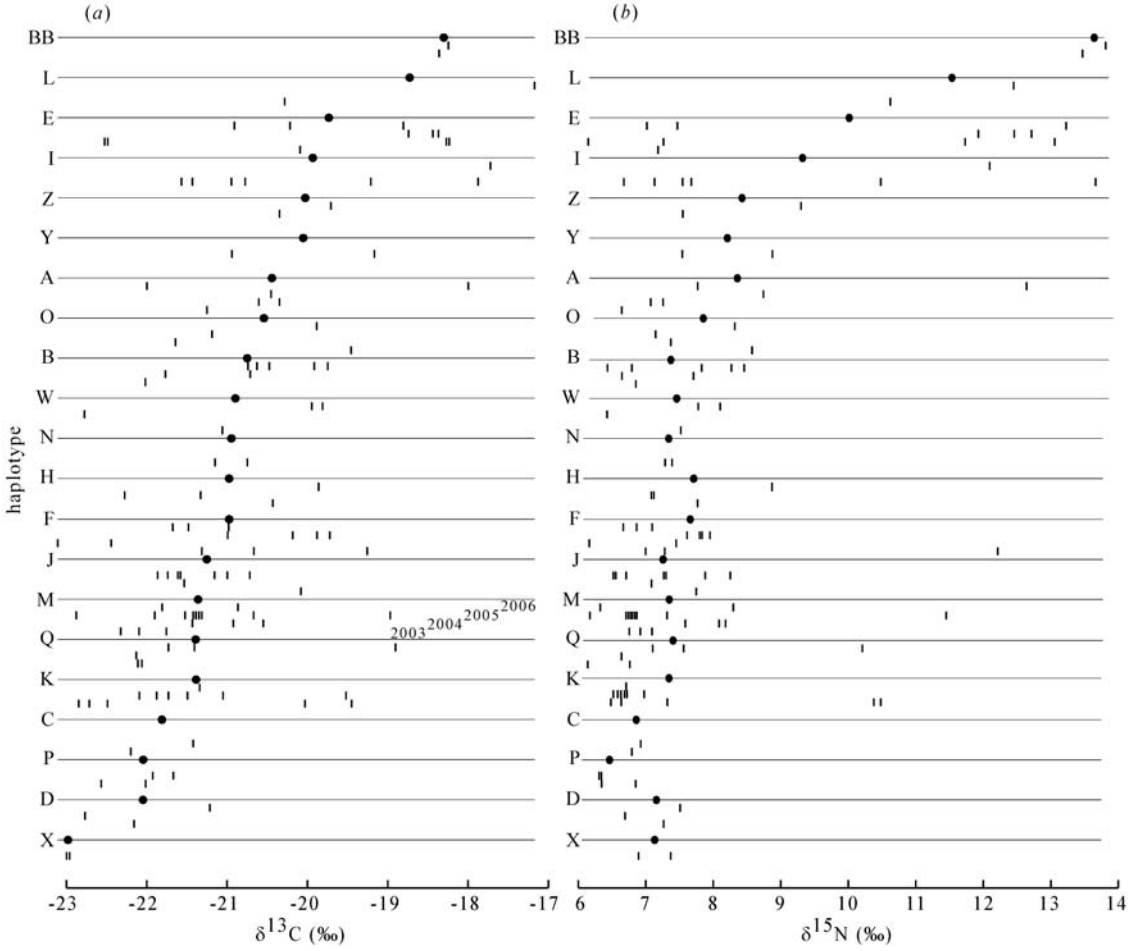

Table 3. Mean pair-wise difference in isotopic values within haplotypes (ΔWH) and between haplotypes (ΔBH) for $\delta^{13}C$ and $\delta^{15}N$, for all samples combined and for each year. W<B? indicates whether (Y, N) ΔWH is smaller than ΔBH. *p* is the significance level of the randomisation test and indicates the proportion of randomly generated values of the difference (D) between ΔWH and ΔBH smaller than or equal to the observed D. *N* is sample size.

