Foraging Segregation Between Adult Female Northern Elephant Seals (*Mirounga angustirostris*) from Guadalupe Island and the San Benito Archipelago, Mexico

Romyna A. Cruz-Vallejo, Fernando R. Elorriaga-Verplancken, Arturo B. Enríquez-García, and Eunice D. Rodríguez-Rafael

Instituto Politécnico Nacional, Centro Interdisciplinario de Ciencias Marinas, La Paz, Baja California Sur, México E-mail: felorriaga@ipn.mx

Abstract

Female northern elephant seals (Mirounga angustirostris) are migratory animals that form colonies along the coasts of California and the Baja California Peninsula, Mexico. A recent decline in abundance has been recorded in this species Mexican distribution, which is an important reason to investigate the different ecological processes operating in these colonies. The aim of this study was to determine values of stable isotope ratios (δ^{13} C and δ^{15} N) in pup fur as foraging maternal indicators. During the same breeding season (2015), pup fur samples were collected to investigate these foraging variations between the two major Mexican colonies-Guadalupe Island (GI) and the San Benito Archipelago (SBA). Isotopic areas were built using the 'SIBER' package in R, and a custom hierarchical Bayesian model was used to compare the values from both localities. Mean (\pm standard deviation [SD]) δ^{13} C values for individuals from GI and the SBA were -16.9 \pm 0.8% and -17.3 \pm 0.4%, respectively, while $\delta^{15}N$ values were $17.4 \pm 1.1\%$ and $16.7 \pm 1.1\%$, respectively. The difference between the posterior means indicated a high probability (P>99%) of GI having higher stable isotope ratio values than the SBA. For the posterior SDs, there were highly probable differences (P = 100%) only for δ^{13} C, where GI had a higher dispersion. Such differences explained why GI presented a wider isotopic niche area than the SBA, indicating more diverse foraging habits along GI's offshore-inshore gradient. Additionally, GI showed higher δ^{15} N values than the SBA. Although this could be related to a slightly higher trophic position for GI individuals, the latitudinal effects of foraging grounds with distinct isotopic baselines remain a plausible explanation for the variations in both isotope ratios, suggesting that individuals from the SBA foraged in a more northerly location than those from GI. This study provides valuable

knowledge about how females from both colonies partition resources, especially regarding habitat use.

Key Words: stable isotopes, isoscapes, trophic ecology, intraspecific variation, pinnipeds

Introduction

The study of foraging habits is critical to understanding aspects regarding the role of each organism in the trophic web (Casper et al., 2006). As top predators are situated in the highest link or close to it, it is possible to infer how they respond to environmental variability individually and at a population level through their diet (Bowen & Iverson, 2013). This includes the possibility of foraging diversification and niche distribution at an intrapopulation level due to phenotypic, physiological, and distribution variations or as a strategy to reduce competition (e.g., Bolnick et al., 2003; Juárez-Ruiz et al., 2018). A case study that could reflect some of these strategies is the northern elephant seal (Mirounga angustirostris; NES), in ontogenetic terms (Riofrío-Lazo et al., 2012) or by sex (Velázquez-Castillo & Elorriaga-Verplancken, 2017). This pelagic species extends throughout a high portion of the Northeast Pacific. However, the islands where it breeds and molts are located on the coasts of California and the Baja California Peninsula. Mexico (Le Boeuf et al., 2000). The NES total population was estimated at 210,000 to 239,000 individuals in 2010 (Lowry et al., 2014). Recent analyses evidence abundance declines in Mexican colonies such as those from Guadalupe Island (GI) and the San Benito Archipelago (SBA) in the western Baja California Peninsula (Elorriaga-Verplancken et al., 2015; García-Aguilar et al., 2018; Rodríguez-Rafael et al., 2023). Adult NESs of both sexes migrate to the North Pacific (ca. 40° and 55° N) for

foraging purposes. These occur twice a year, from and to their reproductive colonies in California and Baja California. The first migration occurs once the breeding season ends in winter, and the second migration is after molting in spring-summer (Le Boeuf et al., 2000; Robinson et al., 2012).

