

STABLE ISOTOPE DIFFERENCES BETWEEN SEA LIONS (*ZALOPHUS*) FROM THE GULF OF CALIFORNIA AND GALÁPAGOS ISLANDS

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Spatial or temporal isotopic variation, or both, in primary producers must be controlled for when investigating the foraging and trophic ecology of top consumers using isotopic data. Populations of the sister species *Zalophus californianus* and *Z. wollebaeki* are separated by approximately 3,350 km in the eastern tropical Pacific Ocean, which prevents contact and mixing between the 2 populations. To explore differences in trophic ecology between these species, as well as the impact of differences in baseline food-web isotope values between the 2 regions, we compared conventional dietary data derived from analyses of scat contents to isotopic values of hair collected from pups at 13 rookeries in the Gulf of California (*Z. californianus*) and 11 rookeries on the Galápagos Islands (*Z. wollebaeki*). Mean ± 1 SD $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values were $-15.9\text{‰} \pm 0.5\text{‰}$ and $21.8 \pm 0.7\text{‰}$ in the Gulf of California, whereas for the Galápagos they were $-14.5\text{‰} \pm 0.5\text{‰}$ and $13.1\text{‰} \pm 0.5\text{‰}$. Examination of scat data suggested overlap in 6 of the 10 most common prey consumed by sea lions. Trophic level (TL) derived from scat analysis was positively related with $\delta^{15}\text{N}$ values for the Gulf of California rookeries, but estimates of TL for each region were similar (4.4 for Galápagos and 4.1 for Gulf of California), suggesting that foraging behavior makes a limited contribution to the large difference in $\delta^{15}\text{N}$ value between the 2 populations. Particulate organic matter $\delta^{15}\text{N}$ values near the Galápagos Islands are $\sim 5.3\text{‰}$ lower than values in the Gulf of California, suggesting that the baseline food-web values account for approximately two-thirds of the observed difference in pup hair $\delta^{15}\text{N}$ values. This study may provide clues to better understand isotopic values of marine top predators migrating across the eastern Pacific Ocean.

Key words: carbon, feeding habits, nitrogen, sea lions, stable isotopes, trophic level

Natural variation in stable carbon and nitrogen isotope values ($\delta^{13}\text{C}$ and $\delta^{15}\text{N}$, respectively) provide information on habitat use and foraging ecology in marine mammals (Hobson et al. 1997; Rau et al. 1983; Walker and Macko 1999). Burton and Koch (1999) and Burton et al. (2001) measured $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values in bone collagen in 4 northeastern Pacific pinniped species to assess isotopic gradients with latitude and distance from shore. The $\delta^{13}\text{C}$ values in nearshore

foragers (e.g., harbor seals [*Phoca vitulina*]) were approximately 2‰ higher than those in offshore foragers (e.g., northern fur seals [*Callorhinus ursinus*] or northern elephant seals [*Mirounga angustirostris*]), with California sea lions (*Zalophus californianus*) having intermediate values. Both $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values were 1–2‰ lower in high-latitude (45–50°N) versus mid-latitude (30–40°N) offshore foragers. Newsome et al. (2007) documented that these spatial isotopic differences were detectable through much of the last 5,000 years, suggesting that the underlying oceanographic factors contributing to regional isotopic differences among animals were stable features of the North Pacific, at least since the end of the last glacial period. These studies interpreted isotopic differences in top carnivores as chiefly reflecting geographic

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differences in the isotopic composition of phytoplankton at the base of the food web ultimately related to differences in productivity and vertical mixing of the water column.

Oceanographic studies have shown that there is a significant correlation between the $\delta^{13}\text{C}$ values of particulate organic matter (POM) or phytoplankton with latitude (or water temperature) at a global scale (Goericke and Fry 1994). Spatial patterns in the $\delta^{15}\text{N}$ values of POM and phytoplankton are more complex, reflecting contributions from different potential sources of nitrogen (deepwater nitrate, nitrate from zones of denitrification, continental inputs, and nitrogen fixation) and differences in nitrate utilization (reviewed in Montoya 2007). A review of isotope data from sediment traps and surface sediment cores along the eastern Pacific coast suggested a statistically significant 1‰ increase in $\delta^{13}\text{C}_{\text{POM}}$ value for approximately every 5° decrease in latitude, and 1‰ increase in $\delta^{15}\text{N}_{\text{POM}}$ values for approximately every 4° decrease in latitude (Auriolas-Gamboa et al. 2006). They used these environmental isotopic trends to explain differences in the $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ values of hair from elephant seals from Año Nuevo (California) and from San Benito Islands (Baja California, Mexico). Values at Año Nuevo relative to San Benito suggested a separation of foraging areas between the populations of approximately 8° in latitude.

These studies and others on other taxa (e.g., Jennings et al. 2008) reveal that significant differences in isotope values may occur among individuals in different populations that feed on similar prey but forage in different regions. Distinct dietary preferences also may lead to differences in isotopic values, however, because predator tissues become enriched in ^{13}C and especially ^{15}N compared to those of their prey (i.e., trophic fractionation—reviewed in Koch 2007). In pinnipeds, ^{13}C - and ^{15}N -enrichment in keratin-rich tissues such as hair or nails has been estimated to be roughly +2–3‰ (Hobson et al. 1996; Lesage et al. 2002), in the range seen for other mammals (Kelly 2000).

Determining the relative influence of diet versus location on the isotopic composition of consumers in marine ecosystems is vital to improving our ability to use isotopes to understand the foraging and migratory behavior of marine mammals as well as wide-ranging fish and seabirds with marine diets. To explore the impact of these factors, we collected hair samples from 1- to 2-month-old sea lion pups in the Gulf of California and Galápagos Islands (*Zalophus californianus* and *Zalophus wollebaeki*, respectively) when they were nutritionally dependent on their mother's milk for nourishment. Thus, a pup's hair should reflect the average isotopic composition of prey ingested by its mother over the preceding several months. Mother-to-pup fractionation factors for California sea lion hair are estimated to be 0.8‰ for $\delta^{13}\text{C}$ and 2.1‰ for $\delta^{15}\text{N}$ (Porrás-Peters et al. 2008), and we assume the same fractionations apply to Galápagos sea lions.

