




Variation in $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values of mothers and their calves across southern right whale nursery grounds: The effects of nutritional stress?

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Abstract

Southern right whales (SRW) are capital breeders that use stored energy reserves to sustain themselves and their

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calves on nursery areas. With successful calving events declining in some SRW populations, it has been hypothesized that nutritional stress in adult females causes reproductive failure or death of calves shortly after birth. Here we compared offsets in carbon and nitrogen isotope values of mothers and their offspring ($\Delta^{13}\text{C}_{\text{calf-cow}}$ and $\Delta^{15}\text{N}_{\text{calf-cow}}$) among three SRW populations. SRW from Aotearoa New Zealand, with high population growth rates and body conditions scores, have negative $\Delta^{13}\text{C}_{\text{calf-cow}}$ suggesting calves are utilizing ^{13}C -depleted lipid carbon in milk to fuel the synthesis of nonessential amino acids used to build new tissues and rapidly grow. In contrast, a significantly positive $\Delta^{13}\text{C}_{\text{calf-cow}}$ offset previously reported for SRW from Argentina during a mass die-off event was hypothesized to be due to calves consuming milk with low lipid content. Patterns in $\Delta^{15}\text{N}_{\text{calf-cow}}$ were more difficult to interpret and highlight the complexity in nitrogen transfer between mother and offspring. When combined with similar data collected from Brazil and during a low mortality year in Argentina, we hypothesize this approach provides a way to retrospectively compare nutritional condition of breeding adult female SRW across nursery areas.

KEYWORDS

capital breeder, *Eubalaena australis*, maternal investment, physiology, southern right whale, stable isotope

1 | INTRODUCTION

Most baleen whales are “capital breeders” that use stored energy reserves to finance the cost of reproduction. Southern right whales (SRW, *Eubalaena australis*) may be one of the most extreme examples of this strategy in cetaceans, as calves grow rapidly (between 2.2 and 3.5 cm per day), resulting in a loss of up to 25% in the body volume of nursing females during the winter lactation period (Best & Ruther, 1992; Christiansen et al., 2018). Gestation and lactation are energetically demanding, with female SRWs historically having an average reproductive cycle of three years: one year for gestation, one year for lactation, and a rest year to regain body condition for the next pregnancy (Best, 1994; Burnell, 2001; Davidson et al., 2018; Thomas & Taber, 1984).

In recent years, there has been an increase in the average interval between successful calving events from three to four or five years in SRW that use the South African wintering grounds (Vermeulen et al., 2020). This is hypothesized to be due to a decrease in prey availability and/or quality leading to SRW females to either defer breeding, thereby lengthening calving intervals, and/or to females losing a calf in its first year of life (Leaper et al., 2006; Rowntree et al., 2013; Seyboth et al., 2016; van den Berg et al., 2021). In this latter case, if a female loses a calf early

in lactation she may recover quickly and mate in the following year, resulting in a five year interval to a successful breeding event (weaned calf) (Marón et al., 2015). Also, unusually high calf mortality events have occurred on the Argentinean wintering ground (Rowntree et al., 2013; Sironi et al., 2018) which has similarly seen a lengthening in successful breeding intervals (Marón et al., 2015), resulting in a decrease in the population growth rate (Crespo et al., 2019). The Brazilian wintering ground is likely demographically distinct from, but linked by high levels of connectivity to the Argentinean wintering ground (Best et al., 1993; Carroll, Ott, et al., 2020; Rowntree et al., 2020). Models linking calf output with conditions on high latitude foraging grounds (Seyboth et al., 2016) suggest SRW in Brazil may have been experiencing nutritional stress. In contrast, the best available data from the Aotearoa New Zealand (hereafter New Zealand) wintering ground shows a high rate of growth of 7% per annum between 1995 and 2009 (Carroll et al., 2013). This is consistent with the New Zealand population having no recorded mortality events and the highest recorded body condition of any studied right whale population (Christiansen et al., 2020).

