

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

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4 Emma L. Carroll^{1,2}, Glenn Dunshea^{3,4}, Paulo H. Ott^{5,6}, Luciano O. Valenzuela^{7,8,9}, C. Scott Baker¹⁰,

5 Simon J. Childerhouse¹¹, Oscar E. Gaggiotti², Paulo A. C. Flores¹², Karina Groch¹³, Darren R.

6 Gröcke¹⁴, Mark A. Hindell¹⁵, David Lundquist¹⁶, Larissa R. Oliveira^{5,17}, Victoria Rowntree⁹, Mariano

7 Sironi^{9,18}, Seth D. Newsome¹⁹

8 1 School of Biological Sciences, University of Auckland, Auckland, New Zealand

9 2 School of Biology and Sea Mammal Research Unit, University of St Andrews, Scotland, UK

10 3 Ecological Marine Services Pty. Ltd., Bundaberg, Queensland, Australia

11 4 NTNU University Museum, Norwegian University of Science and Technology, Trondheim, Norway

12 5 Grupo de Estudos de Mamíferos Aquáticos do Rio Grande do Sul, Torres, RS, Brazil

13 6 Universidade Estadual do Rio Grande do Sul, Osório, RS, Brazil

14 7 School of Biological Sciences, University of Utah, Salt Lake City, Utah, USA

15 8 Consejo Nacional de Investigaciones Científicas y Técnicas (CONICET), Laboratorio de Ecología

16 Evolutiva Humana, Facultad de Ciencias Sociales, UNCPBA, Quequén, Buenos Aires Province,
17 Argentina

18 9 Instituto de Conservación de Ballenas, Buenos Aires, Argentina

19 10 Marine Mammal Institute and Department of Fisheries, Wildlife and Conservation Sciences,

20 Oregon State University, Newport, OR, USA

21 11 Cawthron Institute, Nelson, New Zealand

22 12 Núcleo de Gestão Integrada Florianópolis, ICMBio-MMA, Jurerê, Florianópolis, SC, Brazil

23 13 Instituto Australis, Imbituba, Santa Catarina, Brazil

24 14 Stable Isotope Biogeochemistry Laboratory, Department of Earth Sciences, University of Durham,
25 Durham, UK

26 15 Institute for Marine and Antarctic Studies, University of Tasmania, 20 Castray Esplanade, Battery
27 Point, Tasmania, Australia

28 16 New Zealand Department of Conservation, Wellington, New Zealand

29 17 Laboratório de Ecologia de Mamíferos, Universidade do Vale do Rio dos Sinos, Avenida Unisinos
30 950, Sao Leopoldo, RS - Brazil

31 18 Diversidad Biológica IV, Universidad Nacional de Córdoba, Córdoba, Argentina

32 19 Biology Department, University of New Mexico, Albuquerque, New Mexico

33 Correspondence: Email: carrollemz@gmail.com

34 **KEYWORDS**

35 Capital breeder; maternal investment; physiology; stable isotope

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40 **ABSTRACT**

41 Southern right whales (SRW) are capital breeders that use stored energy reserves to sustain
42 themselves and their calves on nursery areas. With successful calving events declining in some SRW
43 populations, it has been hypothesized that nutritional stress in adult females causes reproductive
44 failure or death of calves shortly after birth. Here we compared offsets in carbon and nitrogen isotope
45 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.
46 SRW from Aotearoa New Zealand, with high population growth rates and body conditions scores,
47 have negative $\Delta^{13}\text{C}_{\text{calf-cow}}$ suggesting calves are utilizing ^{13}C -depleted lipid carbon in milk to fuel the
48 synthesis of nonessential amino acids used to build new tissues and rapidly grow. In contrast, a
49 significantly positive $\Delta^{13}\text{C}_{\text{calf-cow}}$ offset previously reported for SRW from Argentina during a mass
50 die-off event was hypothesized to be due to calves consuming milk with low lipid content. Patterns in
51 $\Delta^{15}\text{N}_{\text{calf-cow}}$ were more difficult to interpret and highlight the complexity in nitrogen transfer between
52 mother and offspring. When combined with similar data collected from Brazil and during a low
53 mortality year in Argentina, we hypothesize this approach provides a way to retrospectively compare
54 nutritional condition of breeding adult female SRW across nursery areas.

