

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?

Emma L. Carroll^{1,2}  | Glenn Dunshea^{3,4} | Paulo H. Ott^{5,6} | Luciano O. Valenzuela^{7,8,9} | C. Scott Baker¹⁰ | Simon J. Childerhouse¹¹ | Oscar E. Gaggiotti² | Paulo A. C. Flores¹² | Karina Groch¹³ | Darren R. Gröcke¹⁴ | Mark A. Hindell¹⁵ | David Lundquist¹⁶ | Larissa R. Oliveira^{5,17}  | Victoria Rowntree⁹  | Mariano Sironi^{9,18} | Seth D. Newsome¹⁹

¹School of Biological Sciences Te Kura Mātauranga Koiora, University of Auckland Waipapa Taumata Rau, Auckland, Aotearoa, New Zealand

²School of Biology and Sea Mammal Research Unit, University of St Andrews, Scotland, UK

³Ecological Marine Services Pty. Ltd, Bundaberg, Queensland, Australia

⁴NTNU University Museum, Norwegian University of Science and Technology, Trondheim, Norway

⁵Grupo de Estudos de Mamíferos Aquáticos do Rio Grande do Sul, Torres, RS, Brazil

⁶Universidade Estadual do Rio Grande do Sul, Osório, RS, Brazil

⁷School of Biological Sciences, University of Utah, Salt Lake City, Utah

⁸Consejo Nacional de Investigaciones Científicas y Técnicas (CONICET), Laboratorio de Ecología Evolutiva Humana, Facultad de Ciencias Sociales, UNCPBA, Buenos Aires Province, Argentina

⁹Instituto de Conservación de Ballenas, Buenos Aires, Argentina

¹⁰Marine Mammal Institute and Department of Fisheries, Wildlife and Conservation Sciences, Oregon State University, Oregon

¹¹Cawthron Institute, Nelson, New Zealand

¹²Núcleo de Gestão Integrada Florianópolis, ICMBio-MMA, Florianópolis, SC, Brazil

¹³Instituto Australis, Imbituba, Santa Catarina, Brazil

¹⁴Stable Isotope Biogeochemistry Laboratory, Department of Earth Sciences, University of Durham, Durham, UK

¹⁵Institute for Marine and Antarctic Studies, University of Tasmania, Tasmania, Australia

¹⁶New Zealand Department of Conservation, Wellington, New Zealand

¹⁷Laboratório de Ecologia de Mamíferos, Universidade do Vale do Rio dos Sinos, Sao Leopoldo, RS, Brazil

¹⁸Diversidad Biológica IV, Universidad Nacional de Córdoba, Córdoba, Argentina

¹⁹Biology Department, University of New Mexico, Albuquerque, New Mexico

Correspondence

Emma L. Carroll, School of Biological Sciences, University of Auckland, Private Bag 92019, Auckland Mail Centre, Auckland 1142,

Abstract

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

New Zealand.

Email: carrollemz@gmail.com

Funding information

Australian Antarctic Division; Australian Marine Mammal Centre; Blue Planet Marine NZ Ltd; Brazilian National Research Council, Grant/Award Number: CNPq proc. n° 144064/98-7; Brian Skerry Photography; EU Horizons 2020, Grant/Award Number: Marie Curie Fellowship; Holsworth Wildlife Research Endowment; Marine Conservation Action Fund; National Geographic Society; New Zealand Department of Conservation; New Zealand Ministry of Foreign Affairs; Royal Society of New Zealand, Grant/Award Number: Rutherford Discovery Fellowship; South Pacific Whale Research Consortium; Winifred Violet Scott Estate Research Grant Fund

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)	$\Delta^{13}\text{C}_{\text{calf-cow}}$ $\pm \text{SD}$ (‰)	$\Delta^{15}\text{N}_{\text{calf-cow}}$ $\pm \text{SD}$ (‰)
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).

