

Isotopic Variation Between Adult Female Guadalupe Fur Seals and Their Offspring: Implications for the Use of Neonates as Proxies for Maternal Foraging

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Abstract

Pinniped neonates are indirect indicators of their mothers' foraging areas and the prey they consume. However, the isotopic difference between neonates and their mothers is often unknown, presenting a substantial obstacle to our understanding of foraging behavior. In this study, we assessed the isotopic differences between Guadalupe fur seal (GFS) neonates and their mothers. Fur was sampled from ten 1-mo-old GFS neonates and their adult female GFS mothers on Guadalupe Island, Mexico. We used a Carlo Erba 1108 elemental analyzer coupled to a ThermoFinnigan Delta Plus XP isotope ratio mass spectrometer to determine the $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$. For each GFS pair, we calculated the isotopic variation using the *SIBER* (*Stable Isotope Bayesian Ellipses in R*) routine included in the *SIAR* package for *R* software. For neonates, the mean values were $17.8 \pm 0.4\text{‰}$ for $\delta^{15}\text{N}$ and $-17.6 \pm 0.4\text{‰}$ for $\delta^{13}\text{C}$, while the values for their mothers were $16.8 \pm 0.1\text{‰}$ for $\delta^{15}\text{N}$ and $-17.4 \pm 0.5\text{‰}$ for $\delta^{13}\text{C}$. The mean variation in $\delta^{15}\text{N}$ between age groups was $+1.0 \pm 0.4\text{‰}$, with most values falling between $+0.5$ and $+1.0\text{‰}$. The mean variation in $\delta^{13}\text{C}$ was $-0.2 \pm 0.6\text{‰}$, with the majority ranging from -0.5 to -0.1‰ . We identified isotopic segregation between the two groups. The variation observed indicated that GFS neonates are effective proxies for their mothers' $\delta^{15}\text{N}$, with values consistently higher in neonates than their mothers. Differences in $\delta^{13}\text{C}$ between the two groups did not follow any apparent pattern. Our results serve as a reference for other studies

using fur from offspring to infer values for adult females and can be used in conjunction with new or existing data. The mother-neonate relationship should be considered with caution as variations may arise from different factors, some of which can be controlled.

Key Words: Guadalupe fur seal, *Arctocephalus philippii townsendi*, stable isotopes, mothers, offspring, isotopic variation

Introduction

Many of the isotopic studies on adult female pinnipeds rely on values from their offspring. As the latter are not yet independent consumers, their tissues form as the result of the catabolism of their mother's fat and muscle during milk production, simulating the relationship between prey and predator (Aurioles-Gamboa et al., 2006, 2009; Newsome et al., 2006; Porras-Peters et al., 2008; Habran et al., 2010; Páez-Rosas & Aurioles-Gamboa et al., 2010; Elorriaga-Verplancken et al., 2013a). This approach to estimating the trophic relationship between mothers and neonates is based on relatively constant isotopic increments, or trophic discrimination factors (TDF), which emulate the differences in δ -values between a consumer's tissues and diet (Martínez del Río et al., 2009). Traditionally, a trophic level change is inferred when this variation is ~ 3 to 5‰ for $\delta^{15}\text{N}$ and ~ 0.5 to 2‰ $\delta^{13}\text{C}$ (Minagawa & Wada, 1984; Newsome et al., 2007; Martínez del Río et al., 2009). These consistent variations between mothers and neonates have been used to assess adult

female foraging habits in different pinniped species (Aurioles-Gamboa et al., 2006; Porrás-Peters et al., 2008; Habran et al., 2010). Regarding this relationship between age classes, there may be a high degree of $\delta^{13}\text{C}$ variation between both groups as the milk of pinniped species has a high lipid content, which is ^{12}C -enriched and results in lower $\delta^{13}\text{C}$ values in offspring (Newsome et al., 2006).

Fur does not grow synchronously in otariid neonates and their mothers; thus, there is a temporal difference in the trophic information provided. Otariid neonates are born with a dark coat, which in California sea lions (*Zalophus californianus*) starts developing in the fetus at around the seventh month of gestation (Odell, 1972). In fur seals, the fur molts to gray at ~3 to 5 mo of age (Stewart et al., 2002). In contrast, adults tend to molt their fur gradually throughout the year (Loch, 2013). Thus, ~1-mo-old neonate fur is an isotopic proxy for maternal foraging only during the final months of gestation and the first weeks of lactation (Aurioles-Gamboa et al., 2006; Newsome et al., 2006; Porrás-Peters et al., 2008; Páez-Rosas & Aurioles-Gamboa et al., 2010), a narrower temporal window than the one provided—a period of several months—by fur samples from their mothers. Hence, the isotopic niche by pups is a subsample of that of their mothers.