The NES forages at sea for months. Moreover, adults fast on land, often on islands (Le Boeuf & Laws, 1994). This species is able to take advantage of productive oceanographic features in the open ocean such as eddies that promote successful foraging activity (Robinson et al., 2012; Adachi et al., 2021). Deeper diving may also help individuals avoid predators, which may be especially difficult in the open ocean where spatial refuges are rare (Beltran et al., 2021). The use of methodologies, such as animal-borne video technology, indicates that NESs predominantly consume small mesopelagic fish (78% of 697 prev items recorded), while squid constitute only 7% of the diet. Prey items identified included fishes such as myctophids, Merluccius sp. and Icosteus aenigmaticus, and squids (e.g., Histioteuthis sp., Octopoteuthis sp., Taningia danae; Yoshino et al., 2020). This is consistent with the fatty acid analysis, which also evidenced fish to be more important in the diet, revealing that mesopelagic fishes, particularly energy-rich myctophids, were a critical prey resource (Goetsch et al., 2018).

Analyzing stable isotope ratios of carbon (δ^{13} C) and nitrogen (δ^{15} N) in trophic ecology studies is useful when stomach contents and feces are scarce. δ^{15} N values provide information regarding the relative trophic level and the consumer's diet breadth by the enrichment relationship between the ¹⁵N content of the consumer and its diet (Owens, 1988). Conversely, δ^{13} C values allow inferences about habitat use by consumers (France, 1995). Both isotope ratios at the base of the trophic web are also associated with latitude due to the presence of isoscapes, which have characteristic baseline isotopic values (Burton & Koch, 1999; Amador-Capitanachi et al., 2017).

Different studies regarding isotope ratios in pinnipeds were based on pup samples for analysis of the trophic habits of their mothers, given that pups were not yet independent consumers at the time of sample collection. Pup tissues result from the catabolism of their mothers' tissues (lipids and muscle) that produce maternal milk, simulating the relation between predator and prey through isotopic increases that are relatively consistent. The latter allows comparisons if the study subjects are only pups and the same tissue is analyzed in every case (Aurioles-Gamboa et al., 2006; Porras-Peters et al., 2008; Páez-Rosas & Aurioles-Gamboa, 2010; Elorriaga-Verplancken et al., 2016b; Amador-Capitanachi et al., 2017, 2020). It has been previously suggested, through stable isotope analysis, that adult female NESs show foraging segregation between different colonies (Aurioles-Gamboa et al., 2006). Therefore, this study aimed to investigate foraging variations between the NESs from GI and those from SBA colonies based on the isotopic values of pups. The presence of differences is expected, thus generating valuable information about how this species partitions (intraspecifically) its niche, especially regarding habitat use.

Methods

The first location, GI (29° 00' N, 118° 26' W), is located 256 km west of the Baja California Peninsula, having a strong influence from the California Current System. The second location, the SBA (28° 18' N, 115° 32' W), is located 31.5 km from Cedros Island and 130 km from the Baja California Peninsula. The archipelago is situated over a long, continental platform that extends from Sebastián Vizcaino Bay in the Baja California Peninsula, including Cedros Island, located at the border of this platform (Figure 1). These locations form part of the Guadalupe Island Biosphere Reserve and the Pacific Islands of the Baja California Peninsula Biosphere Reserve, respectively.

Fieldwork was conducted during the NES 2015 breeding season, from mid-January to early February. Fur samples of weaned pups about 1 mo old were collected (52 from GI and 48 from the SBA). The capture of individuals was unnecessary as pups were molting after their first month of life; thus, it was relatively easy to approach them and obtain a sample using gloves. Samples were stored in labeled manila paper. It was ensured that sampled pups had a similar body mass condition, and we avoided collecting fur from individuals that were emaciated or unhealthy in appearance.