A controversy exists regarding the status of species or subspecies within the genus *Zalophus*. Sivertsen (1953) described the Galápagos sea lions as a species that is distinct from *Z. californianus*, noting that several skull measurements were significantly different. However, some authors consider

Galápagos sea lions as a subspecies of *Z. californianus* (Brunner 2004; Rice 1998). Recent morphological (Zavaleta-Lizarraga 2003) and genetic (Schramm et al. 2009; Wolf et al. 2007) analyses suggest that the differences between populations of *Zalophus* from the Galápagos and the Mexican-Californian region merit their status as separate species. We follow that conclusion here, and consider *Z. californianus* and *Z. wollebaeki* valid sister species.

Sea lion rookeries from the Gulf of California and Galápagos Islands are separated by >24° of latitude and a belt of tropical waters of approximately 3,350 km (Fig. 1). There are pronounced differences in oceanographic conditions between the 2 localities. The Gulf of California is an enclosed basin with high evaporation rates (Álvarez-Borrego 1983) and relatively high $\delta^{15}\text{N}$ values at the base of the food web due to enhanced in situ denitrification and the influence of the highly denitrified intermediate waters of the eastern tropical Pacific Ocean that are carried northward by the Mexican Occidental Current (Altabet et al. 1999; Beier et al. 2003; Voss et al. 2001). Denitrification occurs in relatively stratified water bodies within the oxygen minimum zone, for example, between 22°N, 105°W and 15°N, 110°W along the Pacific coast of Mexico (Voss et al. 2001). Denitrification results in ^{15}N -enrichment of residual nitrate that eventually upwells to the surface and is used by primary producers (Altabet et al. 1999). On the other hand, the areas adjacent to the Galápagos Islands experience open ocean conditions (approximately 950 km offshore) characterized by relatively low $\delta^{15}\text{N}$ values at the base of the food web (Farrell et al. 1995). There is enhanced productivity near the Galápagos, however, resulting from close proximity to the Peruvian Current and from upwelling produced by an "island-mass effect" associated with the flow of the Equatorial Undercurrent (also called Cromwell Current) over the western margin of the archipelago (Feldman 1986; Palacios 2002).

In this study, we evaluate the relative influence of feeding habits (trophic level [TL]) versus natural variations in isotopic values at the base of the food web on the observed differences in $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ values of populations of these sister species of *Zalophus*. Given likely isotopic differences at the base of the food web between marine ecosystems in the Gulf of California and Galápagos, we expect that the isotopic differences between populations of *Zalophus* will principally be driven by differences in oceanography, with a minor influence of diet. We compare dietary data from scat analysis and $\delta^{15}\text{N}$ values from sediment and potential prey from the Gulf of California and Galápagos Islands to estimate their relative influence on $\delta^{15}\text{N}$ values in sea lion tissues. The degree of how each of these 2 factors affect isotopic values of marine top predators has relevance for interpreting isotopic differences of species that experience large migrations across the eastern Pacific area, such as sperm whales, dolphins, tuna, and others.

MATERIALS AND METHODS

Field sampling.—Thirteen and 11 sea lion rookeries were sampled in the Gulf of California and Galápagos Islands,

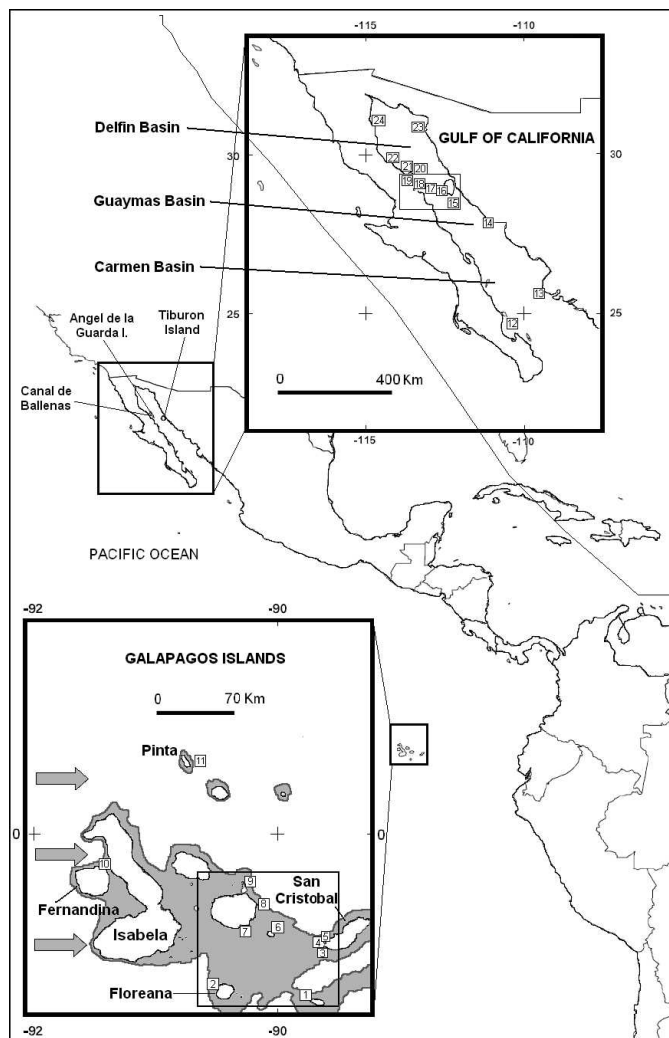


FIG. 1.—Location of sea lion rookeries in the Gulf of California (*Zalophus californianus*) and Galápagos Islands (*Zalophus wollebaeki*) where pup hair was sampled. Numbers correspond to locations listed in Table 1. Rookeries in the small square in the central Gulf of California occupy an area of strong tidal mixing. Arrows in the Galápagos map show the direction of the Equatorial Undercurrent (Cromwell Current) and rookeries in the inner square occupy the extended continental shelf of the central and southern archipelago represented by the shaded area.

respectively (Fig. 1). Approximately 10 pups of both sexes were sampled at each rookery, with a maximum sample size of 29 individuals (Isla Lobos, Galápagos Islands) and a minimum of 4 individuals (Fernandina, Galápagos Islands). Samples were collected during the breeding seasons of 2002 and 2004 in the Gulf of California (July) and 2002, 2003, and 2004 in the Galápagos Islands (February–March). Hair samples from pups and scats were collected in the same areas where adult females are the most abundant sex and age category, followed by pups. Both categories comprise roughly 80% of the total population at each site. Each pup was measured for total length (tip of snout to tip of tail) with a flexible tape (0.5 cm of precision) and weighed with a manual scale (0.05 kg of precision). We measured pups to ensure that their approximate age was equivalent among rookeries and regions, assuming

similar individual growth rates among rookeries within each region. We estimated the age of the pups using a calculation considering the weight at birth and the growth rate for each region. For Galápagos pups, the average weight at birth (males: 7 kg, females: 6 kg) and the growth rate (115 g/day) were based on Trillmich and Wolf (2007). For the Gulf of California pups we used average weight at birth (7 kg) and pup growth rate (160 g/day) from García-Aguilar and Aurióles-Gamboa (2003).