Studies using offspring as proxies for the diet of their mothers are based on the premise that the variation between two or more groups of neonates is the result of variation in their mothers' foraging habits. However, the isotopic difference between mothers and their offspring (M-O) is typically unknown. While inferences may be generated regarding foraging, such studies are limited in the absence of data from adult females. The aim of the present study is to provide information regarding the isotopic variation between Guadalupe fur seal (*Arctocephalus philippii townsendi*) (GFS) M-O. This species' distribution is limited to the breeding area of Guadalupe Island, a recolonized site in the San Benito Archipelago, Baja California, Mexico, and a few sightings on islands off the coast of California (Aurioles-Gamboa et al., 2010). Our results can be useful for studies of other pinnipeds (e.g., sea lions and fur seals) that include isotopic data on offspring, adults, or both, thus strengthening conclusions regarding the trophic ecology of these species. This study also contributes to our knowledge on GFS, which is of particular importance considering the population's endangered status under Mexican law (Secretaría de Medio Ambiente y Recursos Naturales [SEMARNAT], 2010). As a result, this species must be monitored constantly in order to detect any dietary changes during its ongoing recovery.

Methods

On 18 and 19 July 2014, fur was sampled from ten adult female GFSs and their respective ~1-mo-old neonates in Punta Sur (28° 52.746' N, 118° 17.593' W), on the southern tip of Guadalupe Island, Baja California, Mexico (Figure 1). Vocal or olfactory recognition and nursing events were used to confirm the relationship between the adult females and neonates sampled. Due to logistical constraints, it was not possible to take morphometric measurements or determine the sex of the neonates; however, we ensured that all presented a similar body condition, refraining from taking samples from emaciated individuals or those with other obvious differences. Fur samples were taken from the adult females using a 3- to 3.5-m PVC pole fitted with a spherical tip covered with neoprene and glue (Viktor), following Caudron et al.'s (2007) procedure for sampling the fur of New Zealand fur seals (*A. forsteri*). Neonates were immobilized, and fur was sampled from the dorsal area with scissors and stored in labeled paper envelopes.

Stable Isotope Analysis

All samples were processed in the Chemistry Laboratory at the Centro Interdisciplinario de Ciencias Marinas (CICIMAR; Interdisciplinary Center for Marine Sciences) of the Instituto Politécnico Nacional (IPN; National Polytechnic Institute) (www.cicimar.ipn.mx/oasis). Samples were washed with distilled water and chloroform/methanol (1:1) to remove impurities. An agate mortar was used to homogenize the samples and *ca.* 1 mg was weighed on an analytical microbalance precise to 0.001 mg. The samples were stored in 8 × 5 mm tin capsules and sent to the Earth and Planetary Sciences Stable Isotope Laboratory at the University of California at Santa Cruz (UCSC) (<http://es.ucsc.edu/~silab/index.php>), where the $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ were determined using a Carlo Erba 1108 elemental analyzer coupled to a ThermoFinnigan Delta Plus XP isotope ratio mass spectrometer, with an analytical precision of $\pm 0.2\text{‰}$ for both stable isotopes. For both elements, the proportion of stable isotopes is represented using delta (δ) and calculated using DeNiro & Epstein's (1978) equation:

$$\delta^{15}\text{N} \text{ or } \delta^{13}\text{C} = 1,000 [(R_{\text{sample}}/R_{\text{standard}}) - 1]$$

Elemental compositions are estimated relative to standards of known values: Vienna Pee Dee Belemnite ($\delta^{13}\text{C} = 0.011\text{‰}$) for carbon and atmospheric N_2 ($\delta^{15}\text{N} = 0.004\text{‰}$) for nitrogen.

The isotopic niche characteristics of both groups (mothers and their offspring) were estimated using