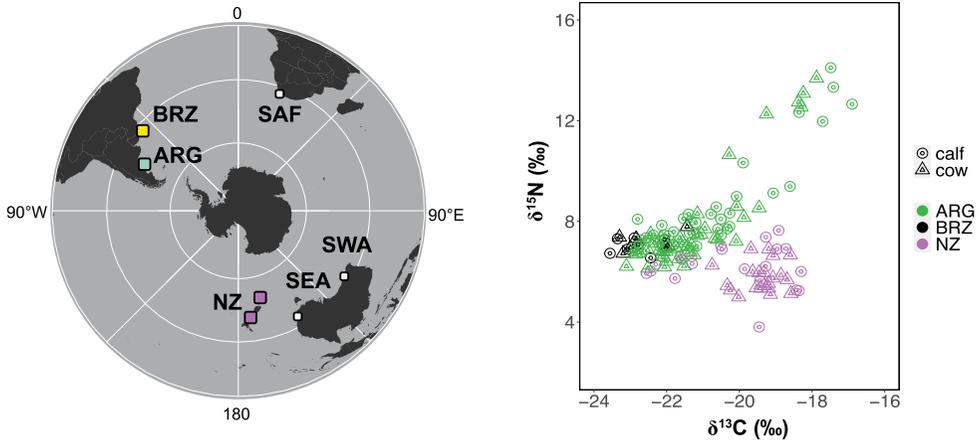


FIGURE 1 Location of southern right whale wintering grounds and skin $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values for the cow (triangles) and calf (circles) samples from Argentina (ARG), Brazil (BRZ) and New Zealand (NZ). Also shown are the locations of the South African (SAF), southwest Australian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

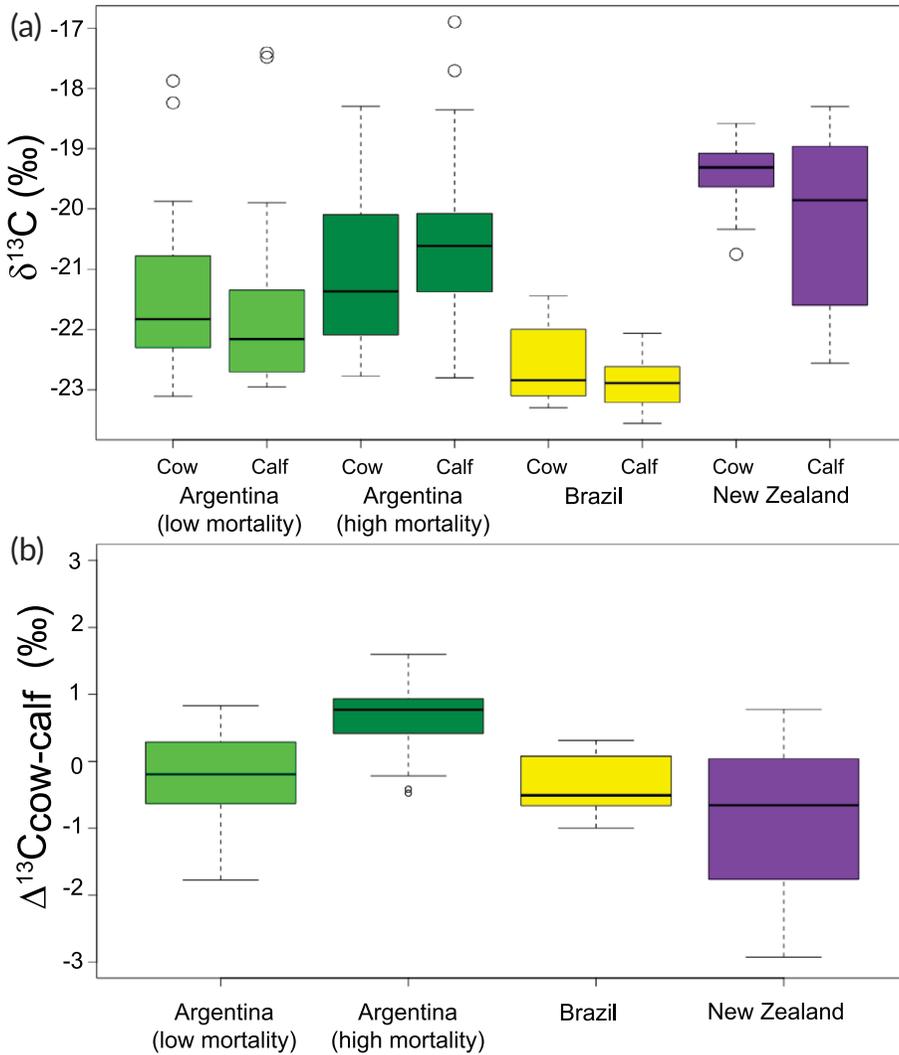


FIGURE 2 (a) Boxplot of cow and calf stable $\delta^{13}\text{C}$ isotope data summarized by wintering ground for Argentina (low and high mortality years), Brazil, and New Zealand. (b) Boxplot of offset between cow and calf for $\delta^{13}\text{C}$ ($\Delta^{13}\text{C}_{\text{calf-cow}}$) by wintering 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