Sample processing and isotope analysis.—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. In the laboratory, hair samples were washed again with distilled water and dried at 80°C for 12 h. Lipids were removed using a microwave-assisted extraction system (microwave oven model 1000 MARS 5 × CEM) using 25 ml of a 1:1 solution of chloroform:methanol in scintillation vials. The extraction continued for 20 min and reached a final temperature of approximately 100°C. Samples were placed in a drying oven at room temperature for 12 h to allow all solvents to volatilize. Dried samples were cut with sterilized scissors and homogenized in an agate mortar.

Dried hair samples (approximately 1.2 ± 0.1 mg SD) were sealed in tin boats and analyzed using an elemental analyzer interfaced with a 20-20 PDZ Europa gas source mass spectrometer (Sercon Ltd., Crewe Trade Park, Gateway, Cheshire, United Kingdom). Results are expressed as δ values, such that $\delta^{13}\text{C}$ or $\delta^{15}\text{N} = [(R_{\text{sample}}/R_{\text{standard}}) - 1] \times 1,000$, 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 for carbon and atmospheric N_2 for nitrogen. The units are expressed as parts per thousand or per mil (‰). Repeated measurements of a gelatin standard yielded a $1\sigma < 0.2\text{‰}$ for both $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values.

Estimates of TL.—Trophic level estimates were based on the relative proportions of different types of prey that were identified by scat analysis. The TL (the relative position of a species within the food web) varies from 1 for POM (Hobson et al. 1995) to about 4.6 for orcas (*Orcinus orca*—Pauly et al. 1998) to 5–5.5 for polar bears (*Ursus maritimus*—Hobson et al. 1995, 2002). Among pinniped species, TL usually ranges between 3.8 and 4.4 (Pauly et al. 1998). We estimated TL using the algorithm of Christensen and Pauly (1992):

$$\text{TL} = 1 + \left(\sum_{i=1}^n \text{IIMP}_{ij} \right) (\text{TL}_i),$$

where IIMP_{ij} is the proportion of the i th prey in the diet at rookery j , TL_i is the TL of the i th prey, and n is the number of prey species in the diet at rookery j . In this approach, detritus and primary producers are defined as having a TL of 1. TLs of the fish are from Fishbase (www.fishbase.org) and those of the cephalopods from the literature (Passarella and Hopkins 1991; Pauly et al. 1998). Because the areas where scat was sampled were dominated by adult females, TL estimates should reflect the feeding habits of this category of the population. All TL estimates were made from scat samples collected during the

breeding season, when pup hair also was sampled, thus part of the window reflected by the isotopic analysis (what the mother ate in the previous weeks or months) matches the TL estimates based on a diet that usually changes on a seasonal basis for these species of sea lions (Dellinger and Trillmich 1999; García-Rodríguez and Auriolas-Gamboa 2004; Lowry et al. 1991; Salazar 2005).

Data analysis.—Statistical tests were performed with JMP (version 5.0) and Statistica (version 7.0). An analysis of variance with a Tukey honestly significant difference post hoc comparison test was used to test for significant differences among mean isotope values of rookeries and age of pups. Isotopic values among regions and subregions were compared using *t*-tests. Significance was assessed using a α -value of 0.05. Latitude and longitude coordinates of sea lion rookeries were converted to decimals to correlate with isotope values.

All field methodologies were approved by Dirección General de Vida Silvestre de la Secretaría de Medio Ambiente y Recursos Naturales throughout research permit granted in Mexico (SGPA/DGVS.-0575) and Parque Nacional Galápagos. We followed the guidelines approved by the American Society of Mammalogists (Gannon et al. 2007).

RESULTS

Size and age of pups.—The average length of pups at the Galápagos Islands ($85.3 \text{ cm} \pm 6.9 \text{ SD}$, $n = 123$) was significantly greater than at the Gulf of California ($81.7 \pm 5.3 \text{ cm}$, $n = 106$; $t = 4.42$, $df. = 227$, $P < 0.001$). Given this difference, we estimated the age of the pups using the calculation described above. The average age for Galápagos pups was $48 \text{ days} \pm 31 \text{ SD}$ (coefficient of variation [CV] = 65%), whereas for the Gulf of California pups the average age was $25 \pm 14 \text{ days}$ (CV = 56%). This difference was statistically significant ($t = -6.21$, $df. = 149$, $P < 0.001$). There were no significant differences in estimated age among colonies within each region ($F = 1.52$, $df. = 5, 49$, $P = 0.20$ for Galápagos and $F = 1.47$, $df. = 10, 84$, $P = 0.16$ for the Gulf). Regardless of the small differences in the age of individuals sampled from the Gulf and Galápagos, the pups from the 2 regions are much younger than the age at which California sea lion pups are typically weaned (8–12 months—Newsome et al. 2006; Peterson and Bartholomew 1967). Thus, all individuals were dependent on milk at the time of sampling. However, we concede that an unknown portion of hair analyzed using our sampling approach was grown in utero, and that the amount of this hair may differ between the Galápagos and Gulf of California pups.

Isotopic differences among rookeries within each region.—No subregional trends in $\delta^{13}\text{C}$ values were apparent in the data set from Galápagos Islands pups when arranged on the latitudinal or longitudinal axis (Table 1). Caamaño in the center of the Archipelago showed the lowest $\delta^{13}\text{C}$ value ($-15.2\text{‰} \pm 0.5\text{‰ SD}$), whereas Pinta, the northernmost rookery, showed the highest value ($-16.4\text{‰} \pm 0.3\text{‰}$).