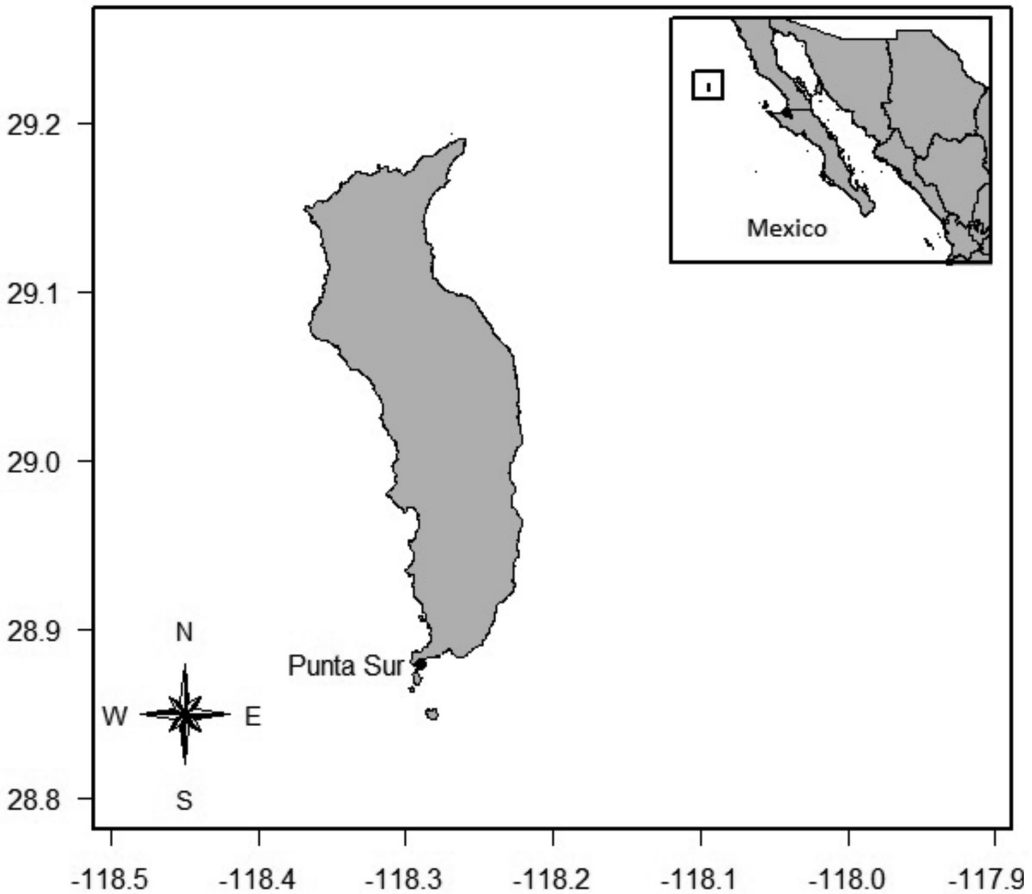


Figure 1. The study area: Punta Sur, on the southern end of Guadalupe Island, Baja California, Mexico

the *Stable Isotope Bayesian Ellipses in R (SIBER)* routine in *SIAR*, a package in *R* (R Development Core Team, 2008; Jackson et al., 2011). This approach involves the use of Markov-Chain Monte Carlo simulations (bootstrapping) to construct ellipse parameters. We used bivariate ellipses and convex hulls to delineate isotopic niche space (95% CI for $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$). We estimated the niche area and overlap based on 100,000 posterior draws of the Bayesian standard ellipse parameters.

We performed paired *t* tests to assess the isotopic differences between both age classes. Significance was tested at the 95% CI ($p < 0.05$). An additional regression was performed (*STATISTICA*, Version 10) to determine the isotopic ($\delta^{15}\text{N}$ and $\delta^{13}\text{C}$) relationship between GFS neonates and their mothers.

Results

The mean (\pm SD) values for GFS neonates were $17.8 \pm 0.4\text{‰}$ for $\delta^{15}\text{N}$ and $-17.6 \pm 0.4\text{‰}$ for $\delta^{13}\text{C}$; for adult females, the values were $16.8 \pm 0.1\text{‰}$

for $\delta^{15}\text{N}$ and $-17.4 \pm 0.5\text{‰}$ for $\delta^{13}\text{C}$. We identified significant differences between neonates and adult females in terms of $\delta^{15}\text{N}$ ($t = 7.3$, $df = 18$, $p < 0.05$); however, there were no significant differences in $\delta^{13}\text{C}$ ($t = -1.0$, $df = 18$, $p > 0.05$).

For all M-O pairs, the mothers' $\delta^{15}\text{N}$ values were lower (0.7 to 2.1‰); however, for $\delta^{13}\text{C}$, this relationship varied considerably (-1.4 to 0.6‰) (Table 1). The mean variation for $\delta^{15}\text{N}$ was $+1.0 \pm 0.4\text{‰}$, with most (70%) cases falling between +0.5 and +1.0‰; whereas the mean variation for $\delta^{13}\text{C}$ was $-0.2 \pm 0.6\text{‰}$, with 50% of the cases falling between -0.5 and -0.1‰. Some positive differences for $\delta^{13}\text{C}$ ($n = 3$) were also recorded.

Based on the results of the *SIBER* analysis, neonates had a broader isotopic niche (polygon = 0.9; ellipse = 0.5) than adult females (polygon = 0.4; ellipse = 0.2). The disparity in $\delta^{15}\text{N}$ values resulted in no overlap (-4.8) between neonates and their mothers (Figure 2).

$\delta^{15}\text{N}$ values of pups and their mothers were linearly correlated ($y = 16.2 + 0.03x$); however,

Table 1. $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ values and trophic discrimination factors (Δ) between Guadalupe fur seal (*Arctocephalus philippii townsendi*) (GFS) adult females (mothers) and neonates (offspring) on Guadalupe Island, Baja California, Mexico

Pair	Neonate $\delta^{15}\text{N}$ (‰)	Mother $\delta^{15}\text{N}$ (‰)	$\Delta^{15}\text{N}$ (‰)	Neonate $\delta^{13}\text{C}$ (‰)	Mother $\delta^{13}\text{C}$ (‰)	$\Delta^{13}\text{C}$ (‰)
1	17.7	16.9	+0.8	-17.6	-18.2	0.6
2	18.2	16.9	+1.3	-17.6	-18.1	0.5
3	18.0	16.9	+1.1	-17.2	-17.7	0.5
4	18.7	16.6	+2.1	-17.3	-16.8	-0.5
5	17.7	16.8	+0.9	-18.2	-16.8	-1.4
6	17.6	16.8	+0.8	-17.0	-16.9	-0.1
7	17.4	16.6	+0.8	-17.7	-17.6	-0.1
8	17.5	16.7	+0.8	-18.0	-17.5	-0.5
9	17.4	16.7	+0.7	-17.4	-16.9	-0.5
10	17.9	17.1	+0.8	-17.7	-17.0	-0.7
Mean \pm SD	17.8 \pm 0.4	16.8 \pm 0.1	+1.0 \pm 0.4	-17.6 \pm 0.4	-17.4 \pm 0.5	-0.2 \pm 0.6