55
56 **RESUMEN**

57 Las ballenas francas australes (BFA) tienen una estrategia de reproducción de “acumulación de
58 capital”, es decir que utilizan las reservas de energía almacenadas para mantenerse a sí mismas y a sus
59 crías en las áreas de cría. Con la disminución de los eventos de partos exitosos en algunas poblaciones
60 de BFA, se ha planteado la hipótesis que el estrés nutricional en las hembras adultas causa fallas
61 reproductivas o la muerte de los ballenatos poco después del nacimiento. En este trabajo comparamos
62 las diferencias en los valores de isótopos de carbono y nitrógeno de las madres y sus crías ($\Delta^{13}\text{C}_{\text{cría-}}\text{madre}$
63 $\text{y } \Delta^{15}\text{N}_{\text{cría-madre}}$) entre tres poblaciones de BFA. Las BFA de Aotearoa Nueva Zelanda, con
64 altas tasas de crecimiento de la población y altos puntajes de condiciones corporales, tiene $\Delta^{13}\text{C}_{\text{cría-}}\text{madre}$
65 negativo, lo que sugiere que las crías están utilizando carbono lipídico empobrecido en ^{13}C en
66 la leche para impulsar la síntesis de aminoácidos no esenciales utilizados para construir nuevos tejidos
67 y crecer rápidamente. En contraste, diferencias significativamente positivas de $\Delta^{13}\text{C}_{\text{cría-madre}}$
68 reportadas previamente para BFA de Argentina durante un evento de muerte masiva han sido
69 hipotetizadas como debido al consumo de leche con bajo contenido de lípidos. Los patrones de
70 $\Delta^{15}\text{N}_{\text{cría-madre}}$ fueron más difíciles de interpretar y resaltan la complejidad en la transferencia de
71 nitrógeno entre las madres y sus crías. Al combinar los datos de este estudio con datos similares
72 recopilados en Brasil y durante un año de baja mortalidad en Argentina, podemos plantear la hipótesis
73 de que este enfoque proporciona una forma de comparar retrospectivamente la condición nutricional
74 de las hembras adultas de BFW en distintas áreas de cría.

75
76 **RESUMO**

77 A baleia-franca-austral (BFA) possui a estratégia de acumular energia para manter a si mesma e aos
78 seus filhotes nas áreas reprodutivas. Devido a diminuição do número de partos bem sucedidos em
79 algumas populações de BFA, foi sugerida a hipótese de que o estresse nutricional nas fêmeas adultas
80 causaria falhas reprodutivas ou a morte dos filhotes logo após o nascimento. Neste estudo
81 comparamos as diferenças nos valores dos isótopos de carbono e nitrogênio das fêmeas e seus filhotes
82 ($\Delta^{13}\text{C}_{\text{filhote-mãe}}$ e $\Delta^{15}\text{N}_{\text{filhote-mãe}}$) entre três populações de BFA. As BFA de Aotearoa Nova
83 Zelândia, com altas taxas de crescimento da população e altos valores de condição corporal, têm
84 $\Delta^{13}\text{C}_{\text{filhote-mãe}}$ negativo, resultado que sugere que os filhotes estão utilizando carbono lipídico
85 empobrecido em ^{13}C do leite para estimular a síntese de aminoácidos não essenciais utilizados para
86 construir novos tecidos e crescer rapidamente. Por outro lado, as diferenças significativas positivas de
87 $\Delta^{13}\text{C}_{\text{filhote-mãe}}$ reportadas previamente para BFA de Argentina, durante um evento de mortalidade
88 em massa, foram atribuídas ao consumo de leite de baixo conteúdo de lípidos. Os padrões de
89 $\Delta^{15}\text{N}_{\text{filhote-mãe}}$ foram mais difíceis de se interpretar e demonstraram a complexidade na
90 transferência de nitrogênio entre as mães e seus filhotes. Ao combinar os dados deste estudo com
91 dados similares coletados no Brasil e durante um ano de baixa mortalidade na Argentina, sugere-se
92 que os estudos isotópicos seriam uma forma de comparar retrospectivamente a condição nutricional
93 das fêmeas de BFA em distintas áreas reprodutivas.

94 1 | INTRODUCTION

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

103

104 In recent years, there has been an increase in the average interval between successful calving events
105 from three to four or five years in SRW that use the South African wintering grounds (Vermeulen et
106 al., 2020). This is hypothesized to be due to a decrease in prey availability and/or quality leading to
107 SRW females to either defer breeding, thereby lengthening calving intervals, and/or to females losing
108 a calf in its first year of life (Leaper et al., 2006; Rowntree et al., 2013; Seyboth et al., 2016; van den
109 Berg et al., 2021). In this latter case, if a females loses a calf early in lactation she may recover
110 quickly and mate in the following year, resulting in a five year interval to a successful breeding event
111 (weaned calf) (Marón et al., 2015). Also, unusually high calf mortality events have occurred on the
112 Argentinean wintering ground (Rowntree et al., 2013; Sironi et al., 2018) which has similarly seen a
113 lengthening in successful breeding intervals (Marón et al., 2015), resulting in a decrease in the
114 population growth rate (Crespo et al., 2019). The Brazilian wintering ground is likely
115 demographically distinct from, but linked by high levels of connectivity to, the Argentinean wintering
116 ground (Best et al., 1993; Carroll, Ott, et al., 2020; Rowntree et al., 2020). Models linking calf output
117 with conditions on high latitude foraging grounds (Seyboth et al., 2016) suggest SRW in Brazil may
118 have been experiencing nutritional stress. In contrast, the best available data from the Aotearoa New
119 Zealand (hereafter New Zealand) wintering ground shows a high rate of growth of 7% per annum
120 between 1995 and 2009 (Carroll et al., 2013). This is consistent with the New Zealand population

121 having no recorded mortality events and the highest recorded body condition of any studied right
122 whale population (Christiansen et al., 2020).

