

Interannual Variation in the Stable Isotope Differences Between Mothers and Their Calves in Southern Right Whales (*Eubalaena australis*)

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Abstract

Lactation is the most energetically expensive aspect of mammalian reproduction. As capital breeders, lactating southern right whales (*Eubalaena australis*) are completely dependent on their stored nutrients. The relative proportion of different endogenous nutrient pools used during lactation could be assessed using stable isotopes. We determined the stable carbon and nitrogen isotope difference between skin samples of 42 southern right whale mothers and their calves. The mean $\delta^{15}\text{N}$ value of calves was 0.51‰ higher than that of their mothers, but their $\delta^{13}\text{C}$ values were identical. However, when analyzed by year, the mother-calf pairs showed no isotope differences in 2004, but calves had higher $\delta^{15}\text{N}$ (0.85‰) and $\delta^{13}\text{C}$ (0.63‰) in 2003 and 2005. We hypothesize that the interannual variability was a consequence of different levels of nutritional stress. A decline in food abundance prior to the nursing seasons could result in mothers with relatively poorer physical condition that would not be able to meet the high energetic demands of their offspring. Thus, the calves would be forced to utilize proteins as well as lipids to meet this demand, increasing their nitrogen and carbon isotope ratios. This hypothesis is supported by an independent assessment of the proportion of stranded whales over the same time period.

Key Words: southern right whales, *Eubalaena australis*, Southern Ocean, stable isotopes, mother-calf pairs, fractionation, nutrition

Introduction

Lactation is the most energetically expensive aspect of mammalian reproduction; it involves the export of significant quantities of maternal nutrients to supply offspring demands (Oftedal,

1993, 2000). For most mammals, this period is accompanied by an increase in food consumption (Oftedal, 1993). However, in capital breeders (those that fast during lactation; e.g., seals, bears, and baleen whales), the large nutrient demand on mothers must be supplied from energy stores such as body fat, blubber, and muscle tissue accumulated during previous feeding events (Oftedal, 2000). Because capital breeders are unable to increase their energy intake during lactation, they have to deal with nutrient demands associated with milk production and with nutrient conservation associated with a fasting metabolism (Sare et al., 2005; Dalerum et al., 2007). If a lactating female is unable to meet these demands, she must either reduce milk production, putting offspring survival at risk, or compromise her own health and future reproductive output (Oftedal, 2000). Thus, the reproductive success of capital breeders is strongly influenced by food abundance prior to lactation, capacity to store nutrients, and maternal ability to balance offspring demands and individual needs.

Southern right whales (*Eubalaena australis*) are capital breeders with an extreme and energetically demanding lifestyle. They migrate between low latitude coastal nursery grounds and higher latitude feeding grounds (International Whaling Commission [IWC], 2001). Calves are born in winter, and females depend exclusively on internal reserves to nurse their young during their first 2 to 3 mo of life (IWC, 2001). During this period when mothers are fasting, calves grow approximately 2.4 cm/d (Best & Rüther, 1992). Their long reproductive cycle reflects the high demands of lactation. The normal cycle includes 1 y of gestation, 1 y of lactation, and 1 y of resting (Knowlton et al., 1994; Cooke et al., 2003). The resting year has been attributed to the need to recover from a long lactation and to accumulate enough energy

to begin the next cycle (Knowlton et al., 1994). Deviations from the mean 3-y calving interval have been attributed to calf loss (Knowlton et al., 1994; Cooke et al., 2003) and environmental variability affecting food abundance during the resting year (Cooke et al., 2003). Leaper et al. (2006) found a reduction in calf output following years with high Sea Surface Temperatures (SST) on the South Georgia feeding ground. High SST anomalies at South Georgia are correlated with periods of low krill abundance, which, in turn, are correlated with the low reproductive output of local populations of Antarctic fur seals (*Arctocephalus gazella*) and gentoo penguins (*Pygoscelis papua*) (Trathan et al., 2006).