Samples were washed and processed (i.e., in the Laboratory of Fish Ecology, Interdisciplinary Center of Marine Sciences [CICIMAR-IPN]) in La Paz Baja California Sur, Mexico. Each sample was washed thrice with a chloroform/methanol solution (1:1 ratio). During the first wash, the solvent was maintained for only 5 min, impurities were removed with tweezers, and the solvent was discarded after use. After this first wash, samples were submerged in the solvent until it evaporated twice.

After the three washes, each sample was finely cut using tweezers and scissors and later homogenized with an agate mortar until a fine powder was obtained. Approximately 1 mg of each sample was weighed in an analytical microbalance (0.0001 mg precision) and stored in $8 \times$



Figure 1. Study area: Guadalupe Island and the San Benito Archipelago in the western region of the Baja California Peninsula, Mexico

5 mm tin capsules. Finally, samples were analyzed with a mass spectrometer. Both stable isotope ratios were represented as proportions using the delta (δ) notation with units expressed as parts per thousand (∞ ; DeNiro & Epstein, 1978):

$\delta^{13}C$ or $\delta^{15}N = 1000 | (Rsample/Rstandard) - 1 |$

where Rsample is the ratio of ${}^{15}N/{}^{4}N$ or ${}^{13}C/{}^{12}C$ of the sample and Rstandard is that of the standard. Elemental compositions of carbon and nitrogen were estimated based on standards with known isotopic values: Vienna Pee Dee Belemnite ($\delta^{13}C$ = 0.011‰) for carbon and atmospheric N₂ ($\delta^{15}N$ = 0.004‰) for nitrogen.

Data were analyzed using Bayesian Inference (BI), which reallocates the credibility of parameters among candidate possibilities, and using Bayes' theorem for evaluation based on the data, the model, and prior knowledge about the parameters (Bolstad, 2004; Kruschke, 2012). A custom Hierarchical Bayesian model was used to compare the isotopic values of both localities in terms of their means and standard deviations (SDs). Hierarchical Bayesian models incorporate the uncertainty around the parameters at the lower hierarchy levels and sequentially transfer it to the next, partially pooling the data and "shrinking" the group-level parameters towards the shared estimates (Gelman et al., 2014). The model was then specified as follows, where *i* represents the isotope ratio and *j* the island (either GI or the SBA):

Shared priors:

- μ_i ~ Normal(μ = δ_i, σ = SD(δ_i) * 100: A regularizing normal distribution centered on the mean and SD (times 100) of each isotopic ratio
- σ_i ~ *Exponential*(λ = 1):
 A weakly informative (i.e., not completely flat) exponential distribution

Group priors:

- μ_{i,j} ~ Normal(μ = μ_i, σ = σ_i):
 A normal distribution centered on each isotope's estimated mean, with an SD based on the global SD
- *σ_{i,j}* ~ *Exponential*(λ = 1):
 A weakly informative exponential distribution
- $v_j \sim Exponential(\lambda = 1/30) + 1$:

A shifted exponential distribution whose posterior mean is centered around 30, spreading the credibility across heavy and light-tailed (normal-like) distributions

Likelihood:

 δ_{i,j} ~ StudentT(μ = μ_{i,j}, σ = σ_{i,j}, ν = ν_j): A Student *t* likelihood that assigns a higher probability to extreme values, which is useful to make robust estimations of the parameters (Kruschke, 2012)

The model was fit using the PyMC module, Version 5.0.1 (Salvatier et al., 2016) for *Python*, Version 3.11.0 (Van Rossum & Drake, 2009). The posterior distributions were sampled with four Marcov-Chains Monte Carlo (MCMC) using a No-U-Turn Sampler (NUTS; Hoffman & Gelman, 2014).

