

DIFFERENCES IN FORAGING LOCATION OF MEXICAN AND CALIFORNIA ELEPHANT SEALS: EVIDENCE FROM STABLE ISOTOPES IN PUPS

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ABSTRACT

Female northern elephant seals, *Mirounga angustirostris*, from Año Nuevo (AN) in central California feed offshore in mid-latitude waters (40°–55°N). Migratory patterns and foraging locations of seals from Mexico are unknown. Rookeries on San Benitos (SB) islands in Baja California Sur, Mexico, are ~1,170 km south of AN. Although the colonies are similar in size, seals from SB begin breeding earlier and have an earlier breeding birthing peak than seals from AN. To determine if the foraging location of seals from Mexico was similar to that of seals from California, we measured $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values in the hair of 48 suckling pups at SB and 37 from AN, assuming that their isotopic signatures reflected those of mothers' milk, their exclusive diet. The mean $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values for SB pups ($-16.1\text{‰} \pm 0.9\text{‰}$ and $17.7\text{‰} \pm 0.9\text{‰}$, respectively) were significantly higher than those for AN pups ($-17.6\text{‰} \pm 0.4\text{‰}$ and $15.6\text{‰} \pm 1.0\text{‰}$, respectively). From data on environmental isotope gradients and known behavior of SB and AN populations, we hypothesize that the isotope differences are due to females in the SB colony foraging ~8° south of seals from AN. This hypothesis can be tested by deployment of satellite tags on adult females from the SB colony.

Key words: elephant seal, *Mirounga angustirostris*, carbon, nitrogen, isotope, migration, feeding areas.

Northern elephant seals (*Mirounga angustirostris*) breed from Point Reyes (38°00'N, 123°00'W) in central California to Isla Asuncion (27°06'N, 114°17'W) off the southern coast of Mexico (Stewart *et al.* 1994). The ecology of the population at Año Nuevo (AN) State Park in California (37°07'N, 122°20'W) has been studied intensively since 1968 (*e.g.*, Le Boeuf and Kaza 1981). Adult elephant seals from AN make two migrations, during which males and females travel to different regions in the north Pacific. Males feed in coastal waters from Vancouver Island in the southeast to the Aleutian Islands in the northwest, whereas females move to, and stay in, mid-latitude waters between 40° and 55°N from several hundred to several thousand kilometers offshore (Le Boeuf *et al.* 2000). The diet of female elephant seals in these offshore locations is not well known, but diving studies indicate that they feed pelagically in the deep scattering layer. Data from gastric lavage of animals returning to AN for their spring/summer molt reveal a diet largely based on epi- and mesopelagic cephalopods, as well as a scattering of other prey (Antonelis *et al.* 1994).

Data are lacking on diet and foraging location for seals in Mexico. In 2001, the San Benitos (SB) islands (28°19'N, 115°33'W) had an elephant seal population of approximately 2,500 individuals (Aurioles-Gamboa and Hernandez-Camacho 2001). The AN and SB islands are near the latitudinal extremes of the northern elephant seal breeding distribution, separated by ~1,170 km (straight line) and 10° of latitude. The breeding season of elephant seals at SB is similar to that at AN with respect to arrival, parturition interval, duration of lactation, length of stay on land, and interval between parturition and mating, but the peak of the breeding season is earlier at SB (SB: 19 January; AN: 26 January to 2 February) and so is the peak of births (SB: 47% of births in the first two weeks of January; AN: 50% in the last two weeks of January) (Le Boeuf *et al.* 1972, Le Boeuf and Panken 1977, Le Boeuf and Reiter 1988, García-Aguilar 2004).

The aim of this study was to address whether SB females feed in the same general area and at the same trophic level as seals from California. There are no studies of the diet, migratory, or diving behavior of elephant seals at the southern edge of their range. Traveling to the same foraging grounds as the seals that breed in the north has important consequences, requiring that the Mexican seals either travel at a faster rate or spend less time feeding in order to adhere to the fixed annual schedule of breeding, feeding, molting, and feeding (Le Boeuf and Laws 1994).

