Differences in the Isotopic Niche and Trophic Position of Female California Sea Lions (*Zalophus californianus*) in Distinct Oceanographic Conditions

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Abstract

Determining the trophic position and trophic width of animals within food webs is essential to defining their ecological role. California sea lions (CSLs; *Zalophus californianus*) are widely distributed along the dynamic coast of the northeast Pacific; thus, their diet is shaped by the unique setting and environmental conditions of each colony. Our goal was to determine the trophic position and isotopic niche of CSLs from two colonies in Mexico in distinct environments (Gulf of California vs west coast of the Baja California peninsula) by examining the carbon and nitrogen isotopic signatures in vibrissae. The Gulf of California is a marginal sea where primary productivity is based on seasonal upwelling and intense tidal mixing. In contrast, primary productivity on the west coast of the Baja California peninsula depends on seasonal upwelling as well as the productive California Current System. One mystacial vibrissa was removed from each CSL captured on San Esteban Island (SEI) ($N = 10$) in the Gulf of California during the 2011 breeding season, and on Santa Margarita Island (SMI) ($N = 16$) on the Pacific coast of the Baja California peninsula during the 2012-2013 breeding season. Bayesian techniques were used to determine the trophic niche and trophic position. The trophic niche was wider at SMI than at SEI as more habitats are available to female CSLs at the former (e.g., coastal, pelagic, and lagoonal). However, despite the wider trophic niche and array of habitat types, the trophic level was the same for both colonies, suggesting that CSLs may maintain their trophic position across variable ecosystems. The accurate evaluation of the geographic variation in the trophic position of female CSLs allows us to better understand how these marine mammals utilize the distinct resources available in the habitats they occupy.

Key Words: Gulf of California, stable isotopes, isotopic niche, vibrissae, San Esteban Island, Santa Margarita Island, foraging, pinniped

Introduction

Four factors determine where a species is found: (1) abiotic conditions, (2) biotic factors, (3) the species' dispersal abilities, and (4) the species' ability to adapt to new conditions (Soberón & Peterson, 2005). In this context, interactions between abiotic and biotic factors lead to unique and distinguishable niches. Determining the trophic position and trophic width of animals within food webs is essential to defining their ecological role; however, most quantitative dietary studies of marine mammals are based on small samples and/or consider only a small fraction of a species' distribution. Thus, the results may not apply to the species' ocean-wide or global distribution (Pauly et al., 1998). California sea lions (CSLs; *Zalophus californianus*) are a clear example. This species' overall range extends throughout the temperate and subtropical waters off the west coast of North America from Alaska to southern Mexico, including the Gulf of California (Aurioles-Gamboa & Hernández-Camacho, 2015).

Environmental conditions vary throughout the CSLs' distribution, modulating the abundance and diversity of their prey (Porras-Peters et al., 2008); this suggests that their trophic niche and trophic position may vary throughout their distribution. The Gulf of California and the west coast of the Baja California peninsula represent two distinct environmental settings that could result in different feeding habits and trophic widths. We focus on female CSLs because they provide information on the prey available near their colonies. Adult females are resident at

their rookeries year-round (Hernández-Camacho et al., 2008) since maternal care of young limits the dispersion of females to *ca*. 60 km around the colony. Thus, their diet depends on the availability and abundance of prey in the immediate area (Newsome et al., 2006; Villegas-Amtmann et al., 2012). As a result, adult female CSLs best reflect the local conditions and feeding habits of each colony (Aurioles-Gamboa et al., 2009, 2017).

Our goal was to estimate and compare the trophic position and trophic width of adult female CSLs from San Esteban Island (SEI) in the Gulf of California and Santa Margarita Island (SMI) on the west coast of the Baja California peninsula based on the stable isotopes in vibrissae. The sea lion colonies in the Gulf of California and on the Pacific coast of Baja California are grouped into subpopulations with similar genetic and ecological characteristics (Ward et al., 2010; Szteren & Aurioles-Gamboa, 2011). The colonies in the Gulf of California have been divided into two to three subpopulations (north, center, and south), and the west coast of the Baja California peninsula has been divided into one to two subpopulations depending on the type of genetic analysis (mitochondrial or nuclear DNA) (Szteren et al., 2006; González-Suárez et al., 2009; Schramm et al., 2009; Ward et al., 2010). SEI is the largest colony in the Gulf of California (*ca*. 5,700 individuals); meanwhile, SMI has a population of *ca*. 2,800 individuals (Lowry & Maravilla-Chávez, 2005; Szteren et al., 2006). The Gulf of California is a marginal sea with a high evaporation rate. Primary productivity is based on seasonal upwelling driven by winds during spring and fall as well as intense tidal mixing, which is particularly evident in the narrower central Gulf of California where SEI is located (Simpson et al., 1994; Salas-de-León et al., 2011). In contrast, the west coast of the Baja California peninsula where SMI is located depends on a major seasonal upwelling during spring as well as the productive California Current System (Álvarez-Borrego et al., 1975; Zaytsev et al., 2003). SMI is also characterized by the proximity of the large coastal lagoon system of Magdalena Bay, an important source of shallow-water prey.