123

124 As SRW reproduction and by extension population growth rate are linked to environmental conditions
125 that influence prey availability on the high latitude foraging grounds (Leaper et al., 2006; Seyboth et
126 al., 2016), several studies have aimed to identify the location of the species' offshore foraging
127 grounds (Mackay et al., 2020; Mate et al., 2011; Valenzuela et al., 2018; van den Berg et al., 2021;
128 Zerbini et al., 2018, 2015). A common tool to investigate the location and trophic level at which
129 baleen whales feed is stable isotope analysis. Early studies reported oscillations of carbon ($\delta^{13}\text{C}$) and
130 nitrogen ($\delta^{15}\text{N}$) isotope values in SRW baleen that was linked to the whale's annual migration across
131 oceanographic regions that varied in their baseline isotopic composition (Best and Schell, 1996;
132 Schell et al., 1989). In addition, because the isotopic composition of skin tissue reflects dietary inputs
133 integrated over several months prior to collection (Busquets-Vass et al., 2017), biopsy samples
134 collected from whales on their winter nursery or socializing grounds reflect recently visited foraging
135 grounds. This approach has been used to identify foraging grounds or foraging traditions, infer diet
136 composition, and characterize migratory patterns for SRW (Carroll et al., 2015; Rowntree et al., 2001,
137 2008; Valenzuela et al., 2018, 2009; van den Berg et al., 2021; Vighi et al., 2014).

138

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

147 nonessential amino acids needed to synthesize new tissue in rapidly growing offspring (Newsome et
148 al., 2014; Wolf et al., 2015).

149

150 The lipid content of marine mammal milk is exceptionally high in comparison to other mammals and
151 varies widely within and among species (Lefèvre et al., 2010; Oftedal, 1993). Many mammalian
152 species show a decline in lipid content of milk when nutritionally stressed (Neville & Picciano, 1997).
153 The point where this decline occurs varies between species, but we hypothesize that capital breeders
154 that have evolved to lactate while fasting would also show a decline in milk lipid when nutritional
155 stress reaches a metabolic tipping point. This decrease in lipid content could result in a slightly
156 positive offset in $\delta^{13}\text{C}$ between calves and their mothers, with the offset defined here as the $\delta^{13}\text{C}$ value
157 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
158 because offspring are directly routing milk proteins rather than using a substantial amount of ^{13}C -
159 depleted lipids to synthesize proteinaceous tissues, a process often cited to explain trophic
160 discrimination in carbon isotopes (Kelly, 2000). This phenomenon may be associated with poor body
161 condition and lower reproductive success, with potential population level consequences. Conversely,
162 when milk lipid content is high, the offset in $\delta^{13}\text{C}$ between calves and their mothers is predicted to be
163 negative as ^{13}C -depleted lipid carbon can be converted into acetyl CoA that enters the tricarboxylic
164 acid cycle and used to synthesize the carbon skeletons of nonessential amino acids that are needed to
165 rapidly build tissues (Newsome et al., 2014). We would assume this would be associated with good
166 maternal body condition and stable population growth rates. Stable isotope analysis of northern
167 elephant seal (*Mirounga angustirostris*) tissues supports the above hypothesized patterns and found
168 that ^{13}C -depletion in offspring relative to their mothers correlated with fasting duration (Habran et al.,
169 2019). While not a primary focus here, a positive offset in $\delta^{15}\text{N}$ in calves relative to their mothers
170 ($\Delta^{15}\text{N}_{\text{calf-cow}}$) is also expected since females catabolize their own tissues to produce milk for their
171 offspring. This pattern often manifests as a significant ^{15}N -enrichment akin to that observed in trophic
172 discrimination in nitrogen isotopes between consumer and prey (Fogel et al., 1989; Fuller et al., 2004;
173 Newsome et al., 2006).

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

181

182 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)
183 wintering grounds, and compare these patterns with previously published data on cow-calf pairs in the
184 Argentinean wintering ground summarized above (Valenzuela et al., 2010). This provides
185 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
186 suspected to have relatively low (New Zealand) and high (Argentina) levels of nutritional stress.

187

188 **2 | METHODS**

189 **2.1 | Sample collection and stable isotope analysis**

190 Skin biopsy samples were collected from SRW in Brazil from 1999–2002 (Carroll, Ott, et al., 2020;
191 Ott, 2002) and in New Zealand from 2007–2009 (Carroll et al., 2013). Data collection from cow-calf
192 pairs was noted in the field and maternity confirmed via microsatellite genotyping (Supplementary
193 Material). A subsample of the skin biopsy sample was freeze-dried and underwent lipid extraction
194 following protocols described in Todd et al. (1997) for the Brazilian samples or Busquets-Vass et al.
195 (2017) for the New Zealand samples. Lipid extraction is also known to correct for effects of
196 preservation medium (Newsome et al., 2018; Todd et al., 1997). Carbon ($\delta^{13}\text{C}$) and nitrogen ($\delta^{15}\text{N}$)
197 isotope values were measured on a Costech 4010 elemental analyzer coupled to a Thermo Scientific
198 Delta V isotope ratio mass spectrometer at the University of Wyoming Stable Isotope Facility
199 (Laramie, WY, USA) or the Durham University Stable Isotope Biogeochemistry Laboratory
200 (Durham, UK); see Carroll et al. (2015) for analytical details. Stable isotope data are expressed as δ
201 values using the equation $\delta X = (R_{\text{Sample}}/R_{\text{Standard}}) - 1$, where X is any isotope system of interest (e.g. C