We sought to gain insight into the foraging behavior of Mexican elephant seals through study of their natural variation in stable carbon and nitrogen isotope values ($\delta^{13}\text{C}$ and $\delta^{15}\text{N}$, respectively).¹ Stable isotopes can provide information on migration and foraging location and trophic level of prey consumed by marine mammals (*e.g.*, Rau *et al.* 1992, Hobson *et al.* 1997, Walker and Macko 1999, Kurlle and Worthy 2002). Burton and Koch (1999) and Burton *et al.* (2001) measured $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values in bone collagen in four northeastern Pacific pinniped species to assess isotopic gradients with latitude and distance from the shore. $\delta^{13}\text{C}$ values in nearshore feeders (*e.g.*, harbor seals) were ~2‰ higher than those in offshore feeders (*e.g.*, northern fur seals or female elephant seals), with intermediate values in California sea lions. Both $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values were 1‰–2‰ lower in high- vs mid-latitude feeders.

¹ $\delta^{13}\text{C}$ or $\delta^{15}\text{N} = 1,000[(R_{\text{sample}}/R_{\text{standard}}) - 1]$, where R_{sample} and R_{standard} are the $^{13}\text{C}/^{12}\text{C}$ or $^{15}\text{N}/^{14}\text{N}$ ratios of the sample and standard, respectively. The standards are Vienna Pee Dee Belemnite limestone (V-PDB) for carbon and atmospheric N_2 for nitrogen. The units are expressed as parts per thousand or per mil (‰).

Because these isotopic differences in top carnivores mirror spatial isotopic gradients in particulate organic matter, Burton and Koch (1999) and Burton *et al.* (2001) argued that geographic differences in isotope values of primary producers (created by differences in productivity, rates of photosynthesis, physical mixing, and other processes) cascade upward to label the top of the food web. Recent work on California sea lions in the Gulf of California indicates even greater ^{13}C and ^{15}N enrichments in these lower latitude populations (Aurióles-Gamboa *et al.* 2004).

Here, we use isotope values in pups to assess similarities and differences in the foraging patterns of their mothers. We compare $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values from the hair of ~ 3 -wk-old suckling elephant seal pups sampled in SB and AN during the 2002 breeding season. We assume that pup hair will have isotopic compositions that reflect those of mothers' milk, the exclusive diet of suckling pups, which in turn will reflect the mothers' diets over the preceding few months. Pups may not have exactly the same isotope values as their mothers because, if hair is biosynthesized during the nursing period, isotope ratios may be subtly shifted from mother to pup by isotope discriminating processes. We argue that there is no reason to expect differences in these processes between pups from the SB and AN colonies.

METHODS

Sample Collection and Processing

We sampled hair from suckling pups, rather than from adult females, because of their accessibility, and ease of capture, which allowed us to obtain a large sample size necessary for statistical testing. A total of 22 and 26 hair samples were collected from pups at San Benitos West (SBW) and San Benitos Center (SBC) islands on 21 and 22 January 2002, respectively. A total of 37 pup hair samples were collected on 8, 11, and 19 March 2002 at AN. Pups varied between 2 and 3 wk of age and included both sexes.

Hair samples were collected with scissors at the base of the hair without removing the follicle and then rinsed with distilled water to eliminate salt and sand residues. The samples were washed again with distilled water and dried at 80°C for 12 h to eliminate excess moisture.

Lipids were removed using a microwave-assisted extraction (model 1000 MARS-5, CEM Microwave Technology Ltd., Matthews, NC.) utilizing 25 mL of a (1:1) solution of chloroform/methanol in scintillation vials. The extraction continued for a total of 20 min to reach a final temperature of $\sim 100^\circ\text{C}$. The samples were then placed in a drying oven at room temperature for 12 h to allow all solvents to volatilize. Dried samples were cut finely with sterilized scissors and homogenized in an agate mortar.

All samples were weighed in tin micro-capsules (8×5 mm) to a target size of 1.2 ± 0.1 mg of hair. The micro-capsules were sealed.

Analysis of Samples

Nitrogen and carbon isotope ratios of the hair samples were determined by a continuous flow mass spectrometer (20–20 PDZ Europa) coupled to an element analyzer (PDZ Europa ANCA-GSL) at the Stable Isotope Laboratory at the University of California, Davis. Analytical error for laboratory standards analyzed along with these samples (measured as ± 1 standard deviation) was $\pm 0.2\%$ for both $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values.

RESULTS

Because pups at AN were sampled over a longer time period (13 d) than at SB (2 d), we were concerned that ontogenetic differences between population samples in factors such as length of the nursing period or molting might be responsible for isotopic differences. $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values decreased from the earliest (AN-1) to the latest sampling (AN-3) (Fig. 1), but the differences were not significant for either $\delta^{13}\text{C}$ or $\delta^{15}\text{N}$ (Kruskal–Wallis, (3) $12_{\text{AN-1}}$, $20_{\text{AN-2}}$, $4_{\text{AN-3}}$ = 2.13_{carbon} , and 39_{nitrogen} , respectively; $\chi^2 = 50.99$, $P < 0.05$, $df = 36$).