Based on these distinct oceanographic conditions, we expected to find differences in the trophic position and trophic width of adult female CSLs. Individuals from SMI are expected to have a wider trophic niche due to the presence of demersal fishes and the variety of environmental settings, including coastal lagoons, the coastline, and the pelagic habitat. Analysis of scat samples collected around Magdalena Bay and SMI indicate that many of the prey species consumed by CSLs are benthic or demersal, including North Pacific hake (*Merluccius productus*), smooth stargazer (*Kathetostoma averruncus*), sumptail searobin (*Prionotus stephanophrys*), California lizardfish (*Synodus luciceps*), plainfin midshipman (*Porichthys notatus*), and octopus (*Octopus bimaculatus*) (Reyes-Márquez, 2014). Based on this diet, CSLs mostly feed along the bottom of the wide continental shelf off Magdalena Bay.

Around SEI, deep basins provide an important pelagic habitat for sardines (*Sardinops sagax*) and other schooling fishes, including the lanternfish (*Benthosema panamense*) and the Humboldt squid (*Dosidicus gigas*) (García-Rodríguez & Aurioles-Gamboa, 2004). Due to the limited presence of coastal lagoons, adult female CSLs are expected to focus more on pelagic prey, thereby reducing their trophic niche.

Stable isotope analysis provides quantitative information on biotic (prey consumed) and abiotic (habitat use) factors commonly used to define ecological niche space (Newsome et al., 2007). In food web ecology, the natural variation in stable isotope ratios (typically of carbon and nitrogen) allow us to identify a species' trophic niche (Layman et al., 2007). Between primary producers with different photosynthetic pathways (e.g., C_3 vs C_4 plants), the $\delta^{13}C$ (ratio of ^{13}C to ^{12}C) varies substantially; however, only minimal variation is observed in trophic transfers (~1‰; parts per thousand). Thus, $\delta^{13}C$ can be used to determine the ultimate sources of dietary carbon (DeNiro & Epstein, 1981; Peterson & Fry, 1987; Post, 2002). In contrast, the $\delta^{15}N$ (ratio of ^{15}N to ^{14}N) can be used to determine the trophic position of a predator as this isotopic ratio undergoes step-wise enrichment with trophic transfers. The $\delta^{15}N$ values in the tissues of consumers tend to be *ca*. 2.5 to 5‰ higher than those of their prey (DeNiro & Epstein, 1981; Bearhop et al., 2002). Due to its utility in determining a species' trophic niche, stable isotope analysis is one of the tools most commonly employed in the study of trophic structure (Layman et al., 2007).

Vibrissae were sampled because this tissue records seasonal and inter-annual changes in feeding habits and diet (Darimont & Reimchen, 2002; Bearhop et al., 2004). Depending on the length and growth rate, a single vibrissa can integrate diet information spanning one to several years (Hirons et al., 2001; Lewis et al., 2006). The isotopic information contained in vibrissae facilitates estimation of the trophic niche width, allowing us to distinguish between different types of environments and the distinct habitats used by individuals as well as to determine their trophic level.

Methods

Sample collection was carried out on SEI in the Gulf of California in 2011 (9-14 June) and on SMI in the Magdalena Bay lagoon complex on the west coast of Baja California Sur, Mexico (Figure 1), in 2012 (23-29 June) and 2013 (30 April-7 May). Female CSLs were captured using hoop nets and anesthetized with a mixture of isoflurane gas and oxygen (0.5 to 2.5%) administered using a cone mask (see Villegas-Amtmann et al., 2008, for details on these methods). Veterinarians from Africam Safari Park and the Brookfield Zoo were present to monitor the animals while the anesthesia was administered and the samples were collected.