The breadth of the isotopic niches of each colony and their probable overlap were analyzed through Bayesian areas of standard ellipses obtained using the 'SIBER' package ('Stable Isotope Bayesian Ellipses in R'; Jackson et al., 2011) in R, Version 3.6.2 (R Core Team, 2018). This package calculates areas of convex hulls (polygons) based on the total area of all data, as well as the Bayesian Standard Ellipse Areas (SEA_B) that reflect the areas with the highest credibility (Jackson et al., 2011). In both cases, the MCMC were run until convergence (i.e., zero divergent posterior samples for NUTS; Betancourt, 2017), and Gelman-Rubin statistics were less than 1.01 for every parameter (Gelman et al., 2014). The posterior samples varied in length due to the differences in the sampling algorithms; however, the effective sample size for every parameter was greater than 28,000. The colonies were then compared by subtracting the SBA's posterior means, SDs, and standard ellipse areas from GI's. Thus, positive differences indicate that the SBA had higher values than GI, while negative differences indicate the opposite.

Results

The mean δ^{15} N and δ^{13} C values (± SD) of NESs from GI were 17.4 ± 1.1‰ and -16.9 ± 0.8‰, respectively, while the mean for SBA individuals was 16.7 ± 1.1‰ and -17.3 ± 0.4‰, respectively (Table 1). NESs' isotopic niche showed that GI individuals had the largest niche area with a total area (convex hull) of 6.3‰², followed by a total area of 5.1‰² for the SBA. Moreover, the SEA_B was 1.06‰² for the SBA and 1.74‰² for GI (Figure 2; Table 1).

The posterior mean differences are summarized in Figure 3. The difference between the posterior means evidenced a high probability (P > 99%) of GI having higher isotopic values than the SBA.

Conversely, there were highly probable differences in δ^{13} C for the SDs, where GI had higher δ^{13} C values than the SBA, but not for δ^{15} N. There was also a high probability (\approx 99%) that GI had a broader isotopic niche than the SBA.

Discussion

The findings and inferences from this study are based on the isotopic analysis of pup fur, which would correspond to the foraging habits of their mothers during their post-molting migrations before parturition (Elorriaga-Verplancken et al., 2016a). Isotopic niche segregation was generally found between the NESs from GI and the SBA. This could potentially be related to distinct habitat use, despite the large proximity (ca. 270 km) between colonies as compared to the greater distances that are likely traveled during migration movements towards their foraging grounds, which could be ten times greater (about 2,000 km; Le Boeuf et al., 2000; Robinson et al., 2012).

The individuals from the GI colony presented a broader isotopic niche area (wider range of δ^{13} C values) than those from the SBA, which suggests that GI individuals have more diverse

Table 1. Mean values, standard deviation (SD), and highest and lowest values of δ^{13} C and δ^{15} N in northern elephant seals (*Mirounga angustirostris*) from Guadalupe Island and the San Benito Archipelago

Colony	Mean δ¹³C‰	$\underset{\delta^{13}C\%}{SD}$	$\begin{array}{c} Max. \ value \\ \delta^{{}^{13}}C\% \end{array}$		$ Mean \\ \delta^{_{15}}N \ \% $	SD δ ¹⁵ N ‰	$\begin{array}{c} Max. \ value \\ \delta^{{}^{15}}\!N \ \% \end{array}$	
Guadalupe	-16.9	0.8	-14.6	-18.2	17.4	1.1	19.4	14.7
San Benito	-17.3	0.4	-15.9	-18.1	16.7	1.1	19.0	13.9



Figure 2. Isotopic niches of the northern elephant seal (*Mirounga angustirostris*) colonies from Guadalupe Island (GI; black) and the San Benito Archipelago (SBA; grey). Convex hulls (dotted lines) represent the entire area; ellipses (solid line) represent the mean of Bayesian standard ellipses.



Figure 3. Forest plot of the differences in posterior means and standard deviations of each isotopic ratio, as well as in niche amplitude (SEA_B). Thin lines represent the 95% Highest Density Intervals ($HDI_{95\%}$), thick lines the $HDI_{50\%}$, and points (circles) the mean of the distribution. Labels present the mean and probability of the differences being lower than zero.

foraging habits along the inshore-offshore gradient. Meanwhile, SBA NESs showed a more restrained area with more offshore habits represented by more negative δ^{13} C values. Nevertheless, a latitudinal factor along the California Current System that could explain the values of δ^{13} C is not discarded. In this regard, CO₂ solubility increases at higher latitudes (colder waters), favoring the fixation of this ¹³C-depleted gas at the base of the trophic web (Schell et al., 1998; Burton & Koch, 1999). Therefore, this would suggest that NESs from the SBA forage in a more northerly location as compared to the NESs from GI.