As SRW reproduction and by extension population growth rate are linked to environmental conditions that influence prey availability on the high latitude foraging grounds (Leaper et al., 2006; Seyboth et al., 2016), several studies have aimed to identify the location of the species' offshore foraging grounds (Mackay et al., 2020; Mate et al., 2011; Valenzuela et al., 2018; van den Berg et al., 2021; Zerbini et al., 2015, 2018). A common tool to investigate the location and trophic level at which baleen whales feed is stable isotope analysis. Early studies reported oscillations of carbon ($\delta^{13}\text{C}$) and nitrogen ($\delta^{15}\text{N}$) isotope values in SRW baleen that was linked to the whale's annual migration across oceanographic regions that varied in their baseline isotopic composition (Best & Schell, 1996; Schell et al., 1989). In addition, because the isotopic composition of skin tissue reflects dietary inputs integrated over several months prior to collection (Busquets-Vass et al., 2017), biopsy samples collected from whales on their winter nursery or socializing grounds reflect recently visited foraging grounds. This approach has been used to identify foraging grounds or foraging traditions, infer diet composition, and characterize migratory patterns for SRW (Carroll et al., 2015; Rowntree et al., 2001, 2008; Valenzuela et al., 2009, 2018; van den Berg et al., 2021; Vighi et al., 2014).

Stable isotopes are also being used to investigate physiology and nutritional stress in marine mammals (e.g., Lübcker, Whiteman, Millar, et al., 2020; Marón et al., 2020). In the case of SRW, we hypothesize that differences between $\delta^{13}\text{C}$ values in the tissues of mothers and their offspring can be used as a proxy for maternal nutritional stress, and that this is correlated with population health and growth rates (Habran et al., 2019; Valenzuela et al., 2010). Changes in the $\delta^{13}\text{C}$ of calves relative to their mothers likely reflects the balance of protein and lipid sources used by adult females to produce milk to fuel calf growth. Lipids have $\delta^{13}\text{C}$ values that are 6‰–8‰ lower than associated proteins (Cherry et al., 2011), and carbon derived from lipids can be used to build the carbon skeletons of nonessential amino acids needed to synthesize new tissue in rapidly growing offspring (Newsome et al., 2014; Wolf et al., 2015).

The lipid content of marine mammal milk is exceptionally high in comparison to other mammals and varies widely within and among species (Lefèvre et al., 2010; Oftedal, 1993). Many mammalian species show a decline in lipid content of milk when nutritionally stressed (Neville & Picciano, 1997). The point where this decline occurs varies between species, but we hypothesize that capital breeders that have evolved to lactate while fasting would also show a decline in milk lipid when nutritional stress reaches a metabolic tipping point. This decrease in lipid content could result in a slightly positive offset in $\delta^{13}\text{C}$ between calves and their mothers, with the offset defined here as the $\delta^{13}\text{C}$ value of calves minus the $\delta^{13}\text{C}$ value of their mothers, or $\Delta^{13}\text{C}_{\text{calf-cow}}$. This slightly positive offset is expected because offspring are directly routing milk proteins rather than using a substantial amount of ^{13}C -depleted lipids to synthesize proteinaceous tissues, a process often cited to explain trophic discrimination in carbon isotopes (Kelly, 2000). This phenomenon may be associated with poor body condition and lower reproductive success, with potential population level consequences. Conversely, when milk lipid content is high, the offset in $\delta^{13}\text{C}$ between calves and their mothers is predicted to be negative as ^{13}C -depleted lipid carbon can be converted into acetyl CoA that enters the tricarboxylic acid cycle and is used to synthesize the carbon skeletons of nonessential amino acids that are needed to rapidly build tissues (Newsome et al., 2014). We assume this would be associated with good maternal body condition and stable population growth rates. Stable isotope analysis of northern elephant seal (*Mirounga*

angustirostris) tissues supports the above hypothesized patterns and found that ^{13}C -depletion in offspring relative to their mothers correlated with fasting duration (Habran et al., 2019). While not a primary focus here, a positive offset in $\delta^{15}\text{N}$ in calves relative to their mothers ($\Delta^{15}\text{N}_{\text{calf-cow}}$) is also expected since females catabolize their own tissues to produce milk for their offspring. This pattern often manifests as a significant ^{15}N -enrichment akin to that observed in trophic discrimination in nitrogen isotopes between consumer and prey (Fogel et al., 1989; Fuller et al., 2004; Newsome et al., 2006).

This hypothesis was previously tested in a study of 42 SRW cow-calf pairs from the Argentinean wintering ground, where Valenzuela et al. (2010) investigated the offset in carbon and nitrogen isotope composition between paired calves and cows ($\Delta^{13}\text{C}_{\text{calf-cow}}$ and $\Delta^{15}\text{N}_{\text{calf-cow}}$, respectively) during years of relatively low (2004: 13 dead calves) and high (2003: 29 dead and 2005: 36 dead) calf mortality. In the years with high calf mortality, the offset between calf and cow was positive in both carbon and nitrogen, whereas in the year with low mortality neither offset was found to be significantly different than zero (Table 1).