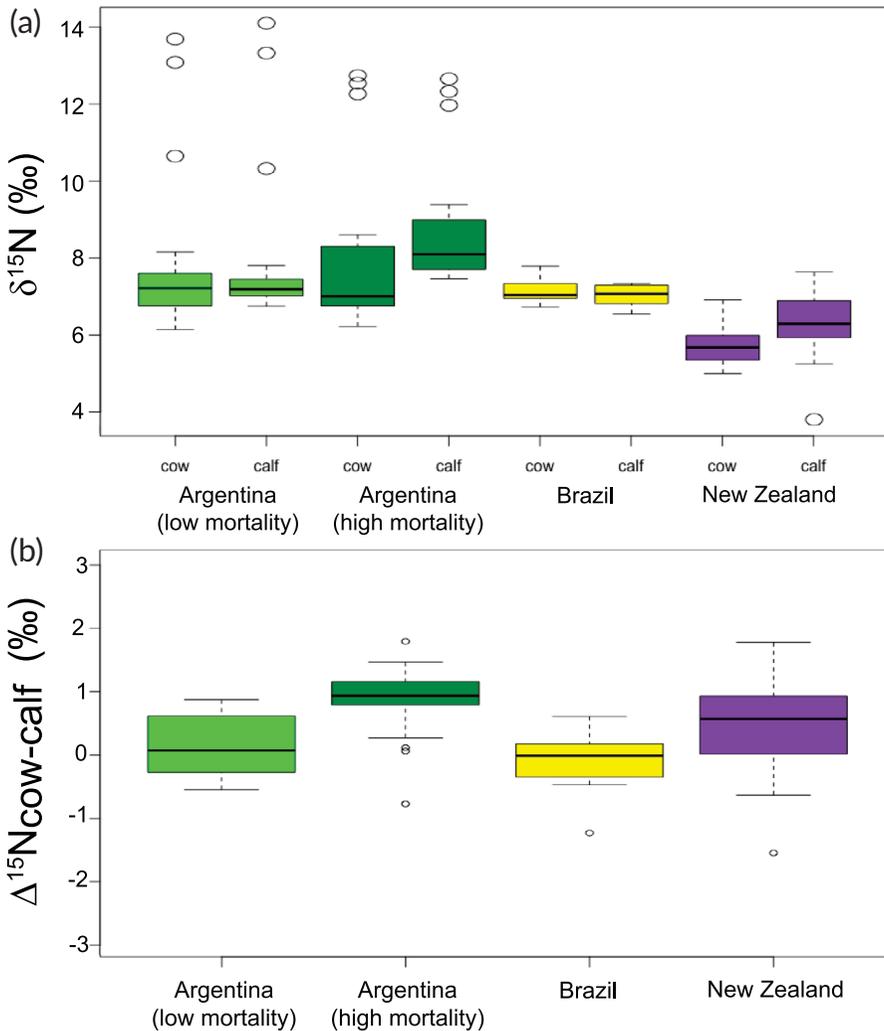


FIGURE 3 (a) Boxplot of cow and calf stable $\delta^{15}\text{N}$ isotope data summarized by wintering ground for Argentina (low and high mortality years), Brazil, and New Zealand. (b) Boxplot of offset between cow and calf for $\delta^{15}\text{N}$ ($\Delta^{15}\text{N}_{\text{calf-cow}}$) by wintering 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.

ACKNOWLEDGMENTS

E.L.C. is supported by a Rutherford Discovery Fellow from the Royal Society of New Zealand Te Apārangi. Stable isotope analyses were supported by a Marie Curie fellowship to E.L.C. (Brazilian samples) and an Australian Marine Mammal Centre grant to G.D., S.C., M.H. (New Zealand samples). P.H.O. was supported by the Brazilian National Research Council (CNPq proc. n° 144064/98-7) and World Wildlife Fund (WWF-Brazil). We thank the Instituto de Conservación de Ballenas and the Southern Right Whale Health Monitoring Program for samples in Argentina. Research permits were issued by Dirección de Fauna y Flora Silvestres and Subsecretaría de Conservación y Areas Protegidas from Chubut for Argentina. The Brazilian samples were collected by GEMARS in collaboration with the Projeto Baleia Franca under permits of the Brazilian Ministry of the Environment. The New Zealand biopsy samples were collected under New Zealand Department of Conservation Marine Mammal Research permit and University of Auckland Animal Ethics Committee approved protocol AEC/02/2005/R334 to CSB. The New Zealand field work was funded by a Winifred Violet Scott Estate Research Grant Fund, Australian Antarctic Division, Marine Conservation Action Fund, Blue Planet Marine NZ Ltd, Holsworth Wildlife Research Endowment, New Zealand Ministry of Foreign Affairs, DOC, South Pacific Whale Research Consortium, National Geographic, and Brian Skerry Photography.