For aging differences in terms of SD (δ^{13} C) and the isotopic niche area (GI > SBA) could be explained by the size of the colonies. From the ca. 22,300 NESs that encompass the Baja California population (García-Aguilar et al., 2018), ca. 54.1% correspond to GI and only ca. 32.6% correspond to the SBA (Arias-Del Razo et al., 2017). Larger populations are more likely to generate distinct foraging groups than smaller groups (Estes et al., 2003), providing a potential explanation for why GI animals were more variable than those from the SBA. In the case of the larger NES colonies in California (e.g., Año Nuevo), female adults have at least three foraging strategies as evidenced through telemetry, including inshore, offshore, and inshore-offshore (Simmons et al., 2007). The above supports the larger δ^{13} C variability by GI in this study, which obeys this horizontal gradient.

The NESs from GI presented higher $\delta^{15}N$ values than those from the SBA, with a similar SD between locations. This difference could be related to a slightly higher trophic position for the GI colony; however, the latitudinal effect throughout the California Current System, as is the case for $\delta^{13}C$, is not discarded. This effect on $\delta^{15}N$ values is due to denitrification (nitrate reduction due to microbial activity) zones, with a higher influence in middle latitudes compared to higher ones, resulting in ¹⁵N-enrichment at the base of the trophic web (Voss et al., 2001), which would suggest that the NESs from the SBA forage in a more northerly location than GI animals.

Foraging variation within the same age class has also been evidenced for the southern elephant seal (Mirounga leonina) from the Valdes Peninsula, Argentina, and the Falkland Islands (Lewis et al., 2006). These authors reported that males of this species presented a broader isotopic spectrum, creating distinct foraging groups along the inshore-offshore gradient. Additional findings regarding dietary diversification within the same sex and age class have also been suggested for other pinniped species such as the harbor seal (Phoca vitulina; Juárez-Rodríguez et al., 2020), the Galapagos sea lion (Zalophus wollebaeki; Villegas-Amtmann et al., 2008), the Antarctic fur seal (Arctocephalus gazella; Kernaléguen et al., 2016), and the Guadalupe fur seal (Arctocephalus townsendi; Juárez-Ruiz et al., 2018). This foraging diversification could be a strategy to prevent potential interindividual competition for resources (Bolnick et al., 2003; Estes et al., 2003; Vander Zanden et al., 2010).

Similarly, previous studies, such as by Aurioles-Gamboa et al. (2006), provided evidence for a segregation between NESs when comparing the SBA colony with Año Nuevo, California. Nevertheless, these authors found greater isotopic differences as compared to our study, possibly due to the considerable distance between these two colonies (approximately 1,200 km).

At the end of 2013 to early 2016, a warm anomaly of the sea surface temperature-the North Pacific heatwave or "The Blob" (Kintisch, 2015; Gentemann et al., 2016)-originated in the Gulf of Alaska and expanded southward, reaching waters off the more southern United States and Mexico. The effect of this anomaly on the findings of our study is unknown. Therefore, comparing both NES colonies over a broader time period is necessary to confirm or refute our findings. Still, the current results relate to a segregation process within the NES population, whose abundance in Mexico is declining (Elorriaga-Verplancken et al., 2015; García-Aguilar et al., 2018; Rodríguez-Rafael et al., 2023), and are significant for the current ecological knowledge of this species. This includes inferences related to an

apparent resource repartition in foraging areas in the Northeast Pacific during the post-molting migration of adult females. Amplifying our understanding of this and other species is a significant tool to inform decisions for their conservation and protect the different natural areas (two biosphere reserves) that the NESs from GI and the SBA inhabit.

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