Stable isotopes have been used to study transfer of maternal nutrients to offspring (Polischuk et al., 2001; Sare et al., 2005; Dalerum et al., 2007). For example, the onset and duration of the weaning period, when maternal nutrients are replaced by food, has been assessed using stable nitrogen and carbon isotopes in polar bear (*Ursus maritimus*) (Polischuk et al., 2001) and meerkat (*Suricata suricatta*) (Dalerum et al., 2007). Stable nitrogen and carbon isotope ratios in animal tissues reflect those of their diet (Peterson & Fry, 1987; Michener & Schell, 1994). In general, the stable nitrogen isotope ratio ($^{15}\text{N}/^{14}\text{N}$) in the tissues of a consumer is enriched (positive fractionation) about 3‰ over the diet, while the stable carbon isotope ratio ($^{13}\text{C}/^{12}\text{C}$) change is relatively small (~1‰; DeNiro & Epstein, 1978, 1981; Peterson & Fry, 1987; Kelly, 2000). In mammals, nitrogen fractionation occurs because there is preferential excretion of the lighter isotope, ^{14}N , during the production of urea, thus leaving the animal's tissues enriched in the heavier isotope, ^{15}N (Kelly, 2000). Nitrogen fractionation is affected mainly by the quality of dietary protein, nutritional stress, and the nitrogen balance of the consumer (DeNiro & Epstein, 1981; Roth & Hobson, 2000; McCutchan et al., 2003; Fuller et al., 2004). The extent of nitrogen and carbon isotope fractionation is also affected

by tissue type, with keratin-rich tissues (i.e., hair, feather, and baleen) generally showing higher values than other tissues (Kelly, 2000). Lipid-rich tissues show lower carbon isotope ratios due to preferential use of the lighter ^{12}C during lipid synthesis (Tieszen & Boutton, 1988). The fact that nitrogen and, to some extent, carbon isotopes can be affected by diet has motivated studies to determine the proportions of exogenous (i.e., food) and endogenous (i.e., maternal reserves) nutrients that are allocated to the offspring (Polischuk et al., 2001; Sare et al., 2005). In capital breeders, for which all transferred nutrients are endogenous, stable isotope analyses have been used to identify the differential use of various nutrient pools (e.g., muscle vs fat) used throughout the lactation period (Polischuk et al., 2001). For example, Polischuk et al. found that nitrogen fractionation between polar bear mothers and cubs was larger in mothers with lower body fat content. The difference among mother-cub families was attributed to relatively higher use of maternal lean tissue (muscle proteins) as compared to fat as an energy source (Polischuk et al., 2001).

Isotope fractionation between mothers and offspring is not well-understood. One attractive idea is that offspring are a trophic level higher than their mothers because, through lactation and milk consumption, the offspring "consume" their mothers (Hobson et al., 1997, 2000; Newsome et al., 2006; Knoff et al., 2008). Nitrogen enrichment from mother to offspring has been detected in all studies in which it has been directly measured (Table 1; Fogel et al., 1989; Hobson et al., 1997, 2000; Jenkins et al., 2001; Polischuk et al., 2001; Sare et al., 2005; Fuller et al., 2006; Dalerum et al., 2007). However, few studies found the expected trophic-level fractionation of 3‰ for nitrogen and 1‰ for carbon, and reported fractionation values show large variability both within and between species (Table 1; Fogel et al., 1989; Hobson et al., 1997, 2000; Fuller et al., 2006). Furthermore, it is important to note that when comparing studies

Table 1. Average values of nitrogen and carbon isotopic differences directly measured from mothers and their offspring

Species	Tissue	$\Delta\delta^{15}\text{N}$ (‰)	$\Delta\delta^{13}\text{C}$ (‰)	Reference
Humans	Fingernails	2.4	NR	Fogel et al., 1989
Humans	Fingernails	1.7-2.8	1.0	Fuller et al., 2006
Northern fur seal	Muscle	1.9	-0.7	Hobson et al., 1997
Eleven species ^a	Plasma	0.9	0.0	Jenkins et al., 2001
Polar bears	Plasma	1.0	-0.8	Polischuk et al., 2001
Black bears	Hair	2.5	0.7	Hobson et al., 2000
Red-backed voles	Hair	1.8	-1.5	Sare et al., 2005
Meerkats	Hair	1.0	NR	Dalerum et al., 2007

^aMoose, caribou, black-tailed deer, coyotes, grizzly bears, domestic rabbits, rats, cows, sheep, pigs, and domestic cats; NR: not reported

that used different tissues, those tissues may potentially have different isotope fractionation factors (Table 1).