The $\delta^{13}\text{C}$ values for samples from SBW and SBC were bimodal (Fig. 2). The $\delta^{15}\text{N}$ values were not as strongly bimodal, but they still did not appear Gaussian (Fig. 2). As a consequence, we tested for differences with a nonparametric Mann–Whitney U test. Differences in median $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values between SBW and SBC were not significantly different (for $\delta^{13}\text{C}$, $U = 367.5$, $P > 0.09$; for $\delta^{15}\text{N}$, $U = 349.5$, $P > 0.18$). As a consequence, we combined data from the two adjacent islands referring to both as SB in subsequent analyses.

The frequency distributions of $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values for SB and AN differed (Fig. 2). Mean $\delta^{13}\text{C}$ values (\pm one standard deviation) were higher for SB pups ($-16.1\text{‰} \pm 0.9\text{‰}$) than AN pups ($-17.6\text{‰} \pm 0.4\text{‰}$). The mean $\delta^{15}\text{N}$ value was also higher at SB ($17.7\text{‰} \pm 0.9\text{‰}$) than at AN ($15.6\text{‰} \pm 1.0\text{‰}$). Because the sample distributions were not Gaussian and variance in $\delta^{13}\text{C}$ values differed between samples, we compared differences between populations with a U test. The differences in median isotope values between these populations were highly significant (for $\delta^{13}\text{C}$, $U = 1,604$, $P < 0.001$; for $\delta^{15}\text{N}$, $U = 1,607$, $P < 0.001$).

DISCUSSION

Ontogenetic Trends in Isotope Values from Pups

To assess maternal foraging habits through isotopic analysis of nursing young, we must evaluate the magnitude of isotopic discrimination from mother to pup, and consider how discrimination might change during the course of nursing and weaning or differ among colonies. Current knowledge of mother-to-pup isotope discrimination in pinnipeds is weak. In humans, where individuals have been tracked from birth, neonates have $\delta^{15}\text{N}$ isotope values similar to their mothers. The $\delta^{15}\text{N}$ values of nursing young rise by $\sim 2.5\text{‰}$ and then fall to values similar to those for adults after weaning (Fogel *et al.* 1989, 1997). ^{15}N -enrichment in young age classes has been documented in many fossil human populations, and is commonly used to assess weaning age (*e.g.*, Katzenberg *et al.* 1993, Schurr 1997, Wright and Schwarcz 1999, Fuller *et al.* 2003). In other species, where different age classes or dental growth layers have been examined, neonates sometimes have higher $\delta^{15}\text{N}$ values than their mothers, but nursing young are always ^{15}N -enriched and these high values only drop after weaning (Balasse *et al.* 2001, Polischuk *et al.* 2001). Among pinnipeds, ^{15}N -enrichment in early age classes has been reported for fossil northern fur seals (Burton *et al.* 2001), extant Steller sea lions (Hobson and Sease 1998), and California sea lions (Aurioles-Gamboa *et al.* 2004) and ranges from 1‰ to 3‰ relative to adult values. ^{15}N -enrichment during nursing is thought to reflect trophic level isotope fractionation between mother's milk and infant tissues, although some question this conclusion (Jenkins *et al.* 2001).

The direction and magnitude of ontogenetic carbon isotope trajectories are less consistent. In a number of mammals, tissues from young animals or early age classes