The $\delta^{15}\text{N}$ values varied from the lowest in Española ($12.2\text{‰} \pm 0.3\text{‰}$) to the highest in Mosquera (13.6 ± 0.6 ; Table 1;

Fig. 2). Because the $\delta^{15}\text{N}$ values were indistinguishable for the 3 rookeries located on San Cristobal (La Loberia, Puerto Baquerizo, and Isla Lobos) and the distance between these locations is $\leq 10 \text{ km}$, we combined all their data to obtain an average representing San Cristobal Island (Fig. 2).

Fernandina (10) and Pinta (11), have features that set them aside with respect to most of the rookeries located in the central Archipelago, where Fernandina Island is the westernmost rookery separated from the other locations by the large island of Isabela and is located in the region with highest productivity and coldest water of the Archipelago (Palacios 2002). Pinta, the northernmost rookery sampled in this study, is separated by 116 km from the nearest rookery in the central Archipelago (Mosquera; Fig. 1) and depths between 1,000 and 2,000 m (Chadwick 2003; Wolf et al. 2008). Both rookeries are influenced by the Equatorial Undercurrent (Cromwell Current), although Fernandina in higher degree (Palacios 2002; D. M. Palacios, Joint Institute for Marine and Atmospheric Research—University of Hawaii and National Oceanic and Atmospheric Administration—National Marine Fisheries Service—Southwest Fisheries Science Center Environmental Research Division, pers. comm.). The remaining rookeries are located on an extended continental shelf (Palacios 2002; Wolf et al. 2008) and in relatively close proximity (Fig. 2). A significant increasing trend of $\delta^{15}\text{N}$ values with latitude ($r = 0.85$, $P = 0.01$) was obtained for the rookeries located in the central part of the Archipelago (Fig. 1).

In the Gulf of California $\delta^{13}\text{C}$ values did not produce a clear pattern when correlated with latitude or longitude. Los Islotes in the south and Los Cantiles in the center had the lowest values (-15.3‰ and -15.4‰ , respectively), whereas the remaining rookeries varied from -14.7‰ to -13.9‰ (Table 1).

However, the $\delta^{15}\text{N}$ values from the Gulf of California showed a pattern (Fig. 3) where a group of 5 rookeries located in a region from the central part of the Gulf from Angel de la Guarda Island to slightly south of Tiburon Island (Fig. 1) produced a range of $\delta^{15}\text{N}$ mean values from 20.1‰ to 20.8‰, whereas the remaining 8 rookeries had higher values ranging from 21.1‰ to 22.4‰. The overall $\delta^{15}\text{N}$ mean \pm SD value for the 5 rookeries in the small central region of the Gulf of California was $20.4\text{‰} \pm 0.5\text{‰}$, significantly lower than the mean $\delta^{15}\text{N}$ value of the remaining rookeries ($21.5\text{‰} \pm 0.5\text{‰}$; $t = 10.32$, $df. = 126$, $P < 0.001$).

Isotopic differences between the regions.—Figure 4 presents a large-scale comparison of $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ values between the Galápagos Islands and the Gulf of California. Mean $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values were $-15.9\text{‰} \pm 0.5\text{‰}$ and $21.8\text{‰} \pm 0.7\text{‰}$, respectively, in the Gulf of California and $-14.5\text{‰} \pm 0.5\text{‰}$ and $13.1\text{‰} \pm 0.5\text{‰}$, respectively, for the Galápagos Islands. The small difference in mean $\delta^{13}\text{C}$ values between the regions was significant ($t = 20.78$, $df. = 242$, $P = 0.001$). There was a large and strongly significant difference in mean $\delta^{15}\text{N}$ values between the regions ($t = -92.79$, $df. = 242$, $P = 0.001$).

Diet and TL.—There is limited information about diet and TL for sea lions at many rookeries in the Galápagos Islands, but it is possible to compare general food structure between

TABLE 1.—Locations (rookery name), number of fur samples (in parentheses), trophic level (TL) estimates, and $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ values (‰) for sea lion pups from the Gulf of California (*Zalophus californianus*) and Galápagos Islands (*Zalophus wollebaeki*). Numbers before rookery name refer to locations in Fig. 1. Superscripted letters indicate sources (estimated by or taken from) of data for calculations of TL.

Location and number of fur samples	TL	$\bar{X} \delta^{15}\text{N}$	$\bar{X} \delta^{13}\text{C}$
Galápagos			
1 Española (17)		12.2 ± 0.3	-16.2 ± 0.2
2 Floreana ^a (10)	4.0	12.7 ± 0.4	-16.2 ± 0.2
3 San Cristobal (Lobería) ^b (14)	4.6	13.2 ± 0.2	-16.3 ± 0.3
4 San Cristobal (Isla Lobos) ^b (19)	4.6	13.3 ± 0.6	-15.8 ± 0.3
5 San Cristobal (P. Baquerizo) ^b (10)	4.3	13.3 ± 0.6	-15.5 ± 0.5
6 Santa Fe (11)	4.6	13.1 ± 0.2	-15.9 ± 0.2
7 Caamaño (11)		13.5 ± 0.5	-15.2 ± 0.5
8 Plaza Sur (10)		13.0 ± 0.5	-16.2 ± 0.1
9 Mosquera (11)		13.6 ± 0.6	-15.6 ± 0.5
10 Fernandina ^c (4)		13.0 ± 0.2	-16.0 ± 0.2
11 Pinta (10)		13.2 ± 0.3	-16.4 ± 0.3
Overall mean and SD	4.4 ± 0.2	13.1 ± 0.5	-15.9 ± 0.5
Gulf of California			
12 Los Islotes ^d (10)	4.3	21.5 ± 0.3	-15.4 ± 0.2
13 Farallón de San Ignacio ^e (10)	4.0	21.6 ± 0.2	-14.1 ± 0.4
14 San Pedro Nolasco ^e (10)	3.6	21.3 ± 0.4	-14.0 ± 0.2
15 San Pedro Martir ^e (10)	4.0	20.6 ± 0.4	-14.3 ± 0.4
16 San Esteban ^f (10)	4.3	20.8 ± 0.4	-14.4 ± 0.4
17 El Rasito ^f (10)	3.5	20.2 ± 0.4	-14.6 ± 0.1
18 El Partido ^f (10)	3.7	20.7 ± 0.5	-13.9 ± 0.3
19 Los Machos ^f (10)	3.2	20.1 ± 0.3	-14.5 ± 0.1
20 Los Cantiles ^f (9)	4.6	21.3 ± 0.6	-15.3 ± 0.4
21 Isla Granito ^f (10)	4.9	21.3 ± 0.4	-14.6 ± 0.3
22 Isla Lobos ^f (10)	4.3	21.5 ± 0.2	-14.7 ± 0.3
23 San Jorge ^g (10)	4.7	21.1 ± 0.7	-14.1 ± 0.4
24 Rocas Consag ^e (9)	4.1	22.4 ± 0.5	-14.0 ± 0.4
$\bar{X} \pm SD$	4.1 ± 0.5	21.0 ± 0.7	-14.5 ± 0.5

^a Okey et al. 2004.