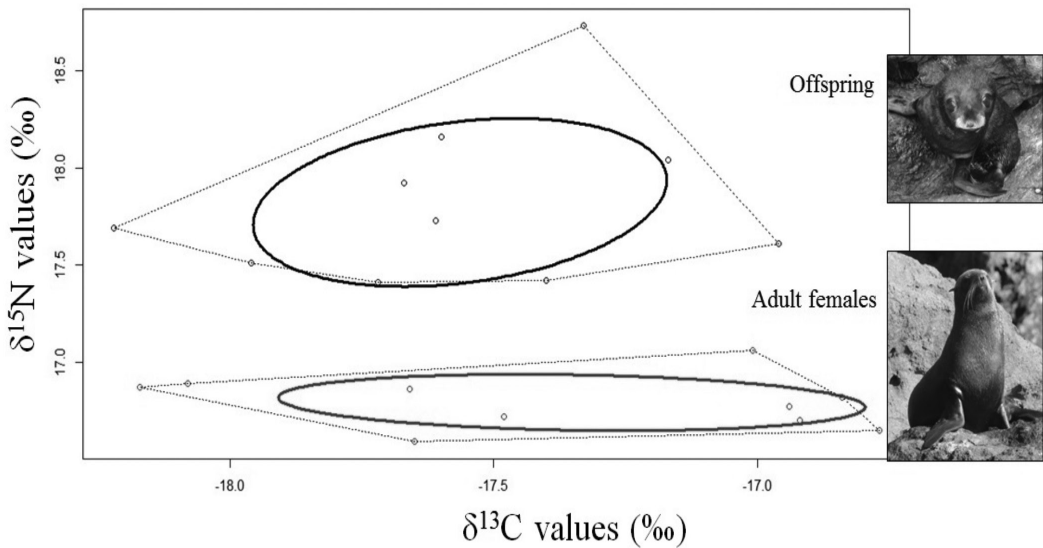


Figure 2. Isotope segregation between adult female (polygon = 0.4; ellipse = 0.2) and neonate (polygon = 0.9; ellipse = 0.5) Guadalupe fur seals (*Arctocephalus philippii townsendi*) (GFSs) from Guadalupe Island; overlap between groups = -4.8.