Here, we measured $\Delta^{13}\text{C}_{\text{calf-cow}}$ and $\Delta^{15}\text{N}_{\text{calf-cow}}$ in the New Zealand ($n = 21$) and Brazilian ($n = 7$) wintering grounds, and compare these patterns with previously published data on cow-calf pairs in the Argentinean wintering ground summarized above (Valenzuela et al., 2010). This provides comparative framework to assess the change in $\Delta^{13}\text{C}_{\text{calf-cow}}$ and $\Delta^{15}\text{N}_{\text{calf-cow}}$ in populations that are suspected to have relatively low (New Zealand) and high (Argentina) levels of nutritional stress.

2 | METHODS

2.1 | Sample collection and stable isotope analysis

Skin biopsy samples were collected from SRW in Brazil from 1999 to 2002 (Carroll, Ott, et al., 2020; Ott, 2002) and in New Zealand from 2007 to 2009 (Carroll et al., 2013). Data collection from cow-calf pairs was noted in the field and maternity confirmed via microsatellite genotyping (Supplementary Material). A subsample of the skin biopsy sample was freeze-dried and underwent lipid extraction following protocols described in Todd et al. (1997) for the Brazilian samples or Busquets-Vass et al. (2017) for the New Zealand samples. Lipid extraction is also known to correct for effects of preservation medium (Newsome et al., 2018; Todd et al., 1997). Carbon ($\delta^{13}\text{C}$) and nitrogen ($\delta^{15}\text{N}$) isotope values were measured on a Costech 4010 elemental analyzer coupled to a Thermo Scientific Delta V isotope ratio mass spectrometer at the University of Wyoming Stable Isotope Facility (Laramie, WY) or the Durham

TABLE 1 Mean and standard deviations ($\pm\text{SD}$) of $\Delta^{13}\text{C}_{\text{calf-cow}}$ and $\Delta^{15}\text{N}_{\text{calf-cow}}$ from southern right whale nursery grounds. Also shown are pairwise comparisons of these values, as well as years with differing levels of calf mortality in Argentina: low (2004) and high (2003 and 2005); acronyms include New Zealand (NZ), Brazil (BRZ), and Argentina (ARG) and sample size (n). The top right and bottom left quadrants show the p -values from t -tests for $\Delta^{13}\text{C}_{\text{calf-cow}}$ and $\Delta^{15}\text{N}_{\text{calf-cow}}$, respectively. Argentinean data from Valenzuela et al. (2010).

	n	NZ	BRZ	ARG (low)	ARG (high)	$\Delta^{13}\text{C}_{\text{calf-cow}}$ \pm SD (%)	$\Delta^{15}\text{N}_{\text{calf-cow}}$ \pm SD (%)
NZ	21		0.125	0.044	<0.001	-0.8 ± 1.1	0.5 ± 0.8
BRZ	7	0.054		0.678	<0.001	-0.3 ± 0.5	-0.1 ± 0.6
ARG (low mortality)	20	0.137	0.266		<0.001	-0.2 ± 0.6	0.2 ± 0.5
ARG (high mortality)	22	0.066	0.003	<0.001		0.8 ± 0.3	0.7 ± 0.7

University Stable Isotope Biogeochemistry Laboratory (Durham, UK); see Carroll et al. (2015) for analytical details. Stable isotope data are expressed as δ values using the equation $\delta X = (R_{\text{Sample}}/R_{\text{Standard}}) - 1$, where X is any isotope system of interest (e.g., C or N) and R_{Sample} and R_{Standard} are the ratios of the heavy to light isotope (e.g., $^{13}\text{C}/^{12}\text{C}$ or $^{15}\text{N}/^{14}\text{N}$) for each sample and standard, respectively. The internationally accepted standards are Vienna Pee Dee Belemnite (V-PDB) for $\delta^{13}\text{C}$, and atmospheric nitrogen for $\delta^{15}\text{N}$; units are expressed as parts per thousand, or per mil (‰). Analytical precision for $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ was assessed via analyses of in-house reference materials for each run, which were stringently calibrated against international standards (e.g., USGS 40, IAEA 600, IAEA N2), and was measured to be $\pm 0.2\text{‰}$ (SD). The calibration of in-house reference materials to international standards ensure isotope data can be compared across laboratories. We also measured the weight percentage carbon ([C]) and nitrogen ([N]) concentrations of each sample via analysis of organic materials with known elemental concentrations.