202 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
203 each sample and standard, respectively. The internationally accepted standards are Vienna Pee Dee
204 Belemnite (V-PDB) for $\delta^{13}\text{C}$, and atmospheric nitrogen for $\delta^{15}\text{N}$; units are expressed as parts per
205 thousand, or per mil (‰). Analytical precision for $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ was assessed via analyses of in-
206 house reference materials for each run, which were stringently calibrated against international
207 standards (e.g., USGS 40, IAEA 600, IAEA N2), and was measured to be $\pm 0.2\text{‰}$ (SD). The
208 calibration of in-house reference materials to international standards ensure isotope data can be
209 compared across laboratories. We also measured the weight percentage carbon ([C]) and nitrogen
210 ([N]) concentrations of each sample via analysis of organic materials with known elemental
211 concentrations.

212

213 **2.2 | Testing for normality**

214 We first used the Shapiro-Wilk test in the statistical programming language R base package (R Core
215 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
216 nursery ground, deviated from the expectation of normality. For the Brazilian samples (n=7 pairs), no
217 isotope values or offsets were found to be significantly different from the expectation of normality
218 ($p > 0.05$). For the New Zealand samples (n=21 pairs), the Shapiro-Wilk test indicated significant
219 deviations from the expectation of normality for $\delta^{13}\text{C}$ ($p < 0.001$), but not for the $\Delta^{13}\text{C}_{\text{calf-cow}}$, $\delta^{15}\text{N}$, or
220 $\Delta^{15}\text{N}_{\text{calf-cow}}$ data sets ($p > 0.05$). Therefore, we assessed the $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ data sets for differences
221 between sampling regions with both parametric and nonparametric statistics and the $\Delta^{13}\text{C}_{\text{calf-cow}}$ or
222 $\Delta^{15}\text{N}_{\text{calf-cow}}$ data sets only with parametric analyses. Data visualisations were done using R package
223 ggplot2 (Wickham, 2016).

224

225 **2.3 | Patterns in $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values across and within nursery grounds**

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

229 **2.4 | Patterns in $\Delta^{13}\text{C}_{\text{calf-cow}}$ and $\Delta^{15}\text{N}_{\text{calf-cow}}$ values across nursery grounds**

230 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
231 the offset in nitrogen and carbon isotope composition between paired calves and cows. The mean and
232 standard deviation for these distributions were calculated, and were tested to see if they were
233 significantly different from zero using a one-sample t-test in R. The distributions of $\Delta^{13}\text{C}_{\text{calf-cow}}$ and
234 $\Delta^{15}\text{N}_{\text{calf-cow}}$ values for different nursery grounds were compared in a pairwise manner using the
235 Kolmogorov-Smirnov test.

236

237 **3 | RESULTS**

238 **3.1 | Data set summary**

239 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
240 from Brazil and New Zealand, respectively. We also included the published data from a low mortality
241 year (2004, $n = 20$) and high mortality years (2003 and 2005, $n = 22$) from Argentina (Valenzuela et
242 al., 2010).

243

244 **3.2 | Patterns in $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values across nursery grounds**

245 We found no significant differences between years within the New Zealand data set (Table 2). There
246 was a significant difference between both South American data sets and the New Zealand data set for
247 cow $\delta^{13}\text{C}$ (Figure 2) and $\delta^{15}\text{N}$ values (Figure 3; $p < 0.001$ for all comparisons: Supplementary Table 1),
248 but not between the Argentina and Brazil data sets (Supplementary Table 1, Figure 1).

249

250 **3.3 | Patterns in $\Delta^{13}\text{C}_{\text{calf-cow}}$ values across nursery grounds**

251 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
252 graphically displayed in Figures 2 and 3. $\Delta^{13}\text{C}_{\text{calf-cow}}$ ($p < 0.01$) for the New Zealand data set was
253 significantly different from zero based on a one-sample t-test, whereas the offsets for the Brazilian
254 dataset were not ($\Delta^{13}\text{C}_{\text{calf-cow}}$: $p = 0.12$). There were significant differences in $\Delta^{13}\text{C}_{\text{calf-cow}}$ across nursery
255 grounds, with the Argentinean high mortality years having significantly higher offsets than all other

256 wintering grounds and the Argentinean low mortality year. We also observed significant differences
257 in $\Delta^{15}\text{N}_{\text{calf-cow}}$ between wintering grounds, with the Argentinean high mortality years having
258 significantly higher offsets than the Argentinean low mortality year or the Brazilian dataset (Table 1).