AUTHOR CONTRIBUTIONS

Emma L Carroll: Conceptualization; data curation; formal analysis; project administration; resources; writing – original draft; writing – review and editing. **Glenn Dunshea:** Conceptualization; data curation; resources; funding acquisition; methodology; writing – review and editing. **Paulo Ott:** Data curation; funding acquisition; resources; writing – review and editing. **Luciano Valenzuela:** Data curation; funding acquisition; investigation; resources; writing – original draft; writing – review and editing. **Scott Baker:** Funding acquisition; resources; writing – review and editing. **Simon Childerhouse:** Conceptualization; funding acquisition; investigation; writing – review and editing. **Oscar Gaggiotti:** Funding acquisition; resources; writing – review and editing. **Paulo André Flores:** Funding acquisition; resources; writing – review and editing. **Karina Groch:** Resources; writing – review and editing. **Darren Grocke:** Methodology; resources; writing – review and editing. **Mark Hindell:** Funding acquisition; methodology; writing – review and editing. **David Lundquist:** Resources; writing – review and editing. **Larissa Oliveira:** Investigation; resources; writing – review and editing. **Victoria Rowntree:** Funding acquisition; resources; writing – review and editing. **Mariano Sironi:** Funding acquisition; resources; writing – review and editing. **Seth Newsome:** Conceptualization; data curation; funding acquisition; investigation; methodology; resources; writing – original draft; writing – review and editing.

ORCID

Emma L. Carroll  <https://orcid.org/0000-0003-3193-7288>

Larissa R. Oliveira  <https://orcid.org/0000-0002-5735-3697>

Victoria Rowntree  <https://orcid.org/0000-0001-6153-8312>

REFERENCES

Best, P. (1994). Seasonality of reproduction and the length of gestation in southern right whales *Eubalaena australis*. *Journal of Zoology*, 232(2), 175–189. <https://doi.org/10.1111/j.1469-7998.1994.tb01567.x>