The *trophic-level* model oversimplifies the many processes acting during nutrient transfer from mother to offspring and assumes implicitly that milk is isotopically similar to the mother's tissues. Jenkins et al. (2001) studied 11 different mammalian species and detected isotopic depletion in carbon and nitrogen from mother to milk, and enrichment from milk to offspring, producing a *balancing effect* with the net effect being a small difference in nitrogen (0.9‰) and no difference in carbon isotopes between mothers and offspring. Milk with high fat content is expected to have lower $\delta^{13}\text{C}$ because fats are depleted in ^{13}C relative to protein and carbohydrates. On the other hand, little is known about the processes by which milk resulted depleted in ^{15}N .

In this paper, we report isotopic differences between lactating right whale mothers and their calves by examining stable nitrogen and carbon isotope ratios measured in skin samples collected during the first months of the nursing period. The isotope differences described here integrate several physiological processes affecting the isotope ratios of carbon and nitrogen in the mothers as well as in their calves. We expected a small isotope difference in nitrogen and no difference in carbon ratios, reflecting the balancing effect described by Jenkins et al. (2001). By examining stable isotope measurements over the course of three consecutive years, we found interannual variability in isotopic differences between mothers and calves. We hypothesize that the interannual variability was a consequence of different average levels of nutritional stress caused by environmental variability. This hypothesis is supported by variation in the proportion of stranded whales during the same sequence of years.

Materials and Methods

Skin samples from each member of 42 mother-calf pairs were collected by biopsy darting whales on their nursery ground off Península Valdés, Argentina (42° 30' S, 64° 10' W). Samples were collected over three consecutive years (2003 to 2005) at the time of peak whale abundance (September and October; Payne, 1986). The start date and duration of sampling differed each year: in 2003, sampling started on 14 September and lasted 21 d ($n_{\text{pairs}} = 12$); in 2004, sampling started on 21 September and lasted 25 d ($n_{\text{pairs}} = 20$); and in 2005, sampling started on 8 September and lasted 33 d ($n_{\text{pairs}} = 10$). All sampled calves were estimated to be older than 1 wk of age based on their size relative to that of their mother (Thomas & Taber, 1984), skin characteristics (Reeb et al.,

2005), and the behavioral patterns of mother-calf pairs (Thomas & Taber, 1984). To avoid including resampled individuals, adult females were photographed for later identification based on callosity patterns (Payne et al., 1983; Best, 1990).

In the field, the top 0.5 to 1 cm of the skin sample was separated for stable isotope analyses. In a few cases, blubber was obtained in the biopsy, in which case the blubber was removed with a clean scalpel. Skin samples were dried, ground to a fine powder, and lipid extracted using Soxhlet extraction following Todd et al. (1997). Approximately 1 mg of material per sample was analyzed for carbon and nitrogen isotopes using a Carlo Erba 1108 elemental analyzer 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. The isotope ratios are expressed as $\delta^{13}\text{C}$ or $\delta^{15}\text{N}$ (‰) = $[(R_{\text{sample}}/R_{\text{standard}}) - 1] \times 10^3$, where R is the $^{13}\text{C}/^{12}\text{C}$ or $^{15}\text{N}/^{14}\text{N}$ for $\delta^{13}\text{C}$ or $\delta^{15}\text{N}$, respectively. Standards were referenced to Pee Dee Belemnite for carbon and atmospheric air for nitrogen. The analytical precision (defined as standard deviation) of these measurements was 0.2‰ for both $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ after repeated analyses of internal laboratory standards. The internal reference was yeast, with carbon and nitrogen isotope values defined as -20.02‰ and -1.24‰, respectively.

The $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values of mothers and calves were not normally distributed (Shapiro-Wilk W test, $p < 0.01$, $n = 42$ for all four distributions). Non-parametric Kruskal-Wallis analysis of variance, Dunn's Multiple Comparison test, and Spearman correlation were used to test for the influence of sampling year and sampling date on isotope values (Dunn, 1964; Sokal & Rohlf, 1981). We used the isotopic difference between calf and mother as an indicator of isotope fractionation, $\Delta\delta^{15}\text{N} = \delta^{15}\text{N}_{\text{calf}} - \delta^{15}\text{N}_{\text{mother}}$, and $\Delta\delta^{13}\text{C} = \delta^{13}\text{C}_{\text{calf}} - \delta^{13}\text{C}_{\text{mother}}$ for nitrogen and carbon differences, respectively. The $\Delta\delta^{15}\text{N}$ and $\Delta\delta^{13}\text{C}$ values were normally distributed (Shapiro-Wilk W test, $p > 0.1$, $n = 42$ for both distributions). Parametric pairwise *t*-tests were used to test for isotopic differences between mothers and calves, and Pearson correlation was used to test for the influence of sampling date and for correlations between nitrogen and carbon isotope differences (Sokal & Rohlf, 1981). Statistical tests were conducted in R (R Development Core Team, 2008) and JMP, Version 7 (SAS, 2007).