2.2 | Testing for normality

We first used the Shapiro–Wilk test in the statistical programming language R base package (R Core Team, 2020) to test whether the distributions of $\delta^{13}\text{C}$, $\delta^{15}\text{N}$, $\Delta^{13}\text{C}_{\text{calf-cow}}$, and $\Delta^{15}\text{N}_{\text{calf-cow}}$, partitioned by nursery ground, deviated from the expectation of normality. For the Brazilian samples ($n = 7$ pairs), no isotope values or offsets were found to be significantly different from the expectation of normality ($p > .05$). For the New Zealand samples ($n = 21$ pairs), the Shapiro–Wilk test indicated significant deviations from the expectation of normality for $\delta^{13}\text{C}$ ($p < .001$), but not for the $\Delta^{13}\text{C}_{\text{calf-cow}}$, $\delta^{15}\text{N}$, or $\Delta^{15}\text{N}_{\text{calf-cow}}$ data sets ($p > .05$). Therefore, we assessed the $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ data sets for differences between sampling regions with both parametric and nonparametric statistics and the $\Delta^{13}\text{C}_{\text{calf-cow}}$ or $\Delta^{15}\text{N}_{\text{calf-cow}}$ data sets only with parametric analyses. Data visualizations were done using R package *ggplot2* (Wickham, 2016).

2.3 | Patterns in $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values across and within nursery grounds

We used t -tests (parametric) and Kolmogorov–Smirnov tests (nonparametric) to test for significant differences in the $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values for cows between nursery grounds. As the New Zealand data were collected over 4 years, we used these tests to investigate any interannual variation.

2.4 | Patterns in $\Delta^{13}\text{C}_{\text{calf-cow}}$ and $\Delta^{15}\text{N}_{\text{calf-cow}}$ values across nursery grounds

For each nursery ground, distributions of $\Delta^{13}\text{C}_{\text{calf-cow}}$ or $\Delta^{15}\text{N}_{\text{calf-cow}}$ values were calculated by taking the offset in nitrogen and carbon isotope composition between paired calves and cows. The mean and standard deviation for these distributions were calculated, and were tested to see if they were significantly different from zero using a one-sample t -test in R. The distributions of $\Delta^{13}\text{C}_{\text{calf-cow}}$ and $\Delta^{15}\text{N}_{\text{calf-cow}}$ values for different nursery grounds were compared in a pairwise manner using the Kolmogorov–Smirnov test.

3 | RESULTS

3.1 | Data set summary

There were 7 and 21 cow-calf pairs for which $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ data (Figure 1, Table 1) were produced from Brazil and New Zealand, respectively. We also included the published data from a low mortality year (2004, $n = 20$) and high mortality years (2003 and 2005, $n = 22$) from Argentina (Valenzuela et al., 2010).

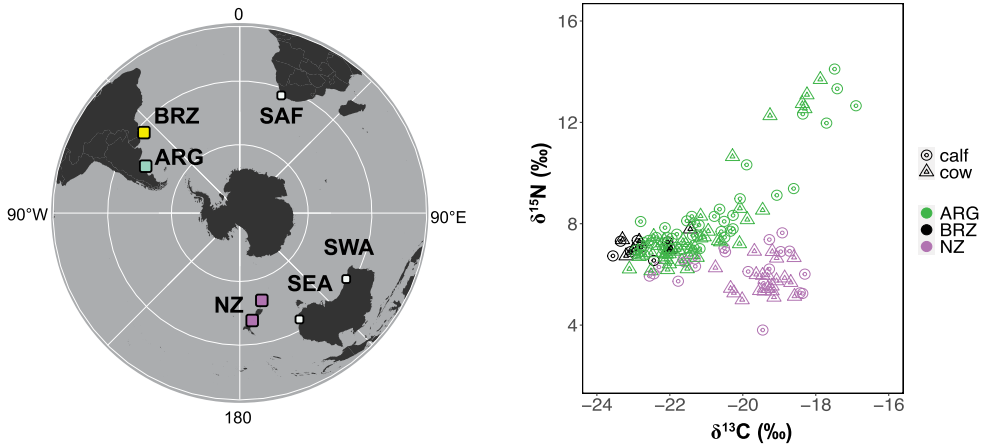


FIGURE 1 Location of southern right whale wintering grounds and skin $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values for the cow (triangles) and calf (circles) samples from Argentina (ARG), Brazil (BRZ) and New Zealand (NZ). Also shown are the locations of the South African (SAF), southwest Australian (SWA) and southeast Australian (SEA) wintering grounds. Argentinean data are from Valenzuela et al. (2010).