Tweezers were used to remove one mystacial vibrissa from the root from each female Californai sea lion. The diameter is fairly consistent close to the root but becomes thinner toward the tip due to erosion (Rogers et al., 2016). Thus, we only analyzed the first 4 cm closest to the root which represent $23.4 \pm 3.7\%$ of the total length of each vibrissa. The time period represented by this length is 571 d based on the linear model growth rate (0.07 mm d^{-1}) reported by McHuron et al. (2016). The 4 cm sample was divided into 20 segments measuring 2 mm each because segments of this length weigh *ca.* 1.0 ± 0.2 mg, the weight requested by the stable isotope laboratory. Each vibrissa segment was stored in a tin
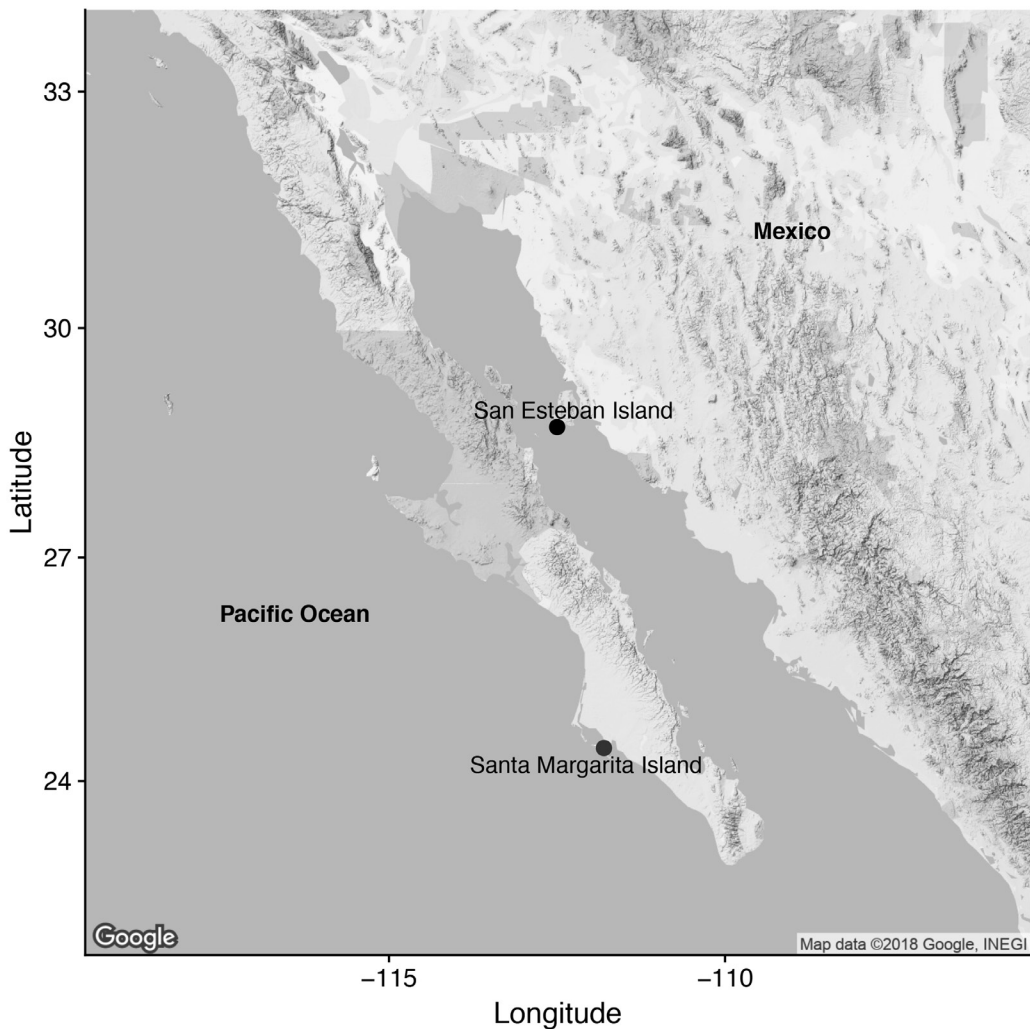
Figure 1. Location of San Esteban Island (SEI) in the Gulf of California and Santa Margarita Island (SMI) on the west coast of the Baja California Peninsula in Mexico

capsule for isotopic analysis. Prior to the isotopic analysis, the cuticle surrounding the root was extracted to remove any lipids present in this layer; each vibrissa was then washed with phosphate-free soap, distilled water, and a 2:1 chloroform:methanol mixture to remove any contaminants or lipid residue (Newsome et al., 2009).