Results

Stable Isotope Ratios

Average stable nitrogen and carbon isotope ratios of calves varied among years (Kruskal-Wallis $n = 42$: $H_{\text{nitrogen}} = 14$, $p < 0.001$; $H_{\text{carbon}} = 9$, $p = 0.012$; Figure

1). Dunn's Multiple Comparison test showed that calves sampled in 2004 had significantly lower values of $\delta^{15}\text{N}$ (mean = $8.0 \pm 2.1\text{‰}$) and $\delta^{13}\text{C}$ (mean = $-21.6 \pm 1.6\text{‰}$) than calves sampled in 2003 and 2005 (mean $\delta^{15}\text{N}_{2003} = 8.7 \pm 1.3$, mean $\delta^{13}\text{C}_{2003} = -20.5 \pm 1.4\text{‰}$, and mean $\delta^{15}\text{N}_{2005} = 8.7 \pm 1.9\text{‰}$, mean $\delta^{13}\text{C}_{2005} = -20.3 \pm 1.7\text{‰}$). Mothers sampled in different years showed no significant differences in nitrogen (mean $\delta^{15}\text{N} = 7.8 \pm 2.0\text{‰}$) or carbon (mean $\delta^{13}\text{C} = -21.2 \pm 1.3\text{‰}$) isotope values (Kruskal-Wallis $n = 42$, $H = 1$, $p > 0.1$ for both nitrogen and carbon; Figure 1). Isotope ratios were not correlated with sampling dates when all samples were analysed together or separately by year (Spearman's $\rho < 0.27$ and $p > 0.5$ for all correlations).

Stable Isotope Differences

The nitrogen ($\Delta\delta^{15}\text{N}$) and carbon ($\Delta\delta^{13}\text{C}$) differences between mothers and their calves were weakly correlated ($r^2 = 0.24$, $p = 0.001$; Figure 2).

Furthermore, when the isotope differences were analysed by year, no correlations were found ($r^2 < 0.18$ and $p > 0.05$ for all years). Total mean $\Delta\delta^{15}\text{N}$ ($0.5 \pm 0.6\text{‰}$) was significantly different from zero ($t = 5.4$, $p < 0.001$), while total mean $\Delta\delta^{13}\text{C}$ ($0.2 \pm 0.7\text{‰}$) was not significantly different ($t = 1.9$, $p = 0.07$; Figure 3). For 2004, neither mean $\Delta\delta^{15}\text{N}$ ($0.2 \pm 0.5\text{‰}$) nor mean $\Delta\delta^{13}\text{C}$ ($-0.2 \pm 0.6\text{‰}$) were significantly different from zero ($p > 0.1$; Figure 3). However, for 2003 and 2005, the mean $\Delta\delta^{15}\text{N}$ and mean $\Delta\delta^{13}\text{C}$ were significantly different from zero ($\Delta\delta^{15}\text{N}_{2003} = 0.9 \pm 0.4\text{‰}$, $t = 7.4$, $p < 0.001$; $\Delta\delta^{13}\text{C}_{2003} = 0.5 \pm 0.7\text{‰}$, $t = 2.4$, $p = 0.03$; $\Delta\delta^{15}\text{N}_{2005} = 0.7 \pm 0.7\text{‰}$, $t = 3.4$, $p = 0.008$; $\Delta\delta^{13}\text{C}_{2005} = 0.8 \pm 0.3\text{‰}$, $t = 8.4$, $p < 0.001$; Figure 3). Total nitrogen and carbon isotope differences appear to be negatively correlated with sampling date ($\Delta\delta^{15}\text{N}$, $r^2 = 0.24$, $p = 0.001$; $\Delta\delta^{13}\text{C}$, $r^2 = 0.10$, $p = 0.04$). However, when the 3 y were considered separately, sampling date did not influence nitrogen ($r^2 < 0.15$