TABLE 2 p -values for pairwise comparisons in $\Delta^{13}\text{C}_{\text{calf-cow}}$ and $\Delta^{15}\text{N}_{\text{calf-cow}}$ between years for the New Zealand data set using Kolmogorov–Smirnov (KS) and t -tests.

Year 1	Year 2	Offset	KS test	t
2007	2008	$\Delta^{13}\text{C}_{\text{calf-cow}}$	0.135	0.316
2007	2009	$\Delta^{13}\text{C}_{\text{calf-cow}}$	0.212	0.316
2008	2009	$\Delta^{13}\text{C}_{\text{calf-cow}}$	0.833	0.235
2007	2008	$\Delta^{15}\text{N}_{\text{calf-cow}}$	0.225	0.235
2007	2009	$\Delta^{15}\text{N}_{\text{calf-cow}}$	0.718	0.873
2008	2009	$\Delta^{15}\text{N}_{\text{calf-cow}}$	0.491	0.873

3.2 | Patterns in $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values across nursery grounds

We found no significant differences between years within the New Zealand data set (Table 2). There was a significant difference between both South American data sets and the New Zealand data set for cow $\delta^{13}\text{C}$ (Figure 2) and $\delta^{15}\text{N}$ values (Figure 3; $p < .001$ for all comparisons: Table S1), but not between the Argentina and Brazil data sets (Table S1, Figure 1).

3.3 | Patterns in $\Delta^{13}\text{C}_{\text{calf-cow}}$ values across nursery grounds

Mean and standard deviations for $\Delta^{13}\text{C}_{\text{calf-cow}}$ and $\Delta^{15}\text{N}_{\text{calf-cow}}$ offsets can be found in Table 1 and graphically displayed in Figures 2 and 3. $\Delta^{13}\text{C}_{\text{calf-cow}}$ ($p < .01$) for the New Zealand data set was significantly different from zero based on a one-sample t -test, whereas the offsets for the Brazilian dataset were not ($\Delta^{13}\text{C}_{\text{calf-cow}}$; $p = .12$). There were significant differences in $\Delta^{13}\text{C}_{\text{calf-cow}}$ across nursery grounds, with the Argentinean high mortality years having significantly higher offsets than all other wintering grounds and the Argentinean low mortality year. We also observed significant differences in $\Delta^{15}\text{N}_{\text{calf-cow}}$ between wintering grounds, with the Argentinean high mortality years having significantly higher offsets than the Argentinean low mortality year or the Brazilian data set (Table 1).