- Best, P., Payne, R., Rowntree, V. J., Palazzo, J., & Both, M. (1993). Long-range movements of South Atlantic right whales *Eubalaena australis*. *Marine Mammal Science*, 9(3), 227–234. <https://doi.org/10.1111/j.1748-7692.1993.tb00451.x>
- Best, P., & Ruther, H. (1992). Aerial photogrammetry of southern right whales *Eubalaena australis*. *Journal of Zoology*, 228(4), 595–614. <https://doi.org/10.1111/j.1469-7998.1992.tb04458.x>
- Best, P., & Schell, D. (1996). Stable isotopes in southern right whale (*Eubalaena australis*) baleen as indicators of seasonal movements feeding and growth. *Marine Biology*, 124, 483–494. <https://doi.org/10.1007/BF00351030>
- Borrell, A., Abad-Oliva, N., Gómez-Campos, E., Giménez, J., & Aguilar, A. (2012). Discrimination of stable isotopes in fin whale tissues and application to diet assessment in cetaceans. *Rapid Communications in Mass Spectrometry*, 26(14), 1596–1602. <https://doi.org/10.1002/rcm.6267>
- Burnell, S. R. (2001). Aspects of the reproductive biology, movements and site fidelity of right whales off Australia. *Journal of Cetacean Research and Management, Special Issue*, 2, 89–102.
- Busquets-Vass, G., Newsome, S. D., Calambokidis, J., Serra-Valente, G., Jacobsen, J. K., Aguiñiga-García, S., & Gendron, D. (2017). Estimating blue whale skin isotopic incorporation rates and baleen growth rates: Implications for assessing diet and movement patterns in mysticetes. *PLoS ONE*, 12, e0177880. <https://doi.org/10.1371/journal.pone.0177880>
- Carroll, E. L., Alderman, R., Bannister, J. L., Bérubé, M., Best, P. B., Boren, L., Baker, C. S., Constantine, R., Findlay, K., Harcourt, R., Lemaire, L., Palsbøll, P. J., Patenaude, N. J., Rowntree, V. J., Seger, J., Steel, D., Valenzuela, L. O., Watson, M., & Gaggiotti, O. E. (2019). Incorporating non-equilibrium dynamics into demographic history inferences of a migratory marine species. *Heredity*, 122(1), 53–68. <https://doi.org/10.1038/s41437-018-0077-y>
- Carroll, E. L., Baker, C. S., Watson, M., Alderman, R., Bannister, J. L., Gaggiotti, O. E., Gröcke, D. R., Patenaude, N. J., & Harcourt, R. (2015). Cultural traditions across a migratory network shape the genetic structure of southern right whales around Australia and New Zealand. *Scientific Reports*, 5, 16182.
- Carroll, E. L., Charlton, C., Vermeulen, E., Jackson, J. A., & Clarke, P. (2020). Roadmap to success for the International Whaling Commission - Southern Ocean Research Partnership (IWC-SORP) Theme 6 - the right sentinel for climate change: linking southern right whale foraging ecology to demographics, health and climate. Report SC/68B/SH07 presented to the Scientific Committee of the International Whaling Commission. <https://doi.org/10.13140/RG.2.2.13001.57441>
- Carroll, E. L., Childerhouse, S. J., Fewster, R., Patenaude, N. J., Steel, D. J., Dunshea, G., Boren, L., & Baker, C. S. S. (2013). Accounting for female reproductive cycles in a superpopulation capture-recapture framework. *Ecological Applications*, 23(7), 1677–1690. <https://doi.org/10.1890/12-1657.1>
- Carroll, E. L., Ott, P. H., McMillan, L., Galletti Vernazzani, B., Nevecealova, P., Vermeulen, E., Gaggiotti, O. E., Andriolo, A., Baker, C. S., Bamford, C., Best, P., Cabrera, E., Calderan, S., Chirife, A., Fewster, R. M., Flores, P. A. C., Frasier, T. R., Freitas, T. R. O., Groch, K. R., ... Jackson, J. A. (2020). Genetic diversity and connectivity of southern right whales (*Eubalaena australis*) found in the Brazil and Chile-Peru wintering grounds and the South Georgia (Islas Georgias del Sur) feeding ground. *Journal of Heredity*, 111(3), 263–276. <https://doi.org/10.1093/jhered/esaa010>
- Cherry, S. G., Derocher, A. E., Hobson, K. A., Stirling, I., & Thiemann, G. W. (2011). Quantifying dietary pathways of proteins and lipids to tissues of a marine predator. *Journal of Applied Ecology*, 48, 373–381. <https://doi.org/10.1111/j.1365-2664.2010.01908.x>
- Christiansen, F., Dawson, S., Durban, J., Fearnbach, H., Miller, C., Bejder, L., Uhart, M., Sironi, M., Corkeron, P., Rayment, W., Leunissen, E., Haria, E., Ward, R., Warick, H., Kerr, I., Lynn, M., Pettis, H., & Moore, M. (2020). Population comparison of right whale body condition reveals poor state of the North Atlantic right whale. *Marine Ecology Progress Series*, 640, 1–16. <https://doi.org/10.3354/meps13299>
- Christiansen, F., Vivier, F., Charlton, C., Ward, R., Amerson, A., Burnell, S., & Bejder, L. (2018). Maternal body size and condition determine calf growth rates in southern right whales. *Marine Ecology Progress Series*, 592, 267–282. <https://doi.org/10.3354/meps12522>
- Corkeron, P., Hamilton, P., Bannister, J., Best, P., Charlton, C., Groch, K. R., Findlay, K., Rowntree, V. J., Vermeulen, E., & Pace, R. M. (2018). The recovery of North Atlantic right whales, *Eubalaena glacialis*, has been constrained by human-caused mortality. *Royal Society Open Science*, 5(11), 180892. <https://doi.org/10.1098/rsos.180892>
- Crespo, E. A., Pedraza, S. N., Dans, S. L., Svendsen, G. M., Degradi, M., & Coscarella, M. A. (2019). The southwestern Atlantic southern right whale, *Eubalaena australis*, population is growing but at a decelerated rate. *Marine Mammal Science*, 35(1), 93–107. <https://doi.org/10.1111/mms.12526>
- Davidson, A. R., Rayment, W., Dawson, S. M., Webster, T., & Sooten, E. (2018). Estimated calving interval for the New Zealand southern right whale (*Eubalaena australis*). *New Zealand Journal of Marine and Freshwater Research*, 52, 372–382. <https://doi.org/10.1080/00288330.2017.1397034>
- Fogel, M. L., Turross, N., & Owsley, D. (1989). Nitrogen isotope tracers of human lactation in modern and archaeological populations. In *Annual Report Geophysical Laboratory, Carnegie Institution of Washington, 1988–1989* (pp. 111–117). Geophysical Laboratory, Carnegie Institution of Washington.
- Fuller, B. T., Fuller, J. L., Sage, N. E., Harris, D. A., O'Connell, T. C., & Hedges, R. E. M. (2004). Nitrogen balance and $\delta^{15}\text{N}$: Why you're not what you eat during pregnancy. *Rapid Communications in Mass Spectrometry*, 18(23), 2889–2896. <https://doi.org/10.1002/rcm.1708>