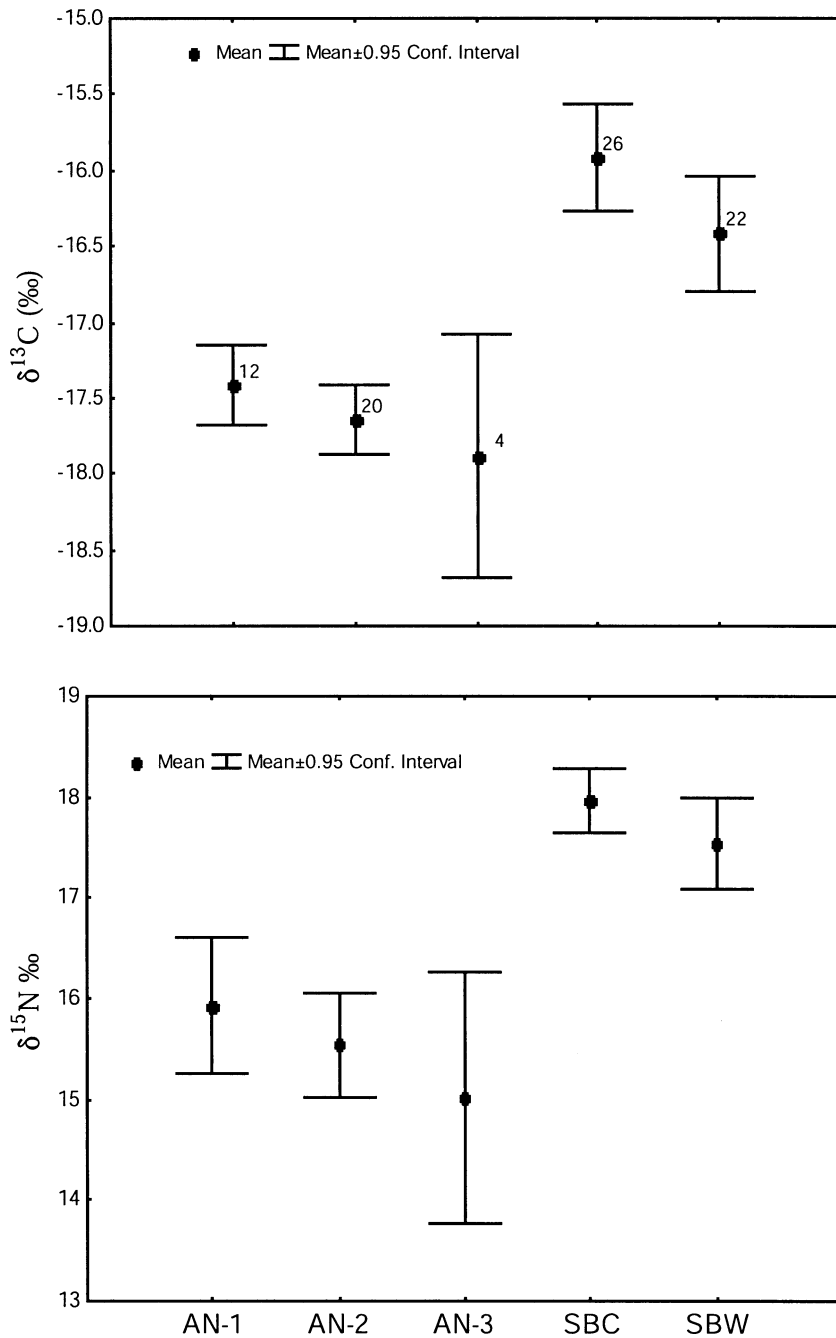


Figure 1. Mean and confidence intervals for $\delta^{13}\text{C}$ (top) and $\delta^{15}\text{N}$ values (below) at the three locations of hair sample collection (SBC = San Benito Center, SBW = San Benito West). AN-1, collected 8 March 2002; AN-2, collected 11 March 2002; AN-2, collected 19 March 2002.