259

260 4 | DISCUSSION

261 Overall, our results suggest a relationship between physiological condition and $\Delta^{13}\text{C}_{\text{calf-cow}}$ across
262 SRW populations calving in three wintering grounds. Specifically, the New Zealand population shows
263 a negative $\Delta^{13}\text{C}_{\text{calf-cow}}$ (Table 1) that is significantly different than zero, suggesting calves are utilizing
264 ^{13}C -depleted lipid carbon in milk to fuel the synthesis of nonessential amino acids needed to build
265 new tissues and rapidly grow. This coincided with a period (1995–2009) of high estimated population
266 growth and no observed cow or calf mortality events (Carroll et al., 2013). In contrast, there were
267 weakly negative mean $\Delta^{13}\text{C}_{\text{calf-cow}}$ values in the data sets from both the Brazilian wintering ground and
268 low mortality year in Argentina (Table 1), both of which were statistically indistinguishable from
269 zero. We hypothesize this represents a decrease in maternal lipid catabolism to fuel growth in calves
270 in the Brazilian wintering grounds relative to those from New Zealand. Modelling suggests that there
271 was a decrease in calf production in the Brazilian wintering ground coincident with our sampling
272 period (1998–2005) of this population, which is believed to be driven by decreases in krill abundance
273 in high latitude foraging areas (Seyboth et al., 2016). If this hypothesis is correct, decreases in calf
274 output were likely driven by higher nutritional stress in females that calved over this time period in
275 the Brazilian wintering ground. Finally, as previously described (Valenzuela et al., 2010), the high
276 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
277 significantly higher than observed in the New Zealand, Brazil, and the low mortality Argentina data
278 sets (see Table 2 for pairwise p-values). This suggests that cows during high mortality years in
279 Argentina were nutritionally stressed and were using fewer lipids to fuel calf development in
280 comparison to the other datasets.

281

282 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
283 ($+0.5 \pm 0.8\text{‰}$) and Argentina high mortality years ($+0.7 \pm 0.7\text{‰}$) showed positive offsets that were

284 significantly higher than zero but statistically indistinguishable from one another. These positive
285 offsets are expected since mammals catabolize their own tissues to produce milk for their offspring,
286 which often manifests as a significant ^{15}N -enrichment akin to trophic discrimination in nitrogen
287 isotopes between consumer and prey (Fogel et al., 1989; Fuller et al., 2004; Newsome et al., 2006).
288 Small but consistent mother-offspring $\Delta^{15}\text{N}$ offsets of 1-2‰ have been observed in a wide range of
289 mammal species (Fogel et al., 1989; Jenkins et al., 2001; Newsome et al., 2009, 2006). In contrast, the
290 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
291 ($0.2 \pm 0.5\text{‰}$) that appear not to be significantly different from zero suggests a more complex
292 relationship between nutritional status, nitrogen balance, and transfer of nitrogen from mother to calf
293 during gestation and lactation. Recent work on healthy southern elephant seal (*Mirounga leonina*)
294 mother-pup pairs utilizing a combination of bulk tissue and amino acid nitrogen isotope analysis
295 highlights this complexity, but also shows that offspring in utero generally have higher $\delta^{15}\text{N}$ values
296 than their mother at parturition (Lübcker, Whiteman, Millar, et al., 2020), an isotopic offset that is
297 likely maintained or enhanced during lactation under healthy conditions. Negligible mother-offspring
298 $\Delta^{15}\text{N}$ offsets may indicate a disruption in nitrogen balance in either offspring or parent. For example,
299 the direct routing of amino acids from diet to tissue with minimal isotopic alteration, resulting in
300 mother-offspring $\Delta^{15}\text{N}$ offsets apparently statistically indistinguishable from zero, could indicate
301 nutritional stress in calves similar to patterns observed in mammals fed diets with low protein content
302 and quality (Robbins et al., 2005). Likewise, fasting has been shown to increase the nitrogen isotope
303 composition of both bulk tissues (Hertz et al., 2015) and individual amino acids catabolized to fuel
304 gluconeogenesis (Lübcker, Whiteman, Newsome, et al., 2020), which could yield increases the $\delta^{15}\text{N}$
305 of mothers over the course of the winter breeding season relative to their calves and produce
306 negligible or even negative $\Delta^{15}\text{N}_{\text{calf-cow}}$. Additional work utilizing amino acid isotope analysis is
307 needed to further explore the potential drivers of $\Delta^{15}\text{N}_{\text{calf-cow}}$ in SRW.

308

309 The interpretation of isotopic differences between calves and cows assumes that the isotopic
310 composition of calf skin largely represents the lactation period, rather than time in utero. While skin

311 isotopic incorporation rates for SRW are unknown, studies of bottlenose dolphins and blue whales
312 report similar estimates of complete isotopic turnover of skin in adults: 163 ± 91 days for $\delta^{15}\text{N}$ in blue
313 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
314 bottlenose dolphins (Giménez et al., 2016). Isotopic incorporation rates for rapidly growing calves are
315 likely faster than in adults, and to ensure that skin sampled from calves primarily reflects the lactation
316 period, we recommend that future work focuses on sampling older calves whose skin tissue reflects
317 time since parturition. Another important assumption of the approach we used to assess maternal
318 physiological condition is that the isotopic composition of cow skin is a reliable proxy for the protein-
319 rich tissues (e.g., muscle) being catabolized to produce milk for their offspring. We believe this
320 assumption is valid because SRW are capital breeders and cows are catabolizing muscle tissue to
321 repair their skin while on the wintering grounds, which is consistent with the lack of significant
322 differences in the isotopic composition of fin whale muscle and skin (Borrell et al., 2012).