^b Páez-Rosas 2008.

^c Dellinger and Trillmich 1999.

^d Elorriaga-Verplancken and Aurióles-Gamboa 2008.

^e Porras-Peters et al. 2008.

^f García-Rodríguez and Aurióles-Gamboa 2004.

^g Mellink and Romero-Saavedra 2005.

Galápagos and Gulf of California regions (Table 2). Diets of sea lions in the Gulf of California (García-Rodríguez and Aurióles-Gamboa 2004) and Galápagos Islands (Dellinger and Trillmich 1999) have been previously characterized using traditional scat analysis. Data from the Gulf include samples from 7 rookeries, whereas data from the Galápagos were derived from Cabo Hammond at Isla Fernandina. Although the data from the Galápagos are not as spatially extensive as those from the Gulf of California, there is considerable overlap in the common types of prey consumed by sea lions in both regions. Of the 10 prey types most commonly consumed by sea lions in each region (Table 2), the genera *Sardinops*, *Engraulis*, *Scomber*, *Trachurus*, and the family Myctophidae are taken by sea lions in both regions. In the case of the genera *Scomber* and *Trachurus*, the same species was consumed in both regions (*Scomber japonicus* and *Trachurus symmetricus*).

Table 1 presents TL estimates and mean $\delta^{15}\text{N}$ values for a subset of sea lion rookeries in the Galápagos Islands and all the sea lion rookeries from the Gulf of California. Some of the TL estimates are derived from previous studies (Elorriaga-Verplancken and Aurióles-Gamboa 2008; Okey et al. 2004; Páez-

Rosas 2008; Porras-Peters et al. 2008); a few were estimated using raw dietary data from previously published studies (Dellinger and Trillmich 1999; García-Rodríguez and Aurióles-Gamboa 2004; Mellink and Romero-Saavedra 2005). In all cases, TL was estimated using the approach of Christensen and Pauly (1992; see "Materials and Methods"). The TL of Galápagos sea lion rookeries ranged from 4 to 4.6, whereas the TL of sea lions in the Gulf of California ranged from 3.2 to 4.9. Mean TL was 4.4 ± 0.2 for 5 rookeries in Galápagos and 4.1 ± 0.5 for the 13 sea lion rookeries in the Gulf of California.

DISCUSSION

The 3 main factors determining isotopic values in marine predators are diet, physiology (which affects diet-to-tissue isotope fractionation), and foraging location. By sampling pups of nearly the same ontogenetic stage, from sister species, we believe that physiological differences between populations will be minimal if the same tissue is used for the analysis, leaving diet and location as the main potentially variable factors.

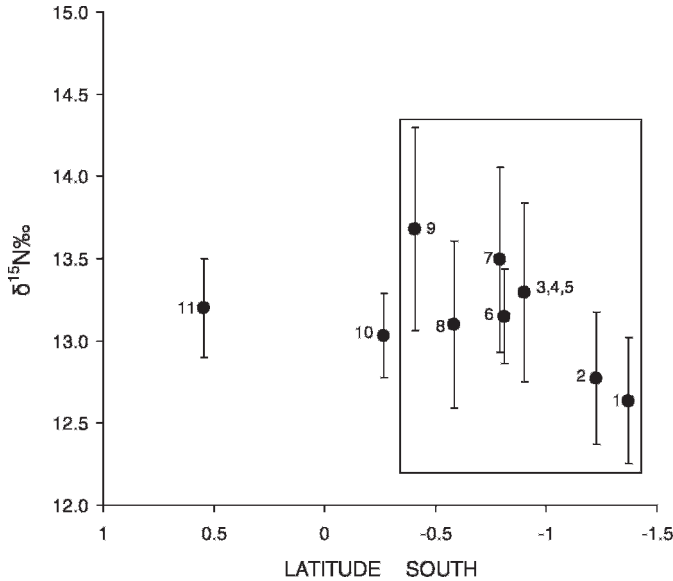


FIG. 2.—Mean $\delta^{15}\text{N}$ values from sea lion (*Zalophus wollebaeki*) pups of the Galápagos Islands ordered along the latitudinal axis. Numbers represent the locations sampled during this study and values within the square correspond to rookeries in the central and southern archipelago (see Fig. 1).

Sea lions in the Gulf of California inhabit a complex, enclosed sea with upwelling along the east coast during winter and upwelling on the west coast during the summer (Álvarez-Borrego 1983; Lluich-Cota et al. 2007). In contrast, Galápagos sea lions inhabit an offshore archipelago adjacent to an extremely productive eastern boundary current system that includes the Panama, Humboldt, and Cromwell currents (Banks 2002).

Effect of diet on isotopic difference in sea lions between and within regions.—Our comparison of the diets of sea lions between the Gulf of California and Galápagos Islands shows that these populations forage on similar prey, albeit in different proportions. In another study, Salazar (2005) conducted an extensive 5-year feeding survey (1997–2001) of several sea lion rookeries on the central and south islands of the Galápagos Archipelago. Although prey was only identified to the family level, Clupeidae, Myctophidae, Serranidae, Chloroptalmidae, and Mugilidae were identified as the dominant fish prey. These results are similar to the diet identified by Dellinger and Trillmich (1999) for rookeries on the northern islands of the Galápagos Archipelago. The similarity in estimated TL (Table 1) between Gulf of California and Galápagos sea lions is further confirmation that the populations share similar dietary habits. Considering the similarities in diet and TL for these 2 sister species of *Zalophus*, we conclude they function as ecological equivalents in their respective ecosystems. As a consequence, differences in diet and TL between the 2 species of *Zalophus* should contribute little to the large $\delta^{15}\text{N}$ difference between pups from the 2 regions.

Effect of isotopic values at the base of the food web on isotope values of sea lions.—In Galápagos sea lion rookeries, there was not a clear geographical pattern for $\delta^{13}\text{C}$ values.