		$\delta^{13}C$				$\delta^{15}N$			
Year	*N*	ΔWH (‰)	ΔBH (‰)	W<B?	*p*	ΔWH (‰)	ΔBH (‰)	W<B?	*p*
All	131	1.22	1.52	Y	0.002	1.52	1.88	Y	0.012
2003	12	0.88	1.30	Y	0.131	1.85	1.27	N	0.569
2004	39	1.67	1.46	N	0.810	2.51	1.74	N	0.987
2005	49	0.87	1.48	Y	0.002	0.83	1.80	Y	0.006
2006	31	0.99	1.54	Y	0.016	1.71	2.35	Y	0.110

The isotopic composition of an animal's tissues can be influenced by its age, nutritional condition and reproductive status (Hobson and Clark, 1992*a*; Roth and Hobson, 2000; Fuller *et al., 200*4). In our study, all the sampled whales were nursing females that had been under similar physiological stresses for at least a year, including twelve months of gestation, migration to the nursery ground, and lactation while fasting (Payne, 1986; Cooke *et al., 200*1). To the degree that these stresses affect the isotopic values, the effect should be similar for all of the sampled whales. Thus, the differences we observed among whales would appear to be caused mainly by differences in the isotopic composition of their foods, not by their metabolism.

The interannual differences in the general distribution of $\delta^{13}C$ and $\delta^{15}N$ detected in this study are most likely a response to variations in the isotopic composition at the base of the food web produced by changes in ocean circulation or by modification of local biogeochemical processes (Peterson and Fry, 1987; Druffel and Griffin, 1999; Brix *et al., 200*4). An alternative explanation is that in 2006 the whales migrated to isotopically distinct feeding regions. If the latter alternative were true, then the isotopic values of the samples from 2006 should not show any particular pattern. However, in 2006 the isotopic values of individual haplotypes were higher (see Fig. 2). For example, in 9 of the 15 haplotypes sampled in 2006, the samples from 2006 had the highest $\delta^{13}C$ values, while 7 of the 15 haplotypes had the highest $\delta^{15}N$ values. The lack of genetic differentiation among years at the haplotype level indicates that the 2006 whales were not a genetically distinct subset of whales.

Our results show an interesting pattern of fine-scale genetic sub-structuring within a breeding population that is most simply explained as a consequence of maternally directed fidelity to different feeding sites. North Atlantic right whales (*Eubalaena glacialis*) and humpback whales (*Megaptera novaeangliae*) show similar site fidelity to feeding grounds, but mix on common breeding grounds (Schaeff *et al., 199*3; Palsbøll *et al., 199*5; Larsen *et al., 199*6; Malik *et al., 199*9). In contrast, Patenaude *et al.* (2007) suggest that southern right whales from different breeding populations within an ocean basin mix on common feeding grounds. For whale species that feed in the Southern Ocean, where there are no land barriers to circumpolar migrations, Hoelzel (1998) suggests that animals from different breeding grounds form mixed genetic assemblages on widely dispersed feeding areas. We suggest that the assemblages detected by Patenaude *et al.* (2007) represent mixed subsets of maternal lineages with site fidelity to specific feeding grounds rather than an unstructured mix of animals migrating randomly from different nursery grounds. Therefore, southern right whale population structure may mirror that of humpback whales in the North Pacific, where the whales are genetically segregated on both the nursery and feeding grounds (Baker *et al., 1998b*).

The correlation of sea surface temperature (SST) anomalies off South Georgia and reduced calf output at Península Valdés (Leaper *et al., 200*6) suggests a strong migratory connection between these two areas, but our isotopic data imply that the whales feed in many different locations distributed over a large geographic range. We see two possible explanations: 1) the SST anomalies detected at South Georgia might affect many other feeding locations, and therefore stress most of the whales that visit Península Valdés; 2) the SST anomalies might affect only the whales that visit South Georgia, but so strongly that calf production is reduced detectably for the population as a whole. These alternatives could be distinguished by analysing the individual reproductive histories of females using Península Valdés to see whether particular matrilines fail to reproduce in years following SST anomalies and low krill abundance near South Georgia.

Strong site fidelity may restrict animals to a set of culturally inherited areas and migratory patterns that represent only a portion of their potential range (Matthiopoulos *et al., 200*5; Clapham *et al., 200*7). The mitochondrial haplotype sub-structuring presented here suggests that the timescale of culturally inherited site fidelity to feeding areas is long (at least several generations). The finding by Leaper *et al.* (2006) raises concerns about the future of southern right whales if krill fisheries and climate change have a significant impact on krill abundance (Atkinson *et al., 200*4). If whales strictly follow the foraging strategies and migratory patterns learned from their mothers, can they be flexible enough to change their strategies and switch to other prey types with different spatial and temporal distributions? Some mitochondrial lineages show relatively large stable isotope ranges, suggesting that a few members of those lineages experimented with different locations (or prey types) in the relatively recent past. If we can better understand the causes and consequences of this limited plasticity, then we may be better able to predict the responses of southern right whales and other marine migrants to global climate change.

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