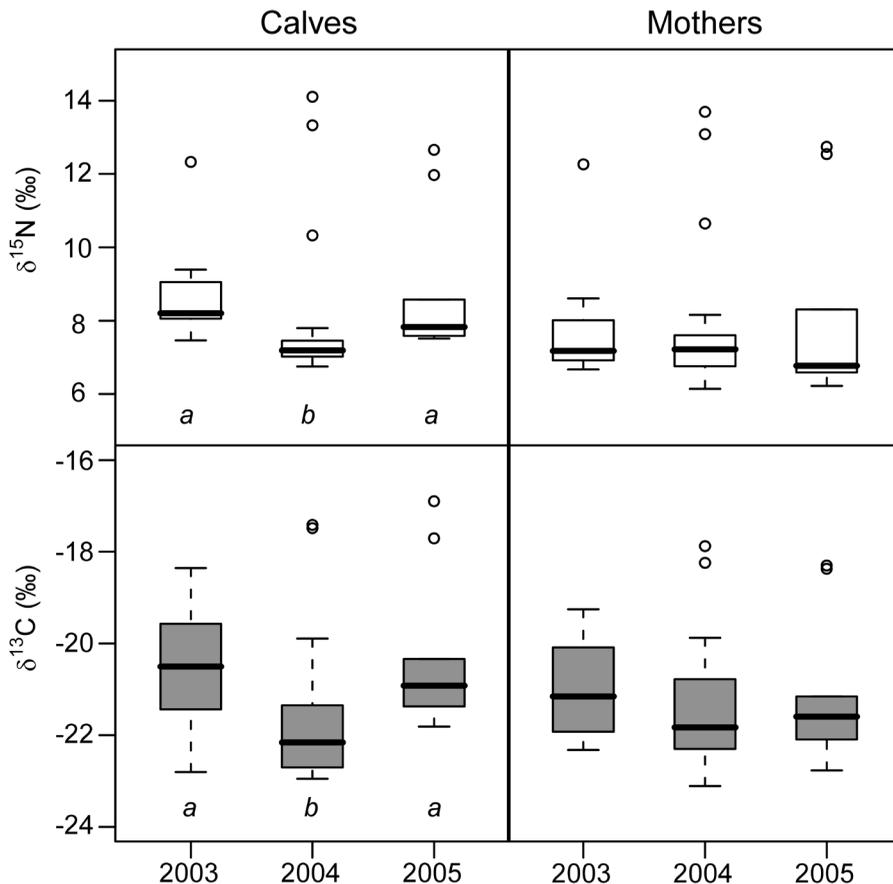


Figure 1. Boxplots of $\delta^{15}\text{N}$ (open boxes) and $\delta^{13}\text{C}$ (grey boxes) for calves (left plots) and mothers (right plots) by year of collection; calves sampled in 2004 ($n = 20$) have isotope values statistically smaller than calves sampled in 2003 ($n = 12$) and 2005 ($n = 10$); nonsignificant differences between years are indicated by the same letter under the boxes. For the mothers, no significant differences in isotope values were detected among years.

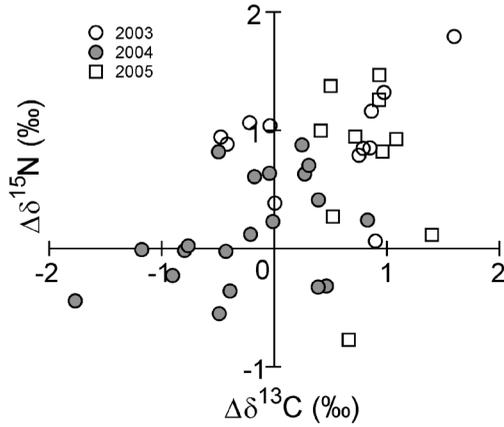


Figure 2. Scatter plot of $\Delta\delta^{15}\text{N}$ vs $\Delta\delta^{13}\text{C}$; each point represents the isotope difference of a calf from its mother. Note that there is a weak but significant correlation; however, this correlation disappears when samples are analysed by year.

and $p > 0.1$ for all years) or carbon isotope differences ($r^2 < 0.1$ and $p > 0.1$ for all years).