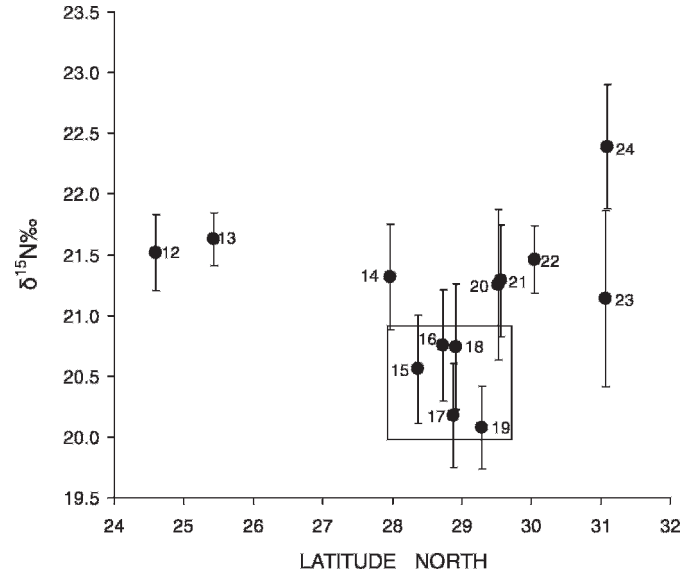


FIG. 3.—Mean $\delta^{15}\text{N}$ values from sea lion (*Zalophus californianus*) pups in the Gulf of California ordered by latitude. Locations numbered from 14 to 18 are located in a small area south of Angel de la Guarda Island (see Fig. 1).

Wolf et al. (2008) reported significant differences in $\delta^{13}\text{C}$ values of skin samples from Galápagos sea lions from Fernandina and Isabela islands in comparison to other rookeries from the central-southern area of the archipelago. These authors concluded that 2 main areas were identified for $\delta^{13}\text{C}$ differentiation: a “central” group, associated to a more benthic-coastal foraging mode (represented by most of the rookeries east of Isabela Island); and a “western” group showing a more pelagic-offshore foraging mode on the west side of Isabela. In our study, the small sample size for Fernandina probably precluded our ability to differentiate this location from the other rookeries because the mean $\delta^{13}\text{C}$ value fell within the values of the other rookeries (Table 1).

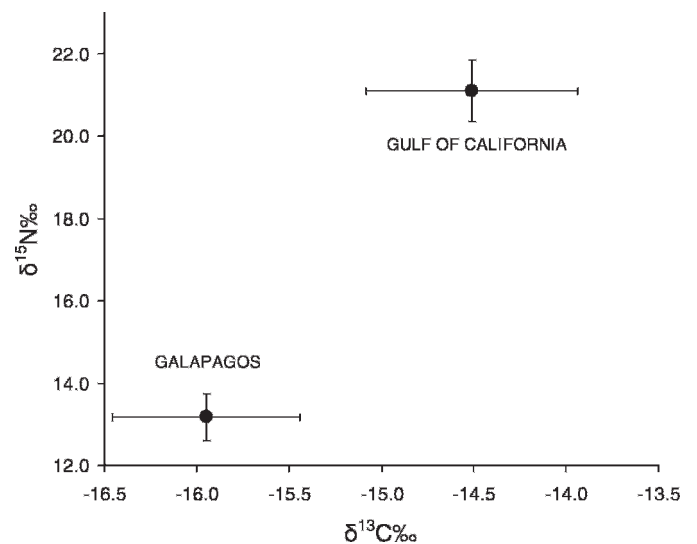


FIG. 4.—Comparison of mean $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ values of all samples of sea lion pups from the regions of the Galápagos Islands (*Zalophus wollebaeki*) and Gulf of California (*Zalophus californianus*).

TABLE 2.—Comparison of diets between *Zalophus californianus* from the Gulf of California^a and *Zalophus wollebaeki* from the Galápagos Islands^b. Only the 10 most important prey items are listed.

Species or family	% in scats
Gulf of California	
<i>Trichiurus lepturus</i>	16.4
<i>Sardinops caeruleus</i>	10.0
<i>Porychthys</i>	9.3
Myctophidae	7.9
<i>Engraulis mordax</i>	5.2
<i>Scomber japonicus</i>	3.4
<i>Cetengraulis mysticetus</i>	2.4
<i>Loliolopsis diomedea</i> ^c	2.4
<i>Trachurus symmetricus</i>	2.3
<i>Merluccius</i>	2.2
Other 93 species	38.5
Galápagos Islands	
<i>Sardinops sagax</i>	81.1
<i>Chlorophthalmus</i>	10.1
<i>Trachurus symmetricus</i>	1.2
<i>Engraulis ringens</i>	1.0
<i>Scomber japonicus</i>	0.8
<i>Pontinus furcirhinus</i>	0.4
Myctophidae	0.4
<i>Lampadaena</i>	0.3
<i>Physiculus talarae</i>	0.3
Bathylagidae	0.1
Other unknown species	4.5

^a From García-Rodríguez and Aurióles-Gamboa (2004).

^b From Dellinger and Trillmich (1999).

^c Squid.

In the Gulf of California, there was a large variation in $\delta^{13}\text{C}$ values among rookeries with no apparent geographical pattern. For example, the 2 rookeries with the lowest mean $\delta^{13}\text{C}$ values are located in the extreme southern (Los Islotes) and central (Los Cantiles) portions of the Gulf (Table 1).

Overall, regional mean $\delta^{13}\text{C}$ values differed significantly, but by a small amount ($\sim 1.5\%$) in comparison to mean $\delta^{15}\text{N}$ values, between *Zalophus* pups from the Gulf of California and the Galápagos Islands. The small difference in $\delta^{13}\text{C}$ values may be explained by the almost uniform $\delta^{13}\text{C}$ values in POM between 0° and 30° in both hemispheres, which average around -20% (Goericke and Fry 1994). Ocean temperature, which impacts dissolved CO_2 concentrations and thereby affects carbon isotope fractionation between dissolved CO_2 and phytoplankton, does not vary greatly across this meridional band. Upwelling promotes phytoplankton blooms that draw down dissolved CO_2 concentration, which tends to reduce discrimination against ^{13}C during photosynthesis (i.e., lead to higher $\delta^{13}\text{C}$ values), perhaps because of diffusional limitation on CO_2 uptake or the uptake of ^{13}C -enriched bicarbonate (Rau et al. 2001; Schell et al. 1998). However, both the Gulf of California and Galápagos experience strong upwelling and high primary production. In the Gulf there is strong upwelling during the winter along the mainland that adds to year-round strong tidal mixing around the large islands in the central region, (e.g., Canal de Ballenas; Fig. 1), producing an

extended area of strong vertical mixing and the flow of cool nutrient-rich water to the surface (Álvarez-Borrego 1983; Lluch-Cota et al. 2007). In the Galápagos, the upwelling produces a phytoplankton bloom on the western margin of the archipelago, covering an approximate area of 25,000 km^2 (Feldman 1986; Palacios 2002; Palacios et al. 2006).