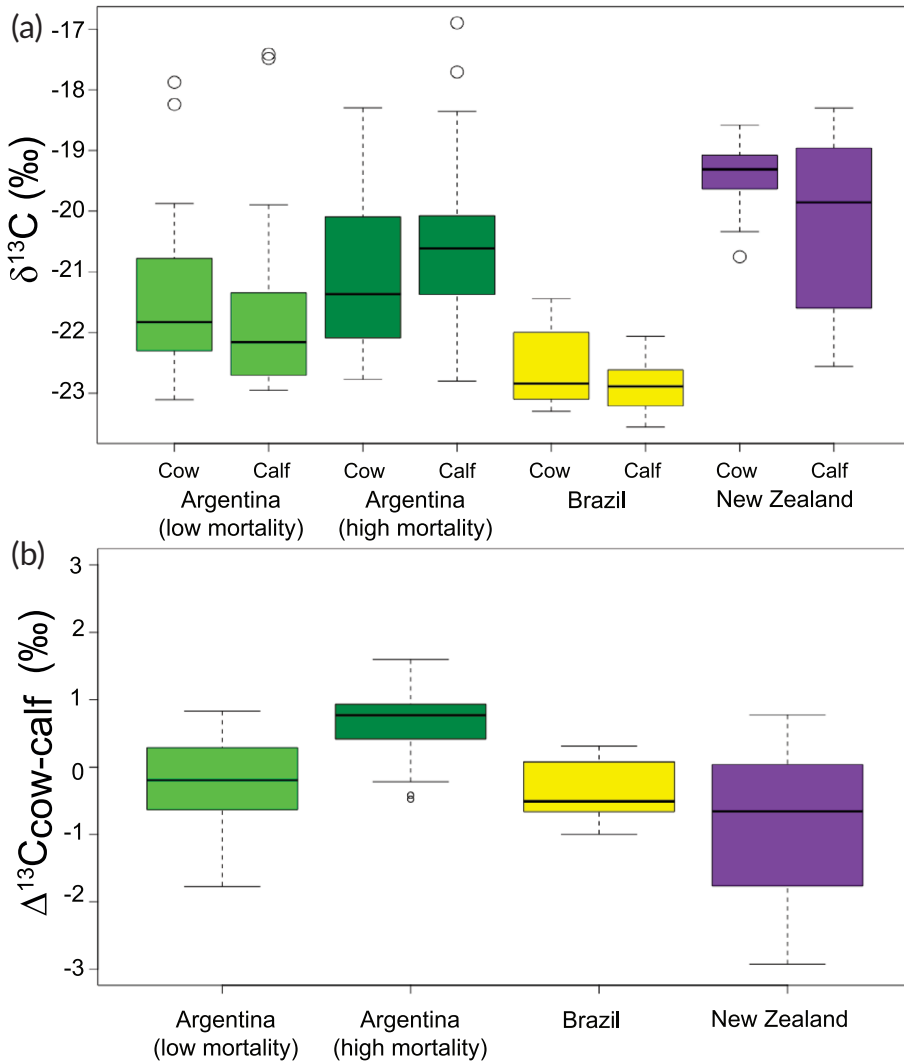


FIGURE 2 (a) Boxplot of cow and calf stable $\delta^{13}\text{C}$ isotope data summarized by wintering ground for Argentina (low and high mortality years), Brazil, and New Zealand. (b) Boxplot of offset between cow and calf for $\delta^{13}\text{C}$ ($\Delta^{13}\text{C}_{\text{calf-cow}}$) by wintering ground for low (low mortality) and high (high mortality) calf mortality years in Argentina, Brazil, and New Zealand. Argentina data from Valenzuela et al. (2010). Boxes defined by 25% and 75% quantile values with median showed by black line, with whiskers extending up to $1.5\times$ the interquartile range and outliers shown by open circles.

4 | DISCUSSION

Overall, our results suggest a relationship between physiological condition and $\Delta^{13}\text{C}_{\text{calf-cow}}$ across SRW populations calving in three wintering grounds. Specifically, the New Zealand population shows a negative $\Delta^{13}\text{C}_{\text{calf-cow}}$ (Table 1) that is significantly different than zero, suggesting calves are utilizing ^{13}C -depleted lipid carbon in milk to fuel the synthesis of nonessential amino acids needed to build new tissues and rapidly grow. This coincided with a period (1995–2009) of high estimated population growth and no observed cow or calf mortality events (Carroll et al., 2013). In contrast, there were weakly negative mean $\Delta^{13}\text{C}_{\text{calf-cow}}$ values in the data sets from both the