Discussion

As predicted, we found a small isotope difference between the skin samples from mothers and calves in nitrogen (mean = 0.5‰) and no difference in carbon isotopes. More importantly, when the stable carbon and nitrogen differences between right whale mothers and calves were analyzed by year, two different scenarios emerged. For the 2004 samples, stable isotope ratios from mothers and calves were statistically indistinguishable from each other. In the other two years, 2003 and 2005, calves showed significant enrichment over their mothers in nitrogen (about 0.8‰) and carbon (about 0.7‰). Jenkins et al. (2001) found small nitrogen differences and no carbon differences between mothers and their offspring across 11 mammalian species. However, the mean nitrogen difference in our study (0.5‰) was smaller than the interspecific mean (0.9‰) estimated by Jenkins et al. (2001). Two other studies (Polischuk

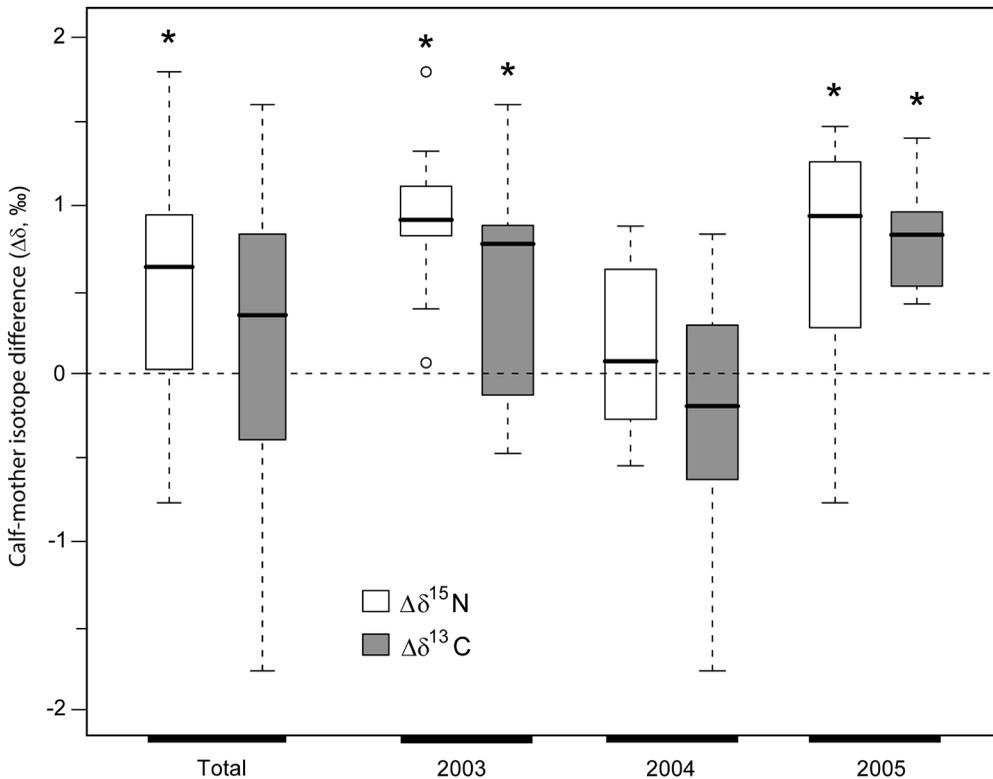


Figure 3. Boxplots of calf-mother isotope differences ($\Delta\delta$) by year of sampling and total; nitrogen differences are presented in open boxes and carbon differences in grey boxes. Isotope differences that are significantly different from zero (paired t -test) are indicated by an *.

et al., 2001; Dalerum et al., 2007) have reported small (1‰) nitrogen fractionation from mother to offspring, but the isotope fractionation of carbon was negative (-0.8‰ for polar bears; Polischuk et al., 2001) or not reported (for meerkats; Dalerum et al., 2007).

The stable isotope ratios measured from the calves' skin likely reflected the lactation period rather than tissue formation *in utero*. The mean date of birth for southern right whales is estimated to be 24 August (Whitehead & Payne, 1981; Best, 1994). According to Reeb et al. (2005), southern right whale calves shed their fetal skin an average of 1 wk after birth. Our earliest sample was taken on 8 September (in 2005), which is about 2 wks after the estimated mean date of birth. Our visual observations of the skin appearance (rough in newborns vs smooth in older calves; Reeb et al., 2005) and the behavior patterns of mother-calf pairs (fast swimming for mothers with newborns vs resting for mothers with older calves; Thomas & Taber, 1984) also indicated that we sampled calves that were at least 2 wks old.