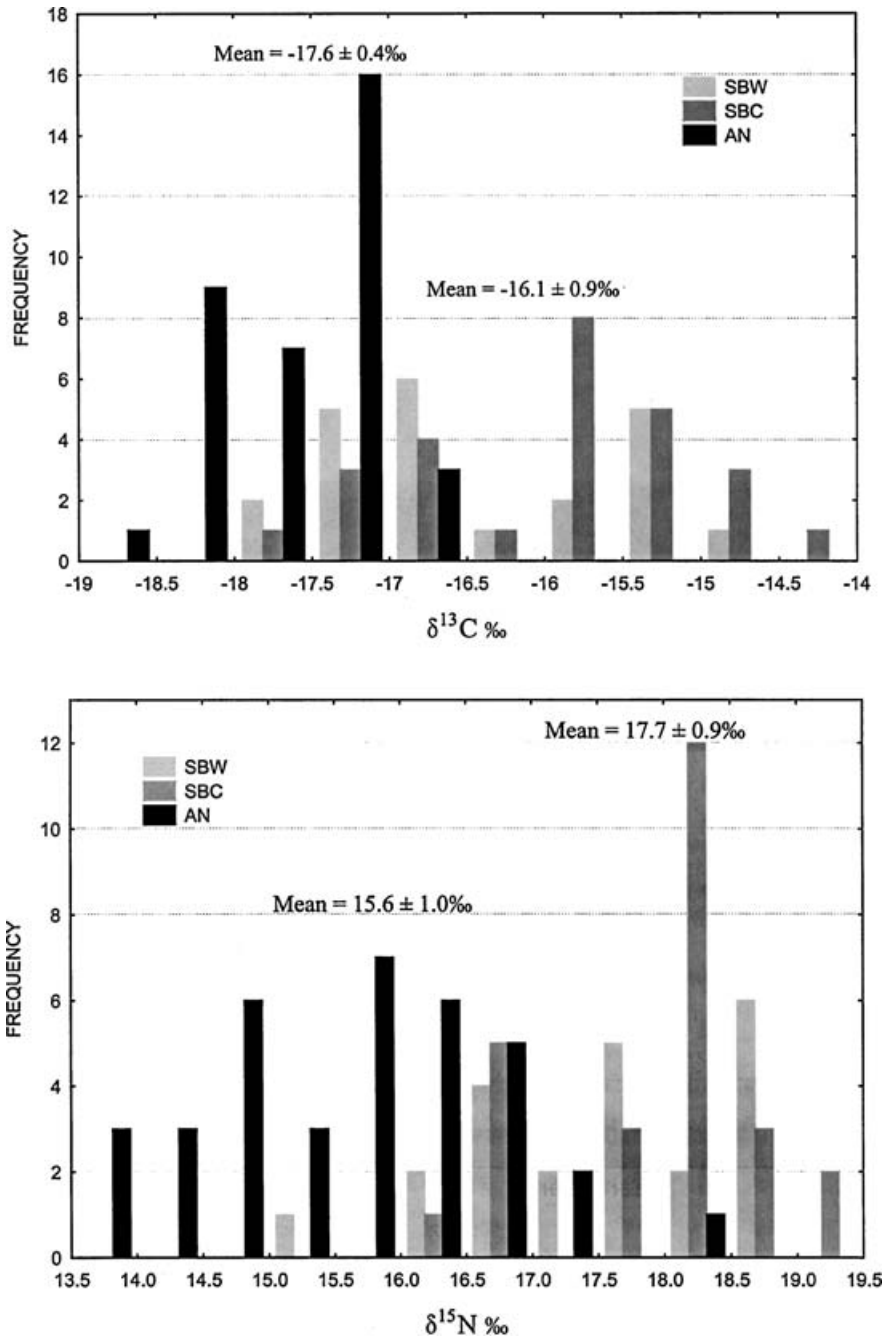


Figure 2. Frequency distributions of $\delta^{13}\text{C}$ (top) and $\delta^{15}\text{N}$ (below) values for elephant seal pup's hair collected at San Benitos (SBC and SBW) and Año Nuevo Reserve (AN) during the breeding season 2002. Means above the $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ graphs represent the overall values for AN and both SB colonies combined.

have lower $\delta^{13}\text{C}$ values than older animals (Polischuk *et al.* 2001, Witt and Ayliffe 2001), but in ancient human populations, the pattern is either reversed (Fuller *et al.* 2003) or inconsistent from individual to individual (Wright and Schwarcz 1999). Work on incremental laminations in sea lion teeth suggests that nursing young have $\delta^{13}\text{C}$ values $\sim 2\%$ lower than older animals (Hobson and Sease 1998; Aurioles, unpublished data). Similarly, bones from young modern Cape fur seals and preweaned fossil northern fur seals have $\delta^{13}\text{C}$ values 1% lower than other age classes (Lee-Thorp *et al.* 1989, Burton *et al.* 2001). Lower $\delta^{13}\text{C}$ values in nursing animals probably occur when the milk is extremely rich in lipids, which are ^{13}C -depleted relative to proteins.

Given these considerations, the gradual temporal decrease in the $\delta^{13}\text{C}$ values of nursing pups at AN is reasonable; as nursing progresses, a greater and greater fraction of the carbon pool in a pup's body is derived from ^{13}C -depleted milk rather than more ^{13}C -enriched tissue formed in utero. The drop in $\delta^{15}\text{N}$ values, in contrast, does not match expectations. We would have expected the $\delta^{15}\text{N}$ values of nursing pups to be either stable or rising with time since birth, not decreasing. As a consequence, we suspect that the small, statistically insignificant $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ shifts among individuals sampled on different days at AN reflect subtle differences "imported" from their mothers that are related to differences in feeding location.