323

324 Finally, the difference between the New Zealand and South American nursery ground cow $\delta^{13}\text{C}$ and
325 $\delta^{15}\text{N}$ values was unsurprising, given that the foraging grounds of SRWs in the two regions are most
326 likely located in the South Atlantic and South Pacific, respectively, that have different isotopic
327 baselines (Mackay et al., 2020; Valenzuela et al., 2018; Vighi et al., 2014; Zerbini et al., 2018). There
328 was no difference in the $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values of cows from Argentina and Brazil (Supplementary
329 Table 1, Figure 1), suggesting that whales that use these two wintering grounds likely share foraging
330 grounds, which contrasts with isotope data from historical samples that suggested SRWs wintering in
331 the two areas used different foraging grounds (Vighi et al., 2014).

332

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

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

344

345 **5 | ACKNOWLEDGEMENTS**

346 ELC is supported by a Rutherford Discovery Fellow from the Royal Society of New Zealand Te
347 Apārangī. Stable isotope analyses were supported by a Marie Curie fellowship to ELC (Brazilian
348 samples) and an Australian Marine Mammal Centre grant to GD, SC, MH (New Zealand samples).
349 PHO was supported by the Brazilian National Research Council (CNPq proc. n° 144064/98-7) and
350 World Wildlife Fund (WWF-Brazil). We thank the Instituto de Conservación de Ballenas and the
351 Southern Right Whale Health Monitoring Program for samples in Argentina. Research permits were
352 issued by Dirección de Fauna y Flora Silvestres and Subsecretaría de Conservación y Areas
353 Protegidas from Chubut for Argentina. The Brazilian samples were collected by GEMARS in
354 collaboration with the Projeto Baleia Franca under permits of the Brazilian Ministry of the
355 Environment. The New Zealand biopsy samples were collected under New Zealand Department of
356 Conservation Marine Mammal Research permit and University of Auckland Animal Ethics
357 Committee approved protocol AEC/02/2005/R334 to CSB. The New Zealand field work was funded
358 by a Winifred Violet Scott Estate Research Grant Fund, Australian Antarctic Division, Marine
359 Conservation Action Fund, Blue Planet Marine NZ Ltd, Holsworth Wildlife Research endowment,
360 New Zealand Ministry of Foreign Affairs, DOC, South Pacific Whale Research Consortium, National
361 Geographic, and Brian Skerry Photography.

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590 Table 1: Mean and standard deviations (\pm SD) of $\Delta^{13}\text{C}_{\text{calf-cow}}$ and $\Delta^{15}\text{N}_{\text{calf-cow}}$ from southern right whale
591 nursery grounds. Also shown are pairwise comparisons of these values between southern right whale
592 wintering grounds, as well as years with differing levels of calf mortality in Argentina: low (2004)
593 and high (2003 and 2005); acronyms include New Zealand (NZ), Brazil (BRZ), and Argentina (ARG)
594 and sample size (n). The top right and bottom left quadrants show the p-values from t-tests for
595 $\Delta^{13}\text{C}_{\text{calf-cow}}$ and $\Delta^{15}\text{N}_{\text{calf-cow}}$, respectively. Argentinean data from Valenzuela et al. (2010).

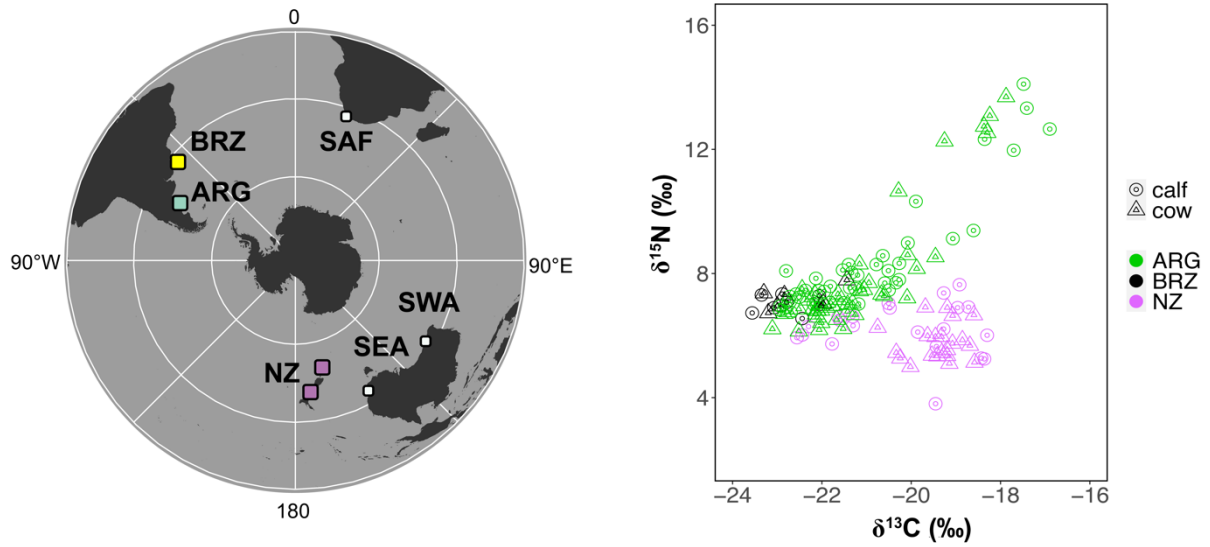
	n	NZ	BRZ	ARG (low)	ARG (high)	$\Delta^{13}\text{C}_{\text{calf-cow}} \pm \text{SD}$ (‰)	$\Delta^{15}\text{N}_{\text{calf-cow}} \pm \text{SD}$ (‰)
NZ	21		0.125	0.044	<0.001	-0.8 \pm 1.1	0.5 \pm 0.8
BRZ	7	0.054		0.678	<0.001	-0.3 \pm 0.5	-0.1 \pm 0.6
ARG (low mortality)	20	0.137	0.266		<0.001	-0.2 \pm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