To calculate the trophic level of the female CSLs, muscle samples were recovered from a variety of fish species collected around each colony. We collected 14 fish species from the area around SEI and 50 fish species from the area around SMI (Table 1). The number of species collected around SEI was notably lower as inclement weather during the sampling period impeded more intensive sampling around the colony. Due to the distance to SEI, it was not possible to return to the study area during the same year. These fish species are potential prey of CSLs (García-Rodríguez & Aurioles-Gamboa, 2004; Porras-Peters et al., 2008). For SMI, fish samples were collected from two different areas of Magdalena Bay that are known to be CSL foraging areas: (1) Alcatraz Harbor and (2) Santa María Bay. Alcatraz Harbor is part of a lagoon zone with mangroves and sea grasses (Bizzarro, 2008) and, thus, it experiences a lesser influx of oceanic waters (Hastings & Fischer, 2001). As such, the C isotope values of the trophic base in this area are more enriched than the corresponding values at Santa María Bay located outside of the Magdalena Bay lagoon complex. Meanwhile, at SEI, fish samples were collected from different points around the colony; thus, they represent distinct habitats (Table 1). Bathymetry strongly influences the marine environments around this island in the central archipelago of the Gulf of California: to the north, the continental shelf is located at 200 m depth; and to the south, there are a series of basins with depths of 2,000 to 3,200 m (Salas-de-León et al., 2011; Hernández-Alcántara et al., 2013). This drastic change in bottom depth, known as the San Esteban Sill, produces intense tidal currents that reach a depth of 500 m and introduce nutrient-rich cold water (Álvarez-Borrego & Lara-Lara, 1991; Simpson et al., 1994).

The muscle samples were frozen for transport to the Pinniped Ecology Laboratory at the Centro Interdisciplinario de Ciencias Marinas (CICIMAR; Interdisciplinary Center for Marine Sciences) of the Instituto Politécnico Nacional (IPN; National Polytechnic Institute) in La Paz, Baja California Sur, Mexico. At the laboratory, the samples were thawed and washed with distilled water to remove impurities, and then dried at 60°C. The dried samples were homogenized to a fine powder in an agate mortar, and

~1.0 ± 0.2 mg of each sample was weighed and stored in tin capsules in preparation for the isotopic analysis (Aurioles-Gamboa et al., 2013). Lipid extraction is commonly used in this type of analysis to eliminate the variability in the $\delta^{13}C$ associated with the lipid content. However, we did not use this technique because it would affect the $\delta^{15}N$ values and, therefore, the estimation of the trophic position (Post et al., 2007; Aurioles-Gamboa et al., 2013). Moreover, it is not necessary to remove lipids from samples from marine mammals when the lipid content is consistently low (< 5%; C:N < 3.5); in our study, the C:N was 3.2 for SEI and 3.0 for SMI (Post et al., 2007).

Isotopic Analysis
Determination of the isotopic ratios of C and N through the combustion of CO_2 and N_2 was undertaken at the Stable Isotope Facility of the University of California at Davis in the United States. The samples were analyzed using a PDZ Europa ANCA-GSL elemental analyzer interfaced to a PDZ Europa 20-20 isotope ratio mass spectrometer (PDZ Europe 20-20; Sercon Ltd, Crewe, Cheshire, UK) with an accuracy of $\pm 0.2‰$ for both isotopes. The isotopic ratios are expressed as delta (δ): $\delta^{15}N$ or $\delta^{13}C = 1,000 * [(R_{sam}/R_{std}) - 1]$, where R_{sam} and R_{std} are the ratios of $^{15}N/^{14}N$ or $^{13}C/^{12}C$ of the sample and the standard, respectively. The standards were Vienna-Pee Dee Belemnite limestone (V-PDB) for carbon and atmospheric N_2 for nitrogen. Units are expressed as parts per thousand (‰).

Linear mixed effects models were used to evaluate isotopic variation in each individual over time, between different individuals from the same colony, and between colonies. The model examined the variance partitioning of the isotopic signatures with the assumption that the variation in the $\delta^{13}C$ and $\delta^{15}N$ measurements for individual vibrissae could be explained by a combination of fixed and random effects. The "lme4" package (Bates et al., 2015) in *R*, Version 3.4.1 (R Development Core Team, 2017) was employed to fit the model using REML or maximum likelihood (lmerMod). Nonsignificant variance components ($p > 0.05$) were assumed to be equal to zero. In our model, the fixed effects were the two colonies (two levels: SEI and SMI), and the random effects were the individual CSLs grouped by region. The residual error term corresponded to within-individual variation, thus accounting for all remaining variance not explained by other terms. Age- and sex-class effects were not assessed because all of the animals analyzed were adult females.

Table 1. $\delta^{13}C$ and $\delta^{15}N$ values (mean and SD) of the prey species consumed by California sea lions (CSLs; *Zalophus californianus*) in Mexico. Samples were collected from San Esteban Island (SEI) and Santa Margarita Island (SMI). Sample size (*N*) is the number of muscle samples from each fish species. FG is the functional group: *Z. californianus* (predator), benthic-demersal prey (B-D), and pelagic prey (pelagic).