- Giménez, J., Ramírez, F., Almunia, J., G. Forero, M., & de Stephanis, R. (2016). From the pool to the sea: Applicable isotope turnover rates and diet to skin discrimination factors for bottlenose dolphins (*Tursiops truncatus*). *Journal of Experimental Marine Biology and Ecology*, 475, 54–61. <https://doi.org/10.1016/j.jembe.2015.11.001>
- Habran, S., Damseaux, F., Pomeroy, P., Debier, C., Crocker, D., Lepoint, G., & Das, K. (2019). Changes in stable isotope compositions during fasting in phocid seals. *Rapid Communications in Mass Spectrometry*, 33(2), 176–184. <https://doi.org/10.1002/rcm.8308>
- Hertz, E., Trudel, M., Cox, M. K., & Mazumder, A. (2015). Effects of fasting and nutritional restriction on the isotopic ratios of nitrogen and carbon: A meta-analysis. *Ecology and Evolution*, 5(21), 4829–4839. <https://doi.org/10.1002/ece3.1738>
- Jenkins, S. G., Partridge, S. T., Stephenson, T. R., Farley, S. D., & Robbins, C. T. (2001). Nitrogen and carbon isotope fractionation between mothers, neonates, and nursing offspring. *Oecologia*, 129(3), 336–341. <https://doi.org/10.1007/s004420100755>
- Kelly, J. F. (2000). Stable isotopes of carbon and nitrogen in the study of avian and mammalian trophic ecology. *Canadian Journal of Zoology*, 78, 1–27. <https://doi.org/10.1007/s00026-012-0134-9>
- Leaper, R., Cooke, J., Trathan, P., Reid, K., Rowntree, V. J., & Payne, R. (2006). Global climate drives southern right whale (*Eubalaena australis*) population dynamics. *Biology Letters*, 2(2), 289–292.
- Lefèvre, C. M., Sharp, J. A., & Nicholas, K. R. (2010). Evolution of lactation: Ancient origin and extreme adaptations of the lactation system. *Annual Review of Genomics and Human Genetics*, 11, 219–238.
- Lübcker, N., Whiteman, J. P., Millar, R. P., de Bruyn, P. J. N., & Newsome, S. D. (2020). Fasting affects amino acid nitrogen isotope values: a new tool for identifying nitrogen balance of free-ranging mammals. *Oecologia*, 193(1), 53–65. <https://doi.org/10.1007/s00442-020-04645-5>
- Lübcker, N., Whiteman, J. P., Newsome, S. D., Millar, R. P., & de Bruyn, P. J. N. (2020). Can the carbon and nitrogen isotope values of offspring be used as a proxy for their mother's diet? Using foetal physiology to interpret bulk tissue and amino acid $\delta^{15}\text{N}$ values. *Conservation Physiology*, 8(1), coaa060. <https://doi.org/10.1093/conphys/coaa060>
- Mackay, A. I., Bailleul, F., Carroll, E. L., Andrews-Goff, V., Baker, C. S., Bannister, J., Boren, L., Carlyon, K., Donnelly, D. M., Double, M. C., Goldsworthy, S. D., Harcourt, R., Holman, D., Lowther, A., Parra, G. J., & Childerhouse, S. J. (2020). Satellite derived offshore migratory movements of southern right whales (*Eubalaena australis*) from Australian and New Zealand wintering grounds. *PLoS ONE*, 15(6), e0231577. <https://doi.org/10.1371/journal.pone.0231577>
- Marón, C., Budge, S., Ward, R., Valenzuela, L., Di Martino, M., Ricciardi, M., Sironi, M., Uhart, M., Seger, J., & Rowntree, V. J. (2020). Fatty acids and stable isotopes ($\delta^{13}\text{C}$, $\delta^{15}\text{N}$) in southern right whale *Eubalaena australis* calves in relation to age and mortality at Península Valdés, Argentina. *Marine Ecology Progress Series*, 646, 189–200. <https://doi.org/10.3354/meps13387>
- Marón, C., Rowntree, V. J., Sironi, M., Uhart, M., Payne, R. S., Adler, F. R., & Seger, J. (2015). *Estimating population consequences of increased calf mortality in the southern right whales off Argentina*. Report SC/66a/BRG/1 presented to the Scientific Committee of the International Whaling Commission.
- Mate, B., Best, P., Lagerquist, B., & Winsor, M. (2011). Coastal, offshore and migratory movements of South African right whales revealed by satellite telemetry. *Marine Mammal Science*, 27(3), 455–476. <https://doi.org/10.1111/j.1748-7692.2010.00412.x>
- Neville, M. C., & Picciano, M. F. (1997). Regulation of milk lipid secretion and composition. *Annual Review of Nutrition*, 17, 159–184. <https://doi.org/10.1146/annurev.nutr.17.1.159>
- Newsome, S. D., Chivers, S. J., & Berman Kowalewski, M. (2018). The influence of lipid-extraction and long-term DMSO preservation on carbon ($\delta^{13}\text{C}$) and nitrogen ($\delta^{15}\text{N}$) isotope values in cetacean skin. *Marine Mammal Science*, 34(2), 277–293. <https://doi.org/10.1111/mms.12454>
- Newsome, S. D., Etnier, M. A., Monson, D. H., & Fogel, M. L. (2009). Retrospective characterization of ontogenetic shifts in killer whale diets via $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ analysis of teeth. *Marine Ecology Progress Series*, 374, 229–242. <https://doi.org/10.3354/meps07747>
- Newsome, S. D., Koch, P. L., Etnier, M. A., & Auriolos-Gamboa, D. (2006). Using carbon and nitrogen isotope values to investigate maternal strategies in Northeast Pacific otariids. *Marine Mammal Science*, 22(3), 556–572. <https://doi.org/10.1111/j.1748-7692.2006.00043.x>
- Newsome, S. D., Wolf, N., Peters, J., & Fogel, M. L. (2014). Amino acid $\delta^{13}\text{C}$ analysis shows flexibility in the routing of dietary protein and lipids to the tissue of an omnivore. *Integrative and Comparative Biology*, 54(5), 890–902. <https://doi.org/10.1093/icb/ucu106>
- Oftedal, O. T. (1993). The adaptation of milk secretion to the constraints of fasting in bears, seals, and baleen whales. *Journal of Dairy Science*, 76, 3234–3246. [https://doi.org/10.3168/jds.S0022-0302\(93\)77660-2](https://doi.org/10.3168/jds.S0022-0302(93)77660-2)
- Ott, P. H. (2002). *Diversidade genética e estrutura populacional de duas espécies de cetáceos do Atlântico Sul Ocidental: Pontoporia blainvillei e Eubalaena australis [Genetic diversity and population structure of two Southwest Atlantic cetacean species: Pontoporia blainvillei and Eubalaena australis] [Doctoral dissertation]*. Universidade Federal do Rio Grande do Sul, Brazil.