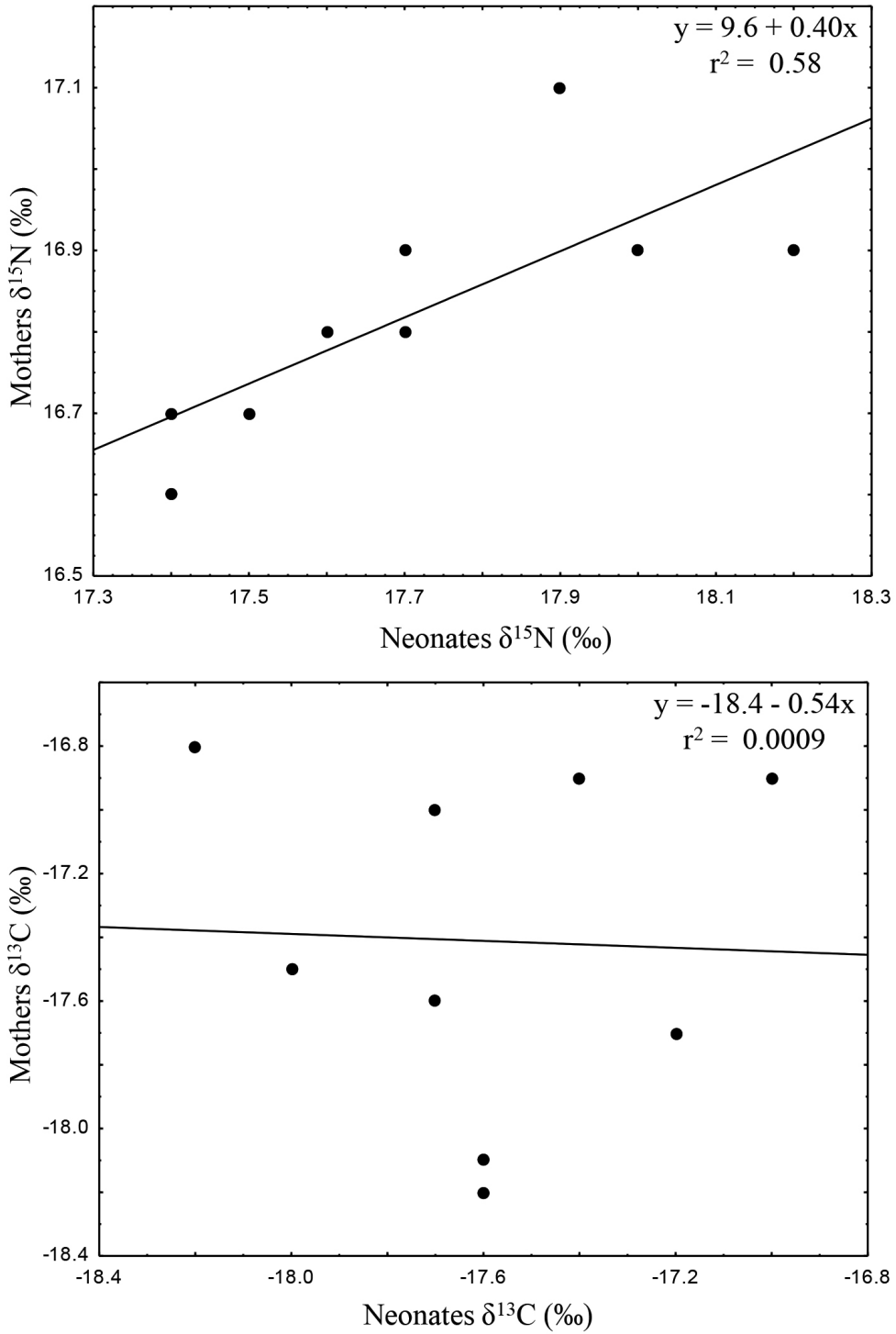


Figure 3. $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ (‰) relationships between fur of adult female GFSs and their neonates

Table 2. Isotopic ($\delta^{15}\text{N}$ and $\delta^{13}\text{C}$) variation between pups and adult females of different pinniped species: (A) mothers-to-offspring; (B) different age classes, unrelated; and (C) individual variation (growth layers in teeth). NS = Nonsignificant.

Species	Tissue	$\delta^{15}\text{N}$ (‰)	$\delta^{13}\text{C}$ (‰)	References
Weddell seal (<i>Leptonychotes weddelli</i>)	Blood (plasma)	~+0.7	~-0.5	Burns et al., 1998 (B)
Northern fur seal (<i>Callorhinus ursinus</i>)	Bone collagen	~+3.0	~-0.7	Newsome et al., 2006 (B)
California sea lion (<i>Zalophus californianus</i>)	Bone collagen	~+2.8	~-1.0	Newsome et al., 2006 (B)
Northern fur seal	Dental collagen	~+1.0 to 4.0	~-1.3 to +0.7	Newsome et al., 2006 (C)
California sea lion	Dental collagen	~+2.0 to 3.0	~-1.4 to -0.2	Newsome et al., 2006 (C)
Northern elephant seal (<i>Mirounga angustirostris</i>)	Blood	~+1.3	~+0.3	Ducatez et al., 2008 (A)
Northern elephant seal	Blood cells and serum	NS to ~+1.3	~+0.2	Habran et al., 2010 (A)
California sea lion	Hair	~+2.1	~-0.8	Porrás-Peters et al., 2008 (B)
Northern elephant seal	Dental collagen	~+1.8	~-0.2	Río-frio-Lazo et al., 2012 (C)
California sea lion	Dental collagen	~+2.6	~-0.2	Elorriaga-Verplancken et al., 2013 (C)

their relationship was not significant ($r = 0.09$, $p > 0.05$); neither was $\delta^{13}\text{C}$ ($y = 0.09x - 15.8$) ($r = 0.06$, $p > 0.05$). The $\delta^{15}\text{N}$ regression was highly influenced by Pair 4, which showed the highest $\delta^{15}\text{N}$ difference (2.1‰) between M-O relative to the rest of the pairs (0.7 to 1.3‰). By removing this pair, the relationship between M-O was significant ($r = 0.76$, $p = 0.01$) for $\delta^{15}\text{N}$ but not for $\delta^{13}\text{C}$ ($r = -0.03$, $p > 0.05$) (Figure 3).

Discussion

This study is the first to estimate the isotopic variation between GFS neonates and their mothers. It represents an important contribution to our limited knowledge on the relationship between adult female pinnipeds and their offspring, and it provides an important tool for future trophic research. On average, $\delta^{15}\text{N}$ values were higher for neonates than their mothers, while the variation in $\delta^{13}\text{C}$ was dispersed and lacked any consistent pattern. Moreover, its SD was larger than the mean.

Variation in $\delta^{15}\text{N}$ Between GFS Mothers and Neonates

Few studies have analyzed the M-O relationship in pinnipeds (Ducatez et al., 2008; Habran et al., 2010). Other analyses examining variation between age classes involve isotopic analysis

of dental growth layers (Newsome et al., 2006; Río-frio-Lazo et al., 2012; Elorriaga-Verplancken et al., 2013a), while other studies have examined individuals from different age classes (e.g., pups and adult females) that are not necessarily related (Burns et al., 1998).