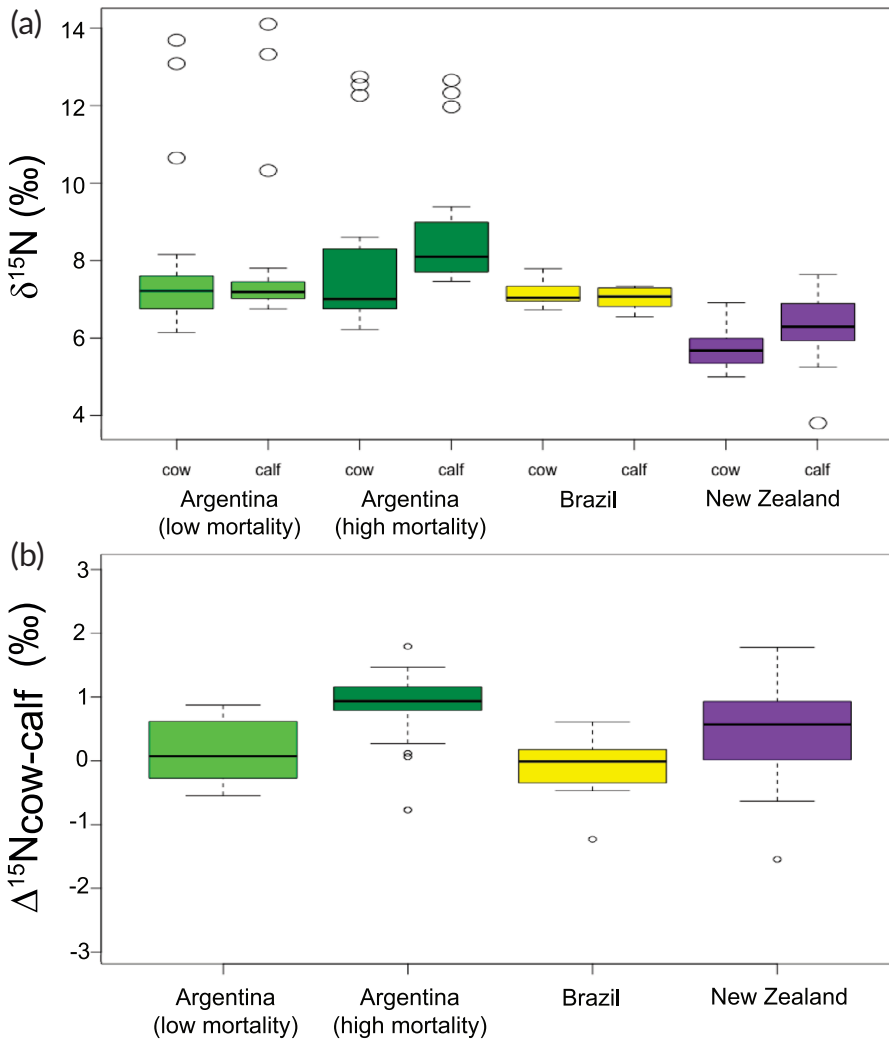


FIGURE 3 (a) Boxplot of cow and calf stable $\delta^{15}\text{N}$ isotope data summarized by wintering ground for Argentina (low and high mortality years), Brazil, and New Zealand. (b) Boxplot of offset between cow and calf for $\delta^{15}\text{N}$ ($\Delta^{15}\text{N}_{\text{calf-cow}}$) by wintering ground for low (low mortality) and high (high mortality) calf mortality years in Argentina, Brazil, and New Zealand. Argentina data from Valenzuela et al. (2010). Boxes defined by 25% and 75% quantile values with median showed by black line, with whiskers extending up to $1.5\times$ the interquartile range and outliers shown by open circles.

Brazilian wintering ground and low mortality year in Argentina (Table 1), both of which were statistically indistinguishable from zero. We hypothesize this represents a decrease in maternal lipid catabolism to fuel growth in calves in the Brazilian wintering grounds relative to those from New Zealand. Modelling suggests that there was a decrease in calf production in the Brazilian wintering ground coincident with our sampling period (1998–2005) of this population, which is believed to be driven by decreases in krill abundance in high latitude foraging areas (Seyboth et al., 2016). If this hypothesis is correct, decreases in calf output were likely driven by higher nutritional stress in females that calved over this time period in the Brazilian wintering ground. Finally, as previously described (Valenzuela et al., 2010), the high mortality years in Argentina had a positive mean offset in $\Delta^{13}\text{C}_{\text{calf-cow}}$ ($+0.8 \pm 0.3\text{‰}$), which was significantly higher than observed in the New Zealand, Brazil, and the low mortality Argentina

data sets (see Table 2 for pairwise p -values). This suggests that cows during high mortality years in Argentina were nutritionally stressed and were using fewer lipids to fuel calf development in comparison to the other data sets.