A possible explanation for differences found in this study is that they reflect differences in the mother-to-pup isotope discrimination. As females fast during birth and lactation, differences in the availability and use of endogenous fat stores *vs.* protein might lead to differences in the isotope composition of milk. Lipids are ^{13}C -depleted relative to other body tissues by 4%–6%, so we might suspect that a higher ratio of endogenous fat-to-protein in milk synthesis would lead to lower milk $\delta^{13}\text{C}$ values and lower pup $\delta^{13}\text{C}$ values. If AN females have greater endogenous fat stores than SB females (*i.e.*, a much better body condition at the start of lactation), pups at AN might have lower $\delta^{13}\text{C}$ values than SB pups, even if females from both regions consumed the same diets. The $\delta^{13}\text{C}$ difference between AN and SB pups, however, is large (1.5%). Fat remobilization, and presumably overall body fat levels, would have to be much higher at AN than at SB (*i.e.*, 25%–40% higher) to explain such low values. Furthermore, all the nitrogen in milk, and consequently pup hair, must come from catabolism of maternal proteins. Even if we accept that AN females have a lower rate of protein catabolism to fuel milk synthesis, there is no reason to expect this to lead to lower milk $\delta^{15}\text{N}$ values. Although no data exist on differences in body condition between AN and SB females, a substantially lower condition for the SB population is unlikely, given that the population weans its young as rapidly as the AN population. In summary, we reason that there is insufficient evidence to attribute the isotopic differences between SB and AN pups to this factor.

Differences in Maternal Foraging

If we accept that the differences in isotope values between pups at SB and AN reflect differences in the foraging habits of adult females, there are three hypotheses that can explain these differences: (1) adult females from the two regions travel to the same areas but feed on different types of prey, (2) females from the two regions feed on ecologically equivalent prey items but feed in different areas, and (3) females from the two regions feed on different types of prey in different regions. The first hypothesis implies that females from SB feed on higher trophic level prey because they have higher $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values. Under this scenario, SB females would be under greater physiological stress than AN females, because SB females would have

to migrate greater distances to breed. This would take longer, and they would spend a shorter amount of time on the feeding grounds. Moreover, their prey is likely to be less abundant, given the decreasing trend of biomass at upper trophic levels.

There are examples of individuals of the same species feeding in the same region on different types of prey such as resident *vs.* transient killer whales, who feed on fish and marine mammals, respectively, or different individual sea otters in populations in California. Yet in the case of killer whales, pod-level differences in foraging ecology are presumably maintained by social interactions and learning between pod members (Ford *et al.* 1999). In the case of otters, differences in feeding behavior are also transmitted along matriline, but there is great diversity in feeding ecology among individuals in a single region (Estes *et al.* 2003). The situation with elephant seals is different from both these cases. If the dietary hypothesis is correct, then animals that segregate during the breeding season would have to exhibit similar behaviors in distant foraging zones. Yet elephant seal females leave their pups at weaning, long before the pups leave the rookery, so it is hard to understand how differences in diet choice while using a distant, common feeding area would come to be sorted by rookery area. In summary, for both energetic and behavioral reasons, it is unlikely that SB and AN females forage in the same region on different prey.

The second and third alternatives suggest that females from the two regions have different feeding grounds. The foraging zone of female elephant seals from AN, California, as determined by satellite tracking, is shown in Figure 3 (Le Boeuf *et al.* 2000). AN adult female seals concentrate in the region between 40° and 50°N, extending several thousand kilometers offshore. $\delta^{15}\text{N}$ values of particulate organic matter from sediment traps are available from offshore regions in the major boundary currents along the northeast Pacific (Fig. 3), and they show a trend of increasing values from north (off British Columbia, 2.8‰) to south (near the tip of the Baja California Peninsula, 10.2‰) (Table 1). Although few data are available from farther offshore, they support a broad north–south gradient in nitrogen isotope values (Saino and Hattori 1987). Using the $\delta^{15}\text{N}$ values from the boundary currents and their latitudinal positions, a statistically significant correlation between these two variables was obtained ($r = -0.91$, $P = 0.001$, $df = 7$; $\text{LAT} = 66.149 - 4.074 \times \delta^{15}\text{N}_{\text{POM}}$), indicating an approximate 4° decrease in latitude for every 1‰ increase in $\delta^{15}\text{N}_{\text{POM}}$.