The $\delta^{15}\text{N}$ values of sea lions in the Galápagos Islands suggest the existence of at least 2 major isotopic zones. One is the central Archipelago where 9 of the 11 sea lion rookeries were sampled (Figs. 1 and 2) and is characterized by an extended continental shelf covering most of the center and southern part of the Archipelago (Palacios 2002; Wolf et al. 2008). The 2nd area is the western and northern part of the Archipelago, exposed to the influence of the Cromwell Current coming from the west, which produces an intense upwelling (island effect) characterized by lower surface temperatures and high productivity (Palacios 2002; Palacios et al. 2006; Wolf et al. 2008). Although in less degree than Fernandina and the west coast of Isabela, Pinta Island is also affected by the Cromwell Current (Fig. 1), and is separated from the central Archipelago by 1,000- to 2,000-m depths, constituting a distinct habitat. Ruttenberg et al. (2005) studied the spatial variation in the ecology of a common reef fish, *Stegastes beebei*, finding regional variations in chlorophyll-*a* (mg/m^3) and sea surface temperature to structure the Archipelago in 4 regions: north (including rookeries of this study such as Pinta), west (including Fernandina and Isabela), south (including Floreana, Española, and San Cristobal), and central (including Santa Fe, Caamaño, Plaza Sur, and Mosquera). These authors demonstrated that a latitudinal gradient-type pattern exists in food availability, along with environmentally mediated life-history trade-offs for *S. beebei*.

In the present study, the highly significant trend suggesting nitrogen enrichment from Española in the south to Mosquera in the north included rookeries from the south (cool) and central (mixed) regions defined by Ruttenberg et al. (2005). At present, limited data from scat analysis or sediment isotopic values in the Galápagos area prevent us from determining whether this trend is driven by differences in sea lion TL among rookeries or variation in baseline $\delta^{15}\text{N}$ values at relatively small spatial scales (<100 km). However, strong environmental gradients may exist over relatively small spatial scales in the Galápagos Archipelago; for example, sea surface temperatures values can vary 5°C or more over only 150 km, whereas similar changes in sea surface temperatures in the tropics usually occur over latitudinal distances of 600–1,000 km (Ruttenberg et al. 2005).

For the Gulf of California, a group of colonies located in a relatively small area in the southern margin of Angel de la Guarda Island has a mean $\delta^{15}\text{N}$ value of $20.4\% \pm 0.57\%$, which was significantly lower than the mean $\delta^{15}\text{N}$ value, $21.5\% \pm 0.50\%$, from the remaining rookeries south and north of this region ($t = 10.32$, $d.f. = 126$, $P = 0.001$). The near permanent upwelling conditions in this subregion supports large stocks of sardines (Lluch-Cota et al. 2007), a relatively high-quality prey that is common in sea lion scats

TABLE 3.—Comparison of $\delta^{15}\text{N}$ values (‰) in sediments, in particulate organic matter (POM) from the euphotic zone, average values for selected fish, and from *Zalophus* pups from the Gulf of California and Galápagos Islands. No data on POM are available for the Galápagos. Superscripted letters indicate sources of isotope data.

	Gulf of California	Galápagos Islands	Difference
Euphotic zone POM $\delta^{15}\text{N}^{\text{a}}$	9.3, 10.0, 12.0		
Bottom sediment $\delta^{15}\text{N}^{\text{b,c}}$	10.8	5.5	5.3
Fishes ^{d,e}	<i>Eucinostomus gracilis</i> , 16.8 <i>Benthoosema panamense</i> , 16.4 <i>Selene peruviana</i> , 16.7 <i>Chloroscombrus orqueta</i> , 16.0 Fish average = 16.4	<i>Selar crumenophthalmus</i> , 11.9 <i>Anchoa</i> , 11.9 <i>Paralabrax albomaculatus</i> , 12.8 Fish average = 12.2	4.2
Sea lion pup hair $\delta^{15}\text{N}$	21.0	13.1	7.9

^a From south to north: Carmen Basin, Guaymas Basin, and Delfin Basin isotopes values, respectively from Altabet et al. (1999).

^b Gulf average value from 2 stations, 10.4‰ and 11.1‰ from Altabet et al. (1999).

^c Galápagos area from Farrell et al. (1995).

^d Data on fish for Gulf of California from Torres-Rojas (2006).

^e Data on fish from the Galápagos Islands provided by Páez-Rosas (2008).

from this particular area (García-Rodríguez and Auriolas-Gamboa 2004; Porrás-Peters et al. 2008). Because sardines primarily forage on plankton, they likely have relatively low $\delta^{15}\text{N}$ values in comparison to other common sea lion prey, such as *Trichiurus lepturus* and *Porychthys*, which feed mostly on other fish and cephalopods (Fitch and Lavenberg 1975; Sheridan and Trimm 1983).

Our study shows a complex pattern of sea lion $\delta^{15}\text{N}$ values among rookeries within the Galápagos Archipelago and Gulf of California. Whether the isotopic trends among rookeries in Galápagos are the result of differences in baseline food-web values or dietary preferences or a combination of both is not clear at present. In the case of the sea lion $\delta^{15}\text{N}$ values in the Gulf of California, they seem to positively correlate with TL, but also to a within-region isotopic enrichment from south to north (Porrás-Peters et al. 2008).