- R Core Team. (2020). *R: A language and environment for statistical computing* [Computer software]. R Foundation for Statistical Computing.
- Robbins, C. T., Felicetti, L. A., & Sponheimer, M. (2005). The effect of dietary protein quality on nitrogen isotope discrimination in mammals and birds. *Oecologia*, 144(4), 534–540. <https://doi.org/10.1007/s00442-005-0021-8>
- Rowntree, V. J., Groch, K. R., Vilches, F., & Sironi, M. (2020). *Sighting histories of 124 southern right whales recorded off both southern Brazil and Península Valdés, Argentina, between 1971 and 2017*. Report SC/68B/CMP/20 presented to the Scientific Committee of the International Whaling Commission.
- Rowntree, V. J., Payne, R., & Schell, D. (2001). Changing patterns of habitat use by southern right whales (*Eubalaena australis*) on their nursery ground at Península Valdés, Argentina, and in their long-range movements. *Journal of Cetacean Research and Management, Special Issue 2*, 133–143.
- Rowntree, V. J., Uhart, M., Sironi, M., Chirife, A., Di Martino, M., La Sala, L., Musmeci, L., Mohamed, N., Andrejuk, J., McAloose, D., Sala, J., Carribero, A., Rally, H., Franco, M., Adler, F., Brownell, R., Jr., Seger, J., & Rowles, T. (2013). Unexplained recurring high mortality of southern right whale *Eubalaena australis* calves at Península Valdés, Argentina. *Marine Ecology Progress Series*, 493, 275–289. <https://doi.org/10.3354/meps10506>
- Rowntree, V. J., Valenzuela, L. O., Fraguas, P. F., & Seger, J. (2008). *Foraging behaviour of southern right whales (Eubalaena australis) inferred from variation of carbon stable isotope ratios in their baleen*. Report SC/60/BRG23 presented to the Scientific Committee of the International Whaling Commission.
- Schell, D. M., Saupe, S. M., & Haubstock, N. (1989). Bowhead whale (*Balaena mysticetus*) growth and feeding as estimated by $\delta^{13}\text{C}$ techniques. *Marine Biology*, 103, 433–443. <https://doi.org/10.1002/9781119072218.ch11>
- Seyboth, E., Groch, K. R., Dalla Rosa, L., Reid, K., Flores, P. A. C., & Secchi, E. R. (2016). Southern right whale (*Eubalaena australis*) reproductive success is influenced by krill (*Euphausia superba*) density and climate. *Scientific Reports*, 6, 28205. <https://doi.org/10.1038/srep28205>
- Sironi, M., Rowntree, V. J., Di Martino, M., Beltramino, L., Rago, V., Franco, M., & Uhart, M. (2018). Southern right whale mortalities at Península Valdés, Argentina: updated information for 2016–2017. Report SC/67B/CMP/06 presented to the Scientific Committee of the International Whaling Commission. https://ballenas.org.ar/descargas/publicaciones-cientificas/2016/Right%20whale%20mortality%20in%20Argentina%202016-2017.%20Sironi%20et%20al.%20-%20SC_67B_CMP_06.pdf
- Thomas, P. O., & Taber, S. M. (1984). Mother-infant interaction and behavioral development in southern right whales, *Eubalaena australis*. *Behaviour*, 88, 42–60.
- Todd, S., Ostrom, P., Lien, J., & Abrajano, J. (1997). Use of biopsy samples of humpback whale (*Megaptera novaeangliae*) skin for stable isotope ($\delta^{13}\text{C}$) determination. *Journal of Northwest Atlantic Fishery Science*, 22, 71–76. <https://doi.org/10.2960/J.v22.a6>
- Valenzuela, L. O., Rowntree, V. J., Sironi, M., & Seger, J. (2018). Stable isotopes in skin reveal diverse food sources used by southern right whales (*Eubalaena australis*). *Marine Ecology Progress Series*, 603, 243–255. <https://doi.org/10.3354/meps12722>
- Valenzuela, L. O., Sironi, M., & Rowntree, V. J. (2010). Interannual variation in the stable isotope differences between mothers and their calves in southern right whales (*Eubalaena australis*). *Aquatic Mammals*, 36(2), 138–147. <https://doi.org/10.1578/AM.36.2.2010.138>
- Valenzuela, L. O., Sironi, M., Rowntree, V. J., & Seger, J. (2009). Isotopic and genetic evidence for culturally inherited site fidelity to feeding grounds in southern right whales (*Eubalaena australis*). *Molecular Ecology*, 18(5), 782–791. <https://doi.org/10.1111/j.1365-294X.2008.04069.x>
- van den Berg, G. L., Vermeulen, E., Valenzuela, L. O., Bérubé, M., Ganswindt, A., Gröcke, D. R., Hall, G., Hulva, P., Neveceralova, P., Palsbøll, P. J., & Carroll, E. L. (2021). Decadal shift in foraging strategy of a migratory southern ocean predator. *Global Change Biology*, 27(5). <https://doi.org/10.1111/gcb.15465>, 1052, 1067
- Vermeulen, E., Wilkinson, C., & Van den Berg, G. (2020). *Report of the southern right whale aerial surveys - 2019*. Report SC/68B/SH02 submitted to the Scientific Committee of the International Whaling Commission.
- Vighi, M., Borrell, A., Crespo, E., Oliveira, L. R., Simões-Lopes, P. C., Flores, P. A. C., García, N., & Aguilar, A. (2014). Stable isotopes indicate population structuring in the Southwest Atlantic population of right whales (*Eubalaena australis*). *PLoS ONE*, 9(6), e90489. <https://doi.org/10.1371/journal.pone.0090489>
- Whiteman, J. P., Smith, E. A. E., Besser, A. C., & Newsome, S. D. (2019). A guide to using compound-specific stable isotope analysis to study the fates of molecules in organisms and ecosystems. *Diversity*, 11(1), 8. <https://doi.org/10.3390/d11010008>
- Wickham, H. (2016). *ggplot2: Elegant graphics for data analysis*. Springer-Verlag.
- Wolf, N., Newsome, S. D., Peters, J., & Fogel, M. L. (2015). Variability in the routing of dietary proteins and lipids to consumer tissues influences tissue-specific isotopic discrimination. *Rapid Communications in Mass Spectrometry*, 29, 1448–1456. <https://doi.org/10.1002/rcm.7239>