If the average feeding latitude for elephant seal females from AN is ~45°N (Fig. 3), we can estimate the latitude at which the SB population is feeding using the difference in $\delta^{15}\text{N}$ values between SB and AN seals and the slope of the relationship between latitude and northeast Pacific sediment $\delta^{15}\text{N}$ values. As SB seals have $\delta^{15}\text{N}$ values ~2‰ higher than AN seals, we estimate that they forage 8° farther south, yielding an average latitude for SB foraging at 37°N (Fig. 3). Because there is overlap in $\delta^{15}\text{N}$ values between SB and AN elephant seals (Fig. 2), a corresponding overlap in the feeding grounds would also be expected between the southern boundary of AN female feeding ground and northern boundary of the SB females (Fig. 3).

Most of the AN $\delta^{15}\text{N}$ values (92%) fall within the range from 14‰ to 17‰. Using the slope established from sediment data, this 3‰ range converts into latitudinal range of ~12°. This fits the known latitudinal feeding range of AN elephant seal females very well as very few females venture above 53°N (Fig. 3). Similar criteria applied to SB seals (94% of $\delta^{15}\text{N}$ values within 16‰–19‰) suggest that their feeding area should be between 43° and 31°N (Fig. 3). This hypothesized difference in foraging zones between SB and AN elephant seals is contingent on two assumptions: (1) no difference in mother-to-pup isotope discrimination, and (2) no major difference in trophic level of prey taken by SB and AN populations.

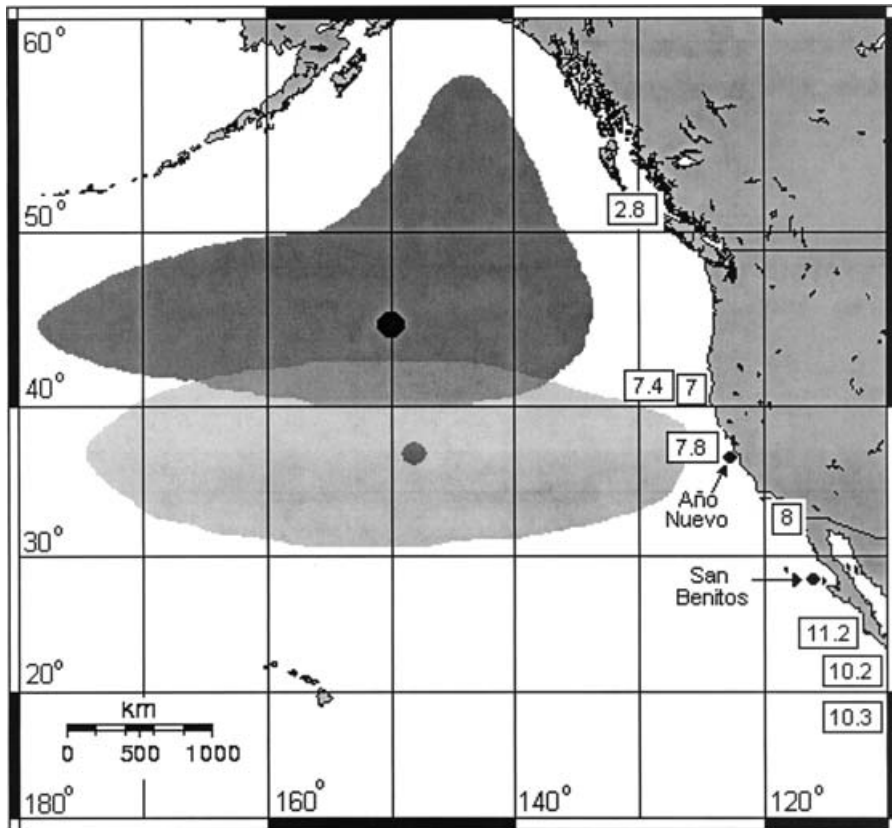


Figure 3. Geographic distribution of AN northern elephant seal females during migration in the northeast Pacific (darker area) and hypothetical center of distribution for the feeding ground (45°N) based on satellite tracking and TDRs (Le Boeuf *et al.* 2000). Lighter area and its center represents the feeding ground for SB elephant seal females as suggested by $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values and comparison with latitudinal variations in $\delta^{15}\text{N}$ from sediments ($\delta^{15}\text{N}$ values shown along the coast in ‰).