The variation in $\delta^{15}\text{N}$ reported herein is lower than that reported in other pinniped studies and also lower than a trophic level if we consider the typical established difference in $\delta^{15}\text{N}$ between two continuous trophic levels (Minagawa & Wada, 1984). However, the variation in $\delta^{15}\text{N}$ was consistently positive (Table 2). The isotopic relationship between mothers and their offspring is complex (Jenkins et al., 2001); physiological and biochemical factors related to nursing may contribute to the variation in $\delta^{15}\text{N}$ between M-O. Physiological stress can lead to ^{15}N -enrichment as a result of nitrogen recycling in either group (Kurle & Worthy, 2001). In contrast, a positive nitrogen balance in protein synthesis, as occurs during pregnancy (Fuller et al., 2005) or lactation (Kurle, 2002), may result in ^{15}N -depleted values. In this study, all subjects were exposed to the same effect (early lactation), eliminating those two effects as a source of variation between individuals. Other factors that may cause variation in $\delta^{15}\text{N}$ include protein quality (Robbins et al., 2005) and nitrogen concentration (C:N) in the diet (Pearson et al.,

2003), both of which may vary by species. Diets with elevated protein and nitrogen concentrations tend to display high $\delta^{15}\text{N}$ values in a consumer, with values reaching up to 4‰. The reduced difference in $\delta^{15}\text{N}$ reported herein may be due to the variability observed in GFS diets compared with the other species considered in Table 2. To reduce any protein or nitrogen-derived variability, our $\delta^{15}\text{N}$ results can be extrapolated for use in other studies involving teuthophagous otariids during the first month of lactation.

Considering the $\delta^{15}\text{N}$ values, the broader isotopic niche identified for neonates may be the result of one or more factors as mentioned above (e.g., protein variability of their mothers' diet). However, a difference in the temporal window provided by neonate fur samples relative to their mothers cannot be discarded as a hypothetical alternative explanation, showing a possible higher foraging variability within the last weeks by the neonates' fur relative to a lower foraging variability within the last several months by the mothers' fur.

Variation in $\delta^{13}\text{C}$ Between GFS Mothers and Neonates

The variability observed in $\delta^{13}\text{C}$ may be the result of two seemingly contradictory factors: (1) ^{13}C -enrichment occurs between trophic links (e.g., offspring that are nourished by adult females) (Minagawa & Wada, 1984); and (2) ^{13}C values can become depleted by the presence of ^{13}C -enriched lipids in milk (Newsome et al., 2006). In our study, we report similar $\delta^{13}\text{C}$ values for offspring and adult females (-17.6 vs -17.4‰). This insignificant difference of 0.2‰ is similar to that reported for California sea lions (Elorriaga-Verplancken et al., 2013a), where it was attributed to milk proteins and their amino acid building blocks rather than lipid-derived carbon (Jenkins et al., 2001; Martínez del Río et al., 2009). In most cases, the difference in $\delta^{13}\text{C}$ between GFS mothers and neonates was near or within the margin of analytical error ($\pm 0.2\text{‰}$). Thus, the presence of both negative and positive $\delta^{13}\text{C}$ values reflects considerable variation between groups. That is, not all neonates demonstrate the same balance between the trophic enrichment and depletion of ^{13}C from lipid-enriched milk. Moreover, individual neonates also may incorporate proteins and lipids differentially based on sex (Luque & Auriolles-Gamboa, 2001) or other factors. Thus, the $\delta^{13}\text{C}$ relationship between M-O should be considered with caution.

As previously mentioned, different physiological or biochemical factors may contribute to the isotopic variation between M-O (Cherel et al., 2005); in fact, these values may be species-specific (Jenkins et al., 2001). The use of neonates as proxies for their mothers' diets involves unknown variables;

thus, this relationship must be qualified (Habran et al., 2010). However, by reducing as many factors of inter-individual variation as possible, it is possible to assess maternal diet using samples from neonates by comparing individuals of similar species, sampling the same types of tissue, and taking all neonate samples during the same period (days) to control for the physiological effect of different states (e.g., pregnancy vs post-natal fasting). By controlling for these factors, most of our M-O pairs showed similar variation in $\delta^{15}\text{N}$. This also may explain the solid inferences on maternal behavior offered by a number of studies relying solely on information from neonates (Auriolles-Gamboa et al., 2006; Porras-Peters et al., 2008; Páez-Rosas & Auriolles-Gamboa, 2010; Elorriaga-Verplancken et al., 2013b, 2016).

Conclusions

Our study focuses on a fur seal species that must be monitored continuously due to its population status. This research also contributes to our understanding of the use of neonates as trophic proxies for pinniped colonies, setting a precedent for future studies that will explore and predict in an approximate manner the M-O isotopic ($\delta^{15}\text{N}$) relationship when values for adult females must be inferred from neonate samples. However, to achieve more solid conclusions in this regard, future research should consider other species, aim for larger sample sizes, sample different types of tissues, know their turnover rates, and consider neonate morphological features and sex. Additionally, experimental research along the lines of the present study would improve our understanding of the physiological and biochemical factors that influence the isotopic variation between adults and neonates.