No Isotopic Differences in 2004

As capital breeders, southern right whales derive all the components of milk from internal reserves, with blubber as the main source of fat and lean body tissue as the main source of protein. The high fat content of whale milk (30 to 40%) serves as the primary source of energy. High protein content is also needed to fulfill the requirements of their extremely rapid growth (Oftedal, 1993, 2000). The growth rate of right whale calves is estimated to be 2.4 cm/d during the first 3 mo of life (Best & R  ther, 1992). The large quantity of lipids consumed by calves probably accounts for the lack of fractionation in $\delta^{13}\text{C}$ observed in the samples collected in 2004 because lipids are ^{13}C -depleted. Our data from 2004 represent the first report of no $\delta^{15}\text{N}$ enrichment between a mother and her offspring. Jenkins et al. (2001) detected $\delta^{15}\text{N}$ depletion from mother to milk, but from mother to offspring, they found a positive fractionation. It is possible that southern right whale milk was so depleted in ^{15}N that a complete balancing effect brought the calves back up to the same isotope values as their mothers. The process by which nitrogen in milk is depleted in comparison to the mother's tissues is unknown.

Another possible cause for the lack of nitrogen fractionation in 2004 is that the positive nitrogen balance of fast growth in the calves reduces the nitrogen isotope fractionation. During anabolic states such as pregnancy and neonatal growth, animals enter positive nitrogen balance, decreasing nitrogen excretion and potentially increasing urea recycling, and as a consequence, $\delta^{15}\text{N}$ fractionation is reduced (Fuller et al., 2004). For

southern right whales, the first months of lactation are critical, and any imbalance due to low energy reserves or high energetic demands could affect isotope ratios in both the mother and the calf.

Isotopic Differences in 2003 and 2005

Alternative hypotheses could explain the isotope differences between mothers and their calves observed in 2003 and 2005. The first hypothesis considers nutritional stress (primarily caused by low food abundance) and the second addresses the possibility of temporal decoupling of mother-calf isotope ratios measured from skin samples.

Nutritional Stress Hypothesis—In 2003 and 2005, nutritional stress could have caused mother-calf pairs to use more energy reserves than in 2004. Calves could suffer nutritional stress if their mothers do not provide enough milk or if the quality of the milk is somehow reduced; the calves would then be forced to utilize milk-derived proteins as well as lipids to meet the energy demands of growing. Catabolism of proteins during periods of nutritional stress increases $\delta^{15}\text{N}$ values (Hobson & Clark, 1992; Hobson et al., 1993). The $\delta^{13}\text{C}$ values of the calves' skin may reflect the catabolism of both the lipid and protein pools. Nutritional stress may also cause mothers to use proteins to meet their own energy demands. This catabolism of proteins would lead to the production of isotopically enriched milk (high values of $\delta^{15}\text{N}$). As a result, calves would have higher isotope ratios than their mothers.

The lack of correlation between isotope differences and sampling date may seem inconsistent with our previous argument of nutritional stress. As the nursing season progresses, the isotope fractionation of fasting animals would be expected to increase as a result of using other body tissues rather than blubber as energy reserves. The lack of seasonal effect was particularly clear in 2005, the year with the broadest sampling time (33 d). It is possible, however, that a month may not be enough time to detect such changes in the isotopic composition of the skin (Ruiz-Cooley et al., 2004). There is, however, the confounding possibility that in periods of nutritional stress, a calf would mobilize internal tissues synthesized *in utero* that may be within the half life of the turnover time to produce the molecules needed to lay down skin. In such a case, we might expect the values of the calf skin to be more similar to those of its mother. So, as the season progresses, the increased use of other tissues would prevent the "fasting signal" to appear. Controlled diet experiments and diet switches using captive cetaceans are needed to understand the turnover rates of different tissues as well as the normal isotopic variability inherent to a complex tissue such as the skin.