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613 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
 614 Zealand data set using Kolmogorov-Smirnov (KS) and t-tests.

Year 1	Year 2	Offset	KS test	t-test
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

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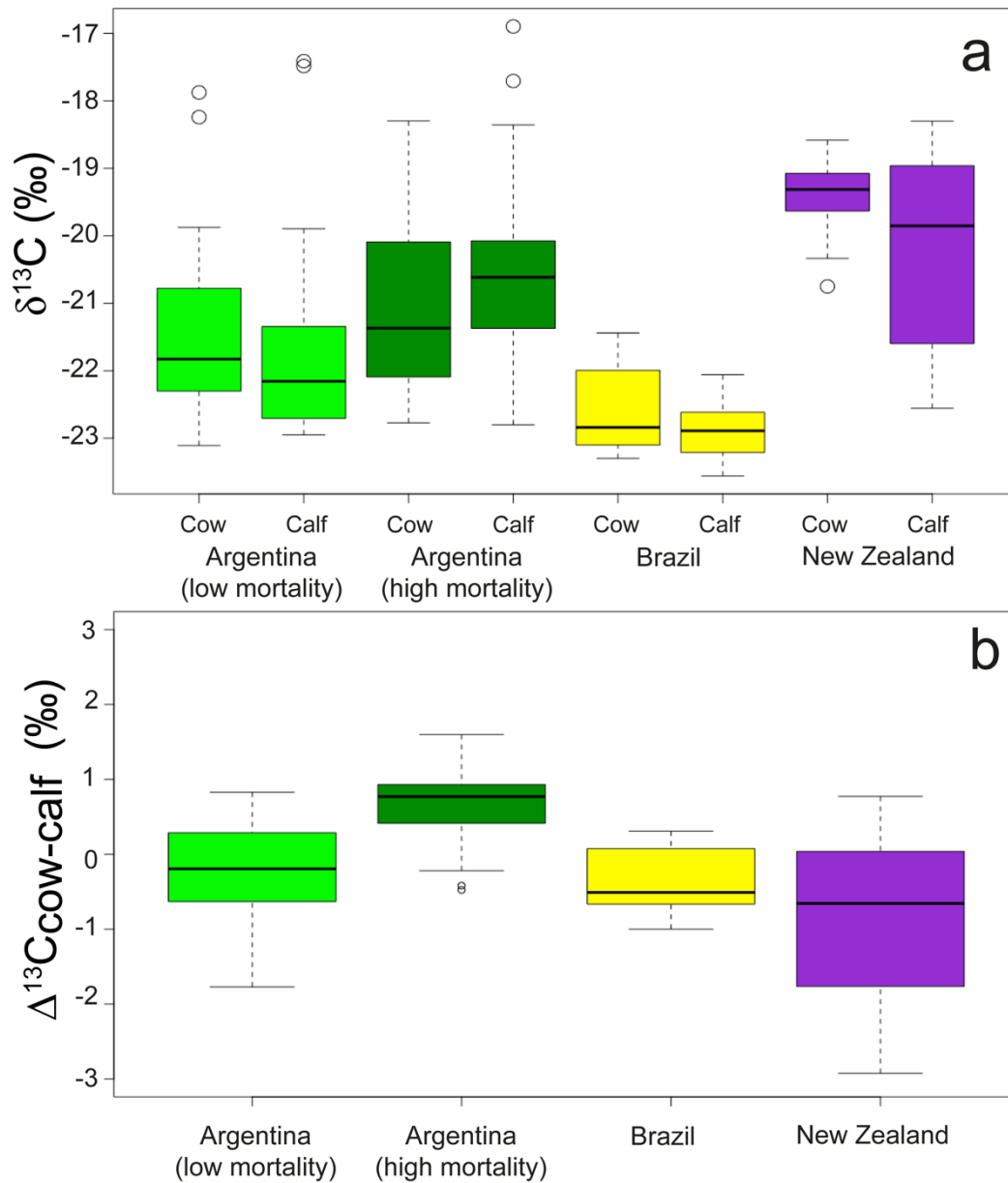
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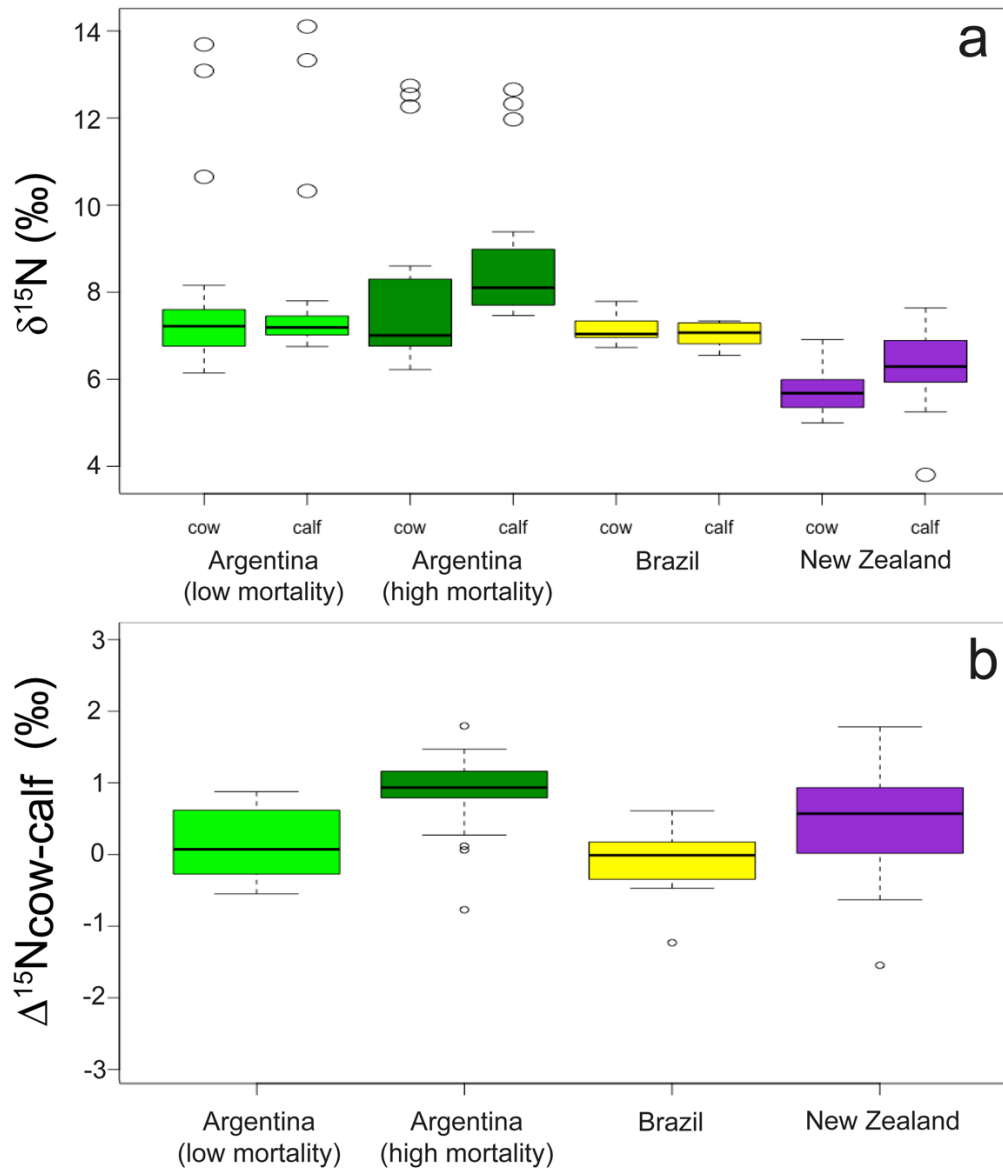
Figure 1: Location of southern right whale wintering grounds and skin $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values for the cow (triangles) and calf (circles) samples from Argentina (ARG), Brazil (BRZ) and New Zealand (NZ). Also shown are the locations of the South African (SAF), southwest Australian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



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641 Figure 2: a. Boxplot of cow and calf stable $\delta^{13}\text{C}$ isotope data summarised by wintering ground for
 642 Argentina (low and high mortality years), Brazil, and New Zealand. b. Boxplot of offset between cow
 643 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)
 644 calf mortality years in Argentina, Brazil and New Zealand. Argentina data from Valenzuela et al.
 645 (2010). Boxes defined by 25% and 75% quantile values with median showed by black line, with
 646 whiskers extending up to 1.5x the interquartile range and outliers shown by open circles.

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649 Figure 3: a. Boxplot of cow and calf stable $\delta^{15}\text{N}$ isotope data summarised by wintering ground for
 650 Argentina (low and high mortality years), Brazil, and New Zealand. b. Boxplot of offset between cow
 651 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)
 652 calf mortality years in Argentina, Brazil and New Zealand. Argentina data from Valenzuela et al.
 653 (2010). Boxes defined by 25% and 75% quantile values with median showed by black line, with
 654 whiskers extending up to 1.5x the interquartile range and outliers shown by open circles.