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Literature Cited

- Aurioles-Gamboa, D., Elorriaga-Verplancken, F. R., & Hernández-Camacho, C. J. (2010). The current population status of Guadalupe fur seal (*Arctocephalus townsendi*) on the San Benito Islands, Mexico. *Marine Mammal Science*, 26(2), 402-408. <http://dx.doi.org/10.1111/j.1748-7692.2009.00350.x>
- Aurioles-Gamboa, D., Koch, P. L., & Le Boeuf, B. J. (2006). Differences in foraging location of Mexican and California elephant seals: Evidence from stable isotopes in pups. *Marine Mammal Science*, 22(2), 326-338. <http://dx.doi.org/10.1111/j.1748-7692.2006.00023.x>
- Aurioles-Gamboa, D., Newsome, S. D., Salazar-Pico, S., & Koch, P. L. (2009). Stable isotope differences between sea lions (*Zalophus*) from the Gulf of California and Galápagos Islands. *Journal of Mammalogy*, 90(6), 1410-1420. <http://dx.doi.org/10.1644/08-MAMM-A-209R2.11>
- Burns, J. M., Trumble, S. J., Castellini, M. A., & Testa, J. W. (1998). The diet of Weddell seals in McMurdo Sound, Antarctica as determined from scat collections and stable isotope analysis. *Polar Biology*, 19(4), 272-282. <http://dx.doi.org/10.1007/s003000050245>
- Caudron, A. K., Negro, S. S., Muller, C. G., Boren, L. J., & Gemmell, N. J. (2007). Hair sampling and genotyping from hair follicles: A minimally-invasive alternative for genetics studies in small, mobile pinnipeds and other mammals. *Marine Mammal Science*, 23(1), 184-192. <http://dx.doi.org/10.1111/j.1748-7692.2006.00084.x>
- Cherel, Y., Hobson, K. A., Bailleul, F., & Groscolas, R. (2005). Nutrition, physiology, and stable isotopes: New information from fasting and molting penguins. *Ecology*, 86(11), 2881-2888. <http://dx.doi.org/10.1890/05-0562>
- DeNiro, M. J., & Epstein, S. (1978). Influence of diet on the distribution of carbon isotopes in animals. *Geochimica et Cosmochimica Acta*, 42, 495-506. [http://dx.doi.org/10.1016/0016-7037\(78\)90199-0](http://dx.doi.org/10.1016/0016-7037(78)90199-0)
- Ducatez, S., Dalloyau, S., Richard, P., Guinet, C., & Cherel, Y. (2008). Stable isotopes document winter trophic ecology and maternal investment of adult female southern elephant seals (*Mirounga leonina*) breeding at the Kerguelen Islands. *Marine Biology*, 155(4), 413-420. <http://dx.doi.org/10.1007/s00227-008-1039-3>
- Elorriaga-Verplancken, F. R., Aurioles-Gamboa, D., Newsome, S. D., & Martínez-Díaz, S. F. (2013a). $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ values in dental collagen as a proxy for age- and sex-related variation in foraging strategies of California sea lions. *Marine Biology*, 160(3), 641-652. <http://dx.doi.org/10.1007/s00227-012-2119-y>
- Elorriaga-Verplancken, F. R., Hadrys, L. M. L., Moreno-Sánchez, X. G., & Mendoza-Salas, I. (2013b). Inferences on the diet of the eastern Pacific harbor seal (*Phoca vitulina richardii*) at the southern end of its distribution: Stable isotopes and scats analyses. *Aquatic Mammals*, 39(4), 415-421. <http://dx.doi.org/10.1578/AM.39.4.2013.415>
- Elorriaga-Verplancken, F. R., Morales-Luna, H. L., Heckel, G., & Schramm, Y. (2016). Foraging ecology of harbor seals (*Phoca vitulina*) and northern elephant seals (*Mirounga angustirostris*) from Baja California, Mexico: Inferences from stable isotopes in pups. *Journal of the Marine Biological Association of the United Kingdom (JMBA)*, 96, 1-6. <http://dx.doi.org/10.1017/S0025315415002143>
- Fuller, B. T., Fuller, J. L., Sage, N. E., Harris, D. A., O'Connell, T. C., & Hedges, R. E. M. (2005). Nitrogen balance and $\delta^{15}\text{N}$: Why you're not what you eat during nutritional stress. *Rapid Communications in Mass Spectrometry: RCM*, 19(18), 2497-2506. <http://dx.doi.org/10.1002/rcm.2090>
- Habran, S., Debier, C., Crocker, D. E., Houser, D. S., Lepoint, G., Bouquegneau, J. M., & Das, K. (2010). Assessment of gestation, lactation and fasting on stable isotope ratios in northern elephant seals (*Mirounga angustirostris*). *Marine Mammal Science*, 26(4), 880-895. <http://dx.doi.org/10.1111/j.1748-7692.2010.00372.x>
- Jackson, A. L., Inger, R., Parnell, A. C., & Bearhop, S. (2011). Comparing isotopic niche widths among and within communities: *SIBER – Stable Isotope Bayesian Ellipses in R*. *Journal of Animal Ecology*, 80(3), 595-602. <http://dx.doi.org/10.1111/j.1365-2656.2011.01806.x>
- 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. <http://dx.doi.org/10.1007/s004420100755>
- Kurle, C. M. (2002). Stable-isotope ratios of blood components from captive northern fur seals (*Callorhinus ursinus*) and their diet: Applications for studying the foraging ecology of wild otariids. *Canadian Journal of Zoology*, 80, 902-909. <http://dx.doi.org/10.1139/z02-069>
- Kurle, C. M., & Worthy, G. A. J. (2001). Stable isotope assessment of temporal and geographic differences in feeding ecology of northern fur seals (*Callorhinus ursinus*) and their prey. *Oecologia*, 126(2), 254-265. <http://dx.doi.org/10.1007/s004420000518>
- Loch, C. (2013). Return to the sea: The life and evolutionary times of marine mammals by Annalisa Berta.