Data from northeast Pacific pinnipeds that forage at different latitudes suggest that $\delta^{13}\text{C}$ values increase from north to south. Thus, the observation that SB elephant seals have higher $\delta^{13}\text{C}$ values than AN seals is consistent with our conclusions regarding differences in latitudinal foraging zone. Data are available on the $\delta^{13}\text{C}$ value of particulate organic matter from sites in the northeastern Pacific Ocean (Fig. 3, Table 1). A statistically significant correlation between $\delta^{13}\text{C}_{\text{‰}}$ (X) and latitude (Y) was obtained ($r = -0.87$, $P = 0.005$, $df = 7$; $\text{LAT} = -76.904 - 5.168 \times \delta^{13}\text{C}_{\text{POM}}$), indicating a $\sim 5^\circ$ decrease in latitude for every 1‰ increase in $\delta^{13}\text{C}_{\text{POM}}$. As SB seals are $\sim 1.5\text{‰}$ ^{13}C -enriched relative to AN seals, this regression would suggest that they feed $\sim 7.8^\circ$ farther south. This value is indistinguishable from the value estimated using $\delta^{15}\text{N}$ values.

SB seals have a wider range of $\delta^{13}\text{C}$ values (3.3‰) than AN seals (1.7‰). Greater variability for SB seals could be due to the fact that we are combining data from

Table 1. Locality information, isotope values, and citations for marine organic matter.

Site	Latitude (°N)	Longitude (°W)	Depth (m)	Type	$\delta^{13}\text{C}$ (‰)	$\delta^{15}\text{N}$ (‰)	Reference
09	17	107	130	trap ^a	-18.4	10.3	Voss <i>et al.</i> (2001)
06	20.5	110.5	130	trap ^a	-20.8	10.2	Voss <i>et al.</i> (2001)
03	23.5	113.5	130	trap ^a	-20.0	11.2	Voss <i>et al.</i> (2001)
S-1	28	155	surface	filter	-20.3	—	Rau <i>et al.</i> (1982)
S-2	33	120	surface	filter	-20.5	—	Rau <i>et al.</i> (1982)
San Pedro	33.55	118.50	500	trap ^b	—	8	Altabet <i>et al.</i> (1999)
S-3	34	119	surface	filter	-20.1	—	Rau <i>et al.</i> (1982)
M2	36.7	122.4	surface	filter ^c	-21.3	—	Rau <i>et al.</i> (2001)
Monterey	36.75	122.05	450	trap ^d	—	7.8	Altabet <i>et al.</i> (1999)
Nearshore	42.1	125.75	1,500–1,800	trap ^e	—	7	Kienast <i>et al.</i> (2002)
Midway	42.2	125.6	500–2,500	trap ^e	—	7.4	Kienast <i>et al.</i> (2002)
OSP	50	135	200	trap ^b	-24.6	2.8	Wu <i>et al.</i> (1999)

^a Traps were deployed for 33–38 h. Data from offshore sites with highest sedimentation rates.

^b Weighted average for biweekly trap samples for 6 mo.

^c Weighted average for data from 4 yr.

^d Weighted average for biweekly trap samples for 3.25 yr.

^e Average for multiple traps left open for 6 mo.

^f Weighted average for 19 (N) or 20 (C) traps spanning 1 yr.

animals on SBW and SBC. The greater $\delta^{13}\text{C}$ variability in the southern population suggests that they forage on a larger range of carbon sources. There are significant $\delta^{13}\text{C}$ differences (1‰–2‰) between pinnipeds that feed in nearshore/coastal *vs* offshore/pelagic habitats (Burton and Koch 1999). Thus the greater $\delta^{13}\text{C}$ range for the SB population might reflect a wider longitudinal feeding area for the SB female elephant seals that includes inshore and offshore habitats, so its center of distribution would be more coastal than to AN females (Fig. 3). It is interesting to note that some AN females also feed nearshore in the Gulf of Alaska (Le Boeuf *et al.* 2000, Fig. 3). Potential near-offshore differences in dietary $\delta^{13}\text{C}$ values complicate the use of this isotope system to estimate the latitude of foraging. Because $\delta^{15}\text{N}$ values do not differ between nearshore and offshore zones, these longitudinal differences in foraging should not bias our estimates of latitudinal foraging zones discussed above.

The distance of migration between our estimated center of foraging zone based on isotopes and the breeding site of SB seals would be $\sim 3,150$ km in a straight line. If these females had to travel to the center of the AN female feeding ground, the distance traveled would be $\sim 3,550$ km or 400 km more than seals from AN. This difference is significant in distance and time for migration when considering a round trip and that AN females alternate travel and foraging. In terms of energy, it seems reasonable to consider a feeding ground for SB females located, on average, 8° south of that known for AN elephant seal females. The hypothesis can be tested by the deployment of satellite tags on females from SB, a study that we initiated in summer 2005.

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