- Zerbini, A. N., Ajos, A. F., Andriolo, A., Clapham, P. J., Crespo, E., Gonzalez, R., Harris, G., Mendez, M., Rosenbaum, H., Sironi, M., Sucunza, F., & Uhart, M. (2018). *Satellite tracking of Southern right whales (Eubalaena australis) from Golfo San Matias, Rio Negro Province, Argentina*. Report SC/67B/CMP17 presented to the Scientific Committee of the International Whaling Commission.
- Zerbini, A. N., Mendez, M., Rosenbaum, H., Sucunza, F., Andriolo, A., Harris, G., Clapham, P. J., Sironi, M., & Uhart, M. (2015). *Tracking southern right whales through the southwest Atlantic: new insights into migratory routes and feeding grounds*. Report SC/66b/BRG26 presented to the Scientific Committee of the International Whaling Commission.

SUPPORTING INFORMATION

Additional supporting information may be found in the online version of the article at the publisher's website.

How to cite this article: Carroll, E. L., Dunshea, G., Ott, P. H., Valenzuela, L. O., Baker, C. S., Childerhouse, S. J., Gaggiotti, O. E., Flores, P. A. C., Groch, K., Gröcke, D. R., Hindell, M. A., Lundquist, D., Oliveira, L. R., Rowntree, V., Sironi, M., & Newsome, S. D. (2021). 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? *Marine Mammal Science*, 1–14. <https://doi.org/10.1111/mms.12871>