- Marine Mammal Science*, 29(1), 236-237. <http://dx.doi.org/10.1111/j.1748-7692.2012.00619.x>
- Luque, S. P., & Aurióles-Gamboa, D. (2001). Sex differences in body size and body condition of California sea lion (*Zalophus californianus*) pups from the Gulf of California. *Marine Mammal Science*, 17(1), 147-160. Retrieved from <http://dx.doi.org/10.1111/j.1748-7692.2001.tb00985.x>
- Martínez del Río, C., Wolf, N., Carleton, S. A., & Gannes, L. Z. (2009). Isotopic ecology ten years after a call for more laboratory experiments. *Biological Reviews*, 84, 91-111. <http://dx.doi.org/10.1111/j.1469-185X.2008.00064.x>
- Minagawa, M., & Wada, E. (1984). Stepwise enrichment of ^{15}N along food chains: Further evidence and the relation between $\delta^{15}\text{N}$ and animal age. *Geochimica et Cosmochimica Acta*, 48(5), 1135-1140. [http://dx.doi.org/10.1016/0016-7037\(84\)90204-7](http://dx.doi.org/10.1016/0016-7037(84)90204-7)
- Newsome, S. D., Martínez del Río, C., Bearhop, S., & Phillips, D. L. (2007). A niche for isotopic ecology. *Frontiers in Ecology and the Environment*, 5(8), 429-436. [http://dx.doi.org/10.1890/1540-9295\(2007\)5\[429:ANFIE\]2.0.CO;2](http://dx.doi.org/10.1890/1540-9295(2007)5[429:ANFIE]2.0.CO;2)
- Newsome, S. D., Koch, P. L., Etnier, M. A., & Aurióles-Gamboa, D. (2006). Using carbon and nitrogen isotope values to investigate maternal strategies in northeast Pacific otariids. *Marine Mammal Science*, 22(3), 556-572. <http://dx.doi.org/10.1111/j.1748-7692.2006.00043.x>
- Odell, D. K. (1972). *Studies on the biology of the California sea lion and the northern elephant seal on San Nicolas Island* (Unpublished doctoral dissertation). University of California, Los Angeles.
- Páez-Rosas, D., & Aurióles-Gamboa, D. (2010). Alimentary niche partitioning in the Galapagos sea lion, *Zalophus wolfebaeki*. *Marine Biology*, 157(12), 2769-2781. <http://dx.doi.org/10.1007/s00227-010-1535-0>
- Pearson, S. F., Levey, D. J., Greenberg, C. H., & Martínez del Río, C. (2003). Effects of elemental composition on the incorporation of dietary nitrogen and carbon isotopic signatures in an omnivorous songbird. *Oecologia*, 135(4), 516-523. <http://dx.doi.org/10.1007/s00442-003-1221-8>
- Porras-Peters, H., Aurióles-Gamboa, D., Cruz-Escalona, V. H., & Koch, P. L. (2008). Trophic level and overlap of sea lions (*Zalophus californianus*) in the Gulf of California, Mexico. *Marine Mammal Science*, 24(3), 554-576. <http://dx.doi.org/10.1111/j.1748-7692.2008.00197.x>
- R Development Core Team. (2008). *R: A language and environment for statistical computing*. Vienna, Austria: R Foundation for Statistical Computing. Retrieved from www.R-project.org. ISBN 3-900051-07-0
- Riofrío-Lazo, M., Aurióles-Gamboa, D., & Le Boeuf, B. J. (2012). Ontogenetic changes in feeding habits of northern elephant seals revealed by $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ analysis of growth layers in teeth. *Marine Ecology Progress Series*, 450, 229-241. <http://dx.doi.org/10.3354/meps09562>
- 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. <http://dx.doi.org/10.1007/s00442-005-0021-8>
- Secretaría de Medio Ambiente y Recursos Naturales (SEMARNAT). (2010). *Protección ambiental: Especies nativas de México de flora y fauna silvestres. Categorías de riesgo y especificaciones para su inclusión, exclusión o cambio: Lista de especies en riesgo* [Environmental protection: Mexican native species of wild flora and fauna. Risk classification and specifications for their inclusion, exclusion, or change: List of species under risk] (Official Report of the Federation, Mexican Official Law NOM-059-SEMARNAT-2010). Jardines de la Montaña, Mexico City: SEMARNAT.
- Stewart, B., Clapham, P., Powell, J., & Reeves, R. R. (2002). *National Audubon Society guide to marine mammals of the world* (National Audubon Society Field Guide Series) (1st ed.). New York: National Audubon Society.