To further investigate the roles of oceanographic versus dietary differences as factors explaining isotopic patterns in these sister species, Table 3 presents a comparison between $\delta^{15}\text{N}$ values in sediment and fish from the Gulf of California and Galápagos Islands. The Gulf of California sediment $\delta^{15}\text{N}$ value is an average from 2 stations located in the south and central Gulf of California (Fig. 1; Altabet et al. 1999); the Galápagos sediment $\delta^{15}\text{N}$ values (Farrell et al. 1995) were collected approximately 250 km south of the archipelago. The sites differ by 5.3‰, on average. The fish species from the 2 regions show an average $\delta^{15}\text{N}$ difference of 4.2‰. With the exception of myctophids, these fish are not the most common prey species consumed by sea lions in either region (Table 2), but all of the species in Table 3 have been reported as sea lion prey (García-Rodríguez and Auriolas-Gamboa 2004). Although the differences in $\delta^{15}\text{N}$ values of sediment and fish from both regions are of similar direction and magnitude (5.3‰ and 4.2‰, respectively), the $\delta^{15}\text{N}$ difference among sea lions (7.9‰) is greater (Table 3). This residual difference cannot be explained by differences in diet or TL, because the feeding habits of these species of *Zalophus* is similar. In fact, examination of scat data suggests that Galápagos sea lions forage at a slightly higher TL than sea lions in the Gulf of California (4.4 versus 4.1; Table 1).

This subtle difference would tend to increase $\delta^{15}\text{N}$ values in the Galápagos relative the Gulf, reducing the residual difference. It seems that a larger sample of $\delta^{15}\text{N}$ values of sediments and fish from both regions is needed to better determine isotope differences between TLs.

Because the pups from the Gulf of California were younger than those from the Galápagos, they might have had more hair formed in utero on their pelts when they were sampled. The expectation, based on previous studies (albeit on other species), is that nursing animals will have $\delta^{15}\text{N}$ values that are higher than or at least equal to those of newborn animals (Balasse et al. 2001; Fogel et al. 1997; Jenkins et al. 2001; Newsome et al. 2006; Polischuk et al. 2001). Thus, if Galápagos animals have more fur formed during nursing, they should have relatively higher $\delta^{15}\text{N}$ values, again reducing, not increasing, the residual difference.

We believe the most likely explanation for the residual difference is that our oceanographic data underestimate the $\delta^{15}\text{N}$ differences at the base of the food chain between the sites. Ideally, when controlling for differences at the base of the food web, we would like data that provide an annually integrated record of the $\delta^{15}\text{N}$ value of nitrogen assimilated by phytoplankton in the region. Spot samples of POM may show large seasonal variations related to upwelling and blooms that make regional intercomparison difficult, and in any case, we lack POM data from near the Galápagos. Sinking particles captured in sediment traps would be the best source, but again, such data are not available for the Galápagos Archipelago. We do have surface sediment samples from both the Gulf of California and near the Galápagos, but again, they may not be entirely comparable. First, the Galápagos data from Farrell et al. (1995) are from approximately 250 km south of the islands and may not reflect conditions in the foraging zone. Information from 9 satellite-tracked Galápagos sea lions indicate that they forage close to the islands, with maximum travel distances from their rookeries of 76 km and a mean foraging distance of 41.7 ± 20 km *SD* (Villegas-Amtmann et al. 2008).

More importantly, nitrogen in surface sediments in deep-ocean sites (such as those near the Galápagos) is subject to

diagenetic alternation that may lead to ^{15}N -enrichment by up to 4‰, whereas sediments at shallow sites more faithfully reflect the descending particle flux, as has been documented at sites in the Gulf (Altabet et al. 1999). Thus, the sinking particle flux near the Galápagos may have $\delta^{15}\text{N}$ values 2–4‰ lower than those recorded in surface sediments, entirely explaining the residual difference relative to the Gulf (D. Sigman, Department of Geosciences, Princeton University, pers. comm.).

Our study shows that small differences in $\delta^{13}\text{C}$ values and large differences in $\delta^{15}\text{N}$ values between predators from 2 regions in the eastern Pacific Ocean are primarily due to differences generated at the base of the food web in their respective ecosystems, and in a much less degree to their trophic or foraging ecology. However, isotopic differences, particularly for $\delta^{15}\text{N}$ values within each of the 2 regions, deserve further investigation. The simultaneous use of distinct approaches to study feeding habits (e.g., stable isotopes, scat analysis, or fatty acids analysis) in both predator and their prey across the 2 regions may provide a better understanding of the differences observed within each region and for top predators that migrate large distances in the eastern Pacific Ocean.

RESUMEN

La variación isotópica espacial y/o temporal en productores primarios debe ser conocida cuando se estudia la ecología trófica de consumidores tope superiores con base en datos isotópicos. Las poblaciones de especies hermanas de *Zalophus californianus* y *Z. wolfebaeki* se encuentran separadas por aproximadamente 3,350 kilómetros de agua tropical que evita su contacto y mezcla. Para explorar las diferencias en ecología trófica de estas especies, así como el impacto de las diferencias en la base de la red trófica, se analizó información de los hábitos alimenticios con base en el análisis de heces y de isótopos estables de carbono y nitrógeno de pelos colectados de crías en 13 colonias en el Golfo de California (*Z. californianus*) en 11 colonias en las Islas Galápagos (*Z. wolfebaeki*). Los valores medios de $\delta^{13}\text{C}$ y $\delta^{15}\text{N}$ fueron $-15.9\text{‰} \pm 0.5\text{‰}$ y $21.8\text{‰} \pm 0.7\text{‰}$ para crías del Golfo de California, mientras que para crías de Galápagos fueron de $-14.5\text{‰} \pm 0.5\text{‰}$ y $13.1\text{‰} \pm 0.5\text{‰}$. El análisis de copros indicó que hay una alta similitud de la dieta entre ambas especies con 6 presas en común de las 10 principales, por tanto explica los valores cercanos de nivel trófico entre ambas especies (Golfo 4.1 y Galápagos 4.4). Aunque se observó una correlación significativa entre los valores de $\delta^{15}\text{N}$ y el nivel trófico, su contribución para explicar las diferencias de $\delta^{15}\text{N}$ entre *Z. californianus* y *Z. wolfebaeki* fueron limitadas. La materia orgánica en sedimentos cercana a Islas Galápagos, fue alrededor de $\sim 5.3\text{‰}$ más baja que los valores de $\delta^{15}\text{N}$ en sedimentos del Golfo de California, sugiriendo que la señal isotópica con la que inicia la red trófica en cada región, explica aproximadamente dos tercios de la diferencia observada en el pelo de las crías de estos depredadores tope. El presente estudio ofrece claves para entender mejor los valores isotópicos de depredadores tope que migran en el Océano Pacífico Oriental.

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