Patterns in $\Delta^{15}\text{N}_{\text{calf-cow}}$ were not as clear as those for carbon isotopes, as the data sets for New Zealand ($+0.5 \pm 0.8\text{‰}$) and Argentina high mortality years ($+0.7 \pm 0.7\text{‰}$) showed positive offsets that were significantly higher than zero but statistically indistinguishable from one another. These positive offsets are expected since mammals catabolize their own tissues to produce milk for their offspring, which often manifests as a significant ^{15}N -enrichment akin to trophic discrimination in nitrogen isotopes between consumer and prey (Fogel et al., 1989; Fuller et al., 2004; Newsome et al., 2006). Small but consistent mother-offspring $\Delta^{15}\text{N}$ offsets of 1‰–2‰ have been observed in a wide range of mammal species (Fogel et al., 1989; Jenkins et al., 2001; Newsome et al., 2006, 2009). In contrast, the negligible mean $\Delta^{15}\text{N}_{\text{calf-cow}}$ in the Brazilian ($-0.1 \pm 0.6\text{‰}$) and low mortality year Argentina data sets ($0.2 \pm 0.5\text{‰}$) that appear not to be significantly different from zero suggests a more complex relationship between nutritional status, nitrogen balance, and transfer of nitrogen from mother to calf during gestation and lactation. Recent work on healthy southern elephant seal (*Mirounga leonina*) mother-pup pairs utilizing a combination of bulk tissue and amino acid nitrogen isotope analysis highlights this complexity, but also shows that offspring in utero generally have higher $\delta^{15}\text{N}$ values than their mother at parturition (Lübcker, Whiteman, Millar, et al., 2020), an isotopic offset that is likely maintained or enhanced during lactation under healthy conditions. Negligible mother-offspring $\Delta^{15}\text{N}$ offsets may indicate a disruption in nitrogen balance in either offspring or parent. For example, the direct routing of amino acids from diet to tissue with minimal isotopic alteration, resulting in mother-offspring $\Delta^{15}\text{N}$ offsets apparently statistically indistinguishable from zero, could indicate nutritional stress in calves similar to patterns observed in mammals fed diets with low protein content and quality (Robbins et al., 2005). Likewise, fasting has been shown to increase the nitrogen isotope composition of both bulk tissues (Hertz et al., 2015) and individual amino acids catabolized to fuel gluconeogenesis (Lübcker, Whiteman, Newsome, et al., 2020), which could yield increases the $\delta^{15}\text{N}$ of mothers over the course of the winter breeding season relative to their calves and produce negligible or even negative $\Delta^{15}\text{N}_{\text{calf-cow}}$. Additional work utilizing amino acid isotope analysis is needed to further explore the potential drivers of $\Delta^{15}\text{N}_{\text{calf-cow}}$ in SRW.

The interpretation of isotopic differences between calves and cows assumes that the isotopic composition of calf skin largely represents the lactation period, rather than time in utero. While skin isotopic incorporation rates for SRW are unknown, studies of bottlenose dolphins and blue whales report similar estimates of complete isotopic turnover of skin in adults: 163 ± 91 days for $\delta^{15}\text{N}$ in blue whales (Busquets-Vass et al., 2017) and 180 ± 71 and 104 ± 35 days for $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$, respectively, in bottlenose dolphins (Giménez et al., 2016). Isotopic incorporation rates for rapidly growing calves are likely faster than in adults, and to ensure that skin sampled from calves primarily reflects the lactation period, we recommend that future work focuses on sampling older calves whose skin tissue reflects time since parturition. Another important assumption of the approach we used to assess maternal physiological condition is that the isotopic composition of cow skin is a reliable proxy for the protein-rich tissues (e.g., muscle) being catabolized to produce milk for their offspring. We believe this assumption is valid because SRW are capital breeders and cows are catabolizing muscle tissue to repair their skin while on the wintering grounds, which is consistent with the lack of significant differences in the isotopic composition of fin whale muscle and skin (Borrell et al., 2012).

Finally, the difference between the New Zealand and South American nursery ground cow $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values was unsurprising, given that the foraging grounds of SRWs in the two regions are most likely located in the South Atlantic and South Pacific, respectively, that have different isotopic baselines (Mackay et al., 2020; Valenzuela et al., 2018; Vighi et al., 2014; Zerbini et al., 2018). There was no difference in the $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values of cows from Argentina and Brazil (Table S1, Figure 1), suggesting that whales that use these two wintering grounds likely share foraging grounds, which contrasts with isotope data from historical samples that suggested SRWs wintering in the two areas used different foraging grounds (Vighi et al., 2014).

Our results contribute to the growing number of comparative studies that use data collected across years and populations to provide insight into broader trends in SRW population health, growth, and genetic diversity (Carroll et al., 2019; Christiansen et al., 2020; Corkeron et al., 2018). Given concern over the decrease in reproductive success and population growth rates in some SRW wintering grounds (Carroll, Charlton, et al., 2020), we recommend

that skin biopsy sampling continues on cow-calf pairs to facilitate a year-to-year understanding of nutritional stress of populations and to increase our understanding of the processes governing isotopic discrimination between mothers and calves. We also anticipate that ongoing work to measure amino acid $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values of these samples, which shows promise as a proxy for nutritional status (Lübcker, Whiteman, Millar, et al., 2020; Whiteman et al., 2019), will provide greater insights into SRW nitrogen balance and the transfer of carbon and nitrogen from mother to offspring during lactation.

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SUPPORTING INFORMATION

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