An independent observation that supports our hypothesis of nutritional stress is an increase in the proportion of stranded whales detected in the same population for the years 2003 and 2005. The proportion of stranded calves (PSC) and whales (PSW) can be estimated as the number of stranded animals (calves or total whales) recorded during the nursing season divided by the total number of live mother-calf pairs counted during annual aerial surveys (Uhart et al., 2008, 2009). Although PSC and PSW are crude estimates of the mortality rate for this population, they serve as a preliminary and comparative tool since both surveys have been conducted for many years, and their methodology and sampling efforts have been consistent across years. PSC and PSW appear to follow a similar pattern to the isotope differences. Although not significantly different, PSC and PSW were lower in 2004 (0.15 for both; see Table 2 for sample sizes and calculations) than in 2003 (0.19 and 0.21, respectively) and 2005 (0.20 and 0.26, respectively). Furthermore, in 2003 and 2005, in addition to calves, adults and juveniles were also reported among the stranded whales, indicating that nutritional stress might have also affected other segments of the population. Years of elevated mortality corresponded with years of larger isotope differences; both increments fit the idea of an increase in nutritional stress caused by reduced food intake during the previous feeding season.

Variability in reproductive success in southern right whales has been tied to changes in sea surface temperature (SST) that, in turn, is correlated with changes in krill abundance off South Georgia. Fewer calves than expected are born following years of high SST and low krill abundance (Leaper et al., 2006). Analysis of calving intervals of known whales suggests that in these years, females appear to extend their resting period but do not appear to suffer increased calf mortality (Cooke et al., 2003). The Antarctic fur seal shows increased pup mortality in years of low krill abundance around South Georgia (Trathan et al., 2006) as well as variation in milk composition (Arnould & Boyd, 1995). Despite being in poorer condition, female fur seals produce milk with higher lipid content in years with reduced prey abundance (Arnould & Boyd, 1995). This paradoxical situation results from the mothers extending the length of their foraging trips. As capital breeders, southern right whales cannot compensate in the same way because there is no food in the nursery area. A nursing female's only option to meet her calf's demands is to adjust nutrient mobilization and milk production from her own body reserves (Ofstedal, 1993, 2000).

Temporal Decoupling Hypothesis—An alternative hypothesis to explain the variation among

Table 2. Proportion of stranded calves (PSC) and of stranded whales (PSW) at Península Valdés during the 3-y period when our study took place; PSC and PSW are calculated by dividing the number of stranded calves or total whales (calves + juveniles + adults) obtained from Uhart et al. (2008, 2009) by the number of live mother-calf pairs counted during annual aerial surveys.

	2003	2004	2005
Stranded calves	29	13	36
Stranded total (C+J+A)	32	13	47
Live mother-calf pairs	154	89	182
PSC	0.19	0.15	0.20
PSW	0.21	0.15	0.26

years in isotope differences between mothers and their offspring addresses the timing of tissue formation and the possible decoupling of isotope ratios. Different tissues have different isotope turnover rates; some turn over within hours or days (e.g., blood plasma and liver), while others take several weeks (e.g., muscles) or years (e.g., bone collagen) (Rubenstein & Hobson, 2004). It is possible that whales in 2003 and 2005 may have fed on an isotopically depleted diet that was integrated during formation of their skin, but fed on an enriched diet when storing nutrients in their blubber and muscle reserves for later milk production. Alternatively, in 2004, the whales could have had isotopically similar diets during both time periods. Hobson et al. (2000) remark on a similar mother-offspring decoupling problem in black bear hair. The turnover rate of cetacean skin is unknown, although it has been suggested to be less than a month (Todd et al., 1997) to several months (Ruiz-Cooley et al., 2004). Because the turnover rate and thus the time for tissue formation are unknown, we cannot determine the influence of this type of decoupling on the interannual isotope differences we have observed between mother-calf pairs.

In summary, stable isotope differences between southern right whale mothers and their calves did not follow a pattern of trophic enrichment (3‰ enrichment in nitrogen and ~1‰ in carbon) but were similar to the values proposed by Jenkins et al. (2001). The substantial interannual variability presented here was probably associated with variability in the nutritional condition of mother-calf pairs. We suggest that nutritional stress, potentially caused by the food shortage, caused some mother-calf pairs to use both protein and lipid stores to meet the energetic demands of calf growth and maintenance. We do not have enough information to reject the decoupling hypothesis, but the association between a higher proportion of stranded animals and larger isotopic differences between mothers and their calves supports

the nutritional stress hypothesis. Regardless of whether one or both of these hypotheses are accurate, the data presented here probably reflect changes in the foraging ecology of southern right whales as a consequence of interannual fluctuations in food abundance or distribution. When we better understand the processes affecting stable isotopes during milk production and consumption, and during offspring growth, it should become possible to study nutritional stress at the individual and population levels, in some detail, by measuring isotopic differences between mothers and their offspring.

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