Location	Species	N	FG	$\delta^{13}C$	±SD	$\delta^{15}N$	±SD
SEI	*Zalophus californianus*	10	Predator	-13.7	0.2	21.2	0.3
SMI	*Zalophus californianus*	16	Predator	-15.0	0.7	20.1	0.3
SEI	*Urobatis halleri*	2	B-D	-15.6	0.1	16.7	0.9
SEI	*Heterodontus franscisi*	2	B-D	-17.9	0.2	18.6	0.4
SEI	*Merluccius productus*	2	B-D	-16.5	0.1	17.9	0.6
SEI	Ophichthidae	2	B-D	-11.8	1.0	13.8	5.3
SEI	*Argentina sialis*	2	Pelagic	-19.4	0.7	17.6	0.8
SEI	*Benthosema panamense*	5	Pelagic	-18.9	0.9	17.2	0.7
SEI	*Coryphaena hippurus*	2	Pelagic	-16.8	0.2	17.7	0.5
SEI	*Euthynnus lineatus*	3	Pelagic	-16.6	0.5	15.6	0.3
SEI	*Fodiator acutus*	2	Pelagic	-16.3	0.8	18.7	0.4
SEI	*Paralabrax aerogutatus*	4	Pelagic	-16.5	0.2	19.1	0.1
SEI	*Paralabrax maculatofasciatus*	3	Pelagic	-15.7	1.2	19.5	1.4
SEI	*Sardinops sagax*	8	Pelagic	-18.2	1.4	15.6	1.2
SEI	*Scomber japonicus*	2	Pelagic	-19.6	0.3	14.9	0.2
SEI	*Serranus* psittacinus	2	Pelagic	-16.3	0.7	18.7	0.6
SMI	*Balistes polylepis*	3	B-D	-15.9	1.1	16.9	1.0
SMI	*Calamus brachysomus*	11	B-D	-15.1	1.6	16.0	1.9
SMI	*Chaetodipterus zonatus*	5	B-D	-15.1	0.8	16.3	0.6
SMI	*Citharichthys gilberti*	3	B-D	-15.9	0.9	15.2	0.5
SMI	*Citharichthys xanthostigma*	9	B-D	-17.8	0.4	16.0	0.2
SMI	*Dasyatis brevis*	3	B-D	-14.2	0.4	15.8	0.3
SMI	*Etropus crossotus*	3	B-D	-15.8	0.3	17.1	0.3
SMI	*Diplectrum labarum*	10	B-D	-18.3	0.3	16.7	0.3
SMI	*Diplectrum rostrum*	3	B-D	-16.3	0.2	17.9	0.4
SMI	*Etropus* sp.	5	B-D	-17.8	1.3	16.9	0.3
SMI	*Eucinostomus argenteus*	3	B-D	-15.6	0.8	17.4	0.7
SMI	*Eucinostomus gracilis*	3	B-D	-17.9	0.1	17.6	0.4
SMI	*Eucinostomus dowii*	4	B-D	-17.0	1.2	16.2	0.3
SMI	*Eucinostomus entomelas*	3	B-D	-16.2	1.4	12.8	1.8
SMI	*Haemulon scudderi*	3	B-D	-16.4	1.0	16.5	1.4
SMI	*Haemulopsis axillaris*	4	B-D	-18.0	0.3	16.3	2.3
SMI	*Hippoglossina stomata*	10	B-D	-17.9	0.2	16.8	0.4
SMI	*Hypsopsetta guttulata*	3	B-D	-17.1	0.1	16.3	0.3
SMI	*Kathetostoma averruncus*	10	B-D	-18.1	0.5	15.7	0.3
SMI	*Lepophidium stigmatistium*	10	B-D	-17.9	0.3	16.9	0.3
SMI	*Merluccius productus*	12	B-D	-18.3	0.3	15.7	0.6
SMI	*Mugil curema*	6	B-D	-14.3	2.6	13.7	2.2
SMI	*Ophidion galeoides*	3	B-D	-16.0	0.3	18.1	0.1
SMI	*Ophioscion* sp.	3	B-D	-16.4	0.3	17.1	0.0
SMI	*Ortopristis chalceus*	3	B-D	-17.0	1.8	14.2	1.9
SMI	*Paralichthys californicus*	6	B-D	-15.5	1.3	17.6	0.7
SMI	*Paralichthys woolmani*	3	B-D	-16.5	1.4	17.2	1.4
SMI	*Peprilus simillimus*	6	B-D	-19.3	0.3	14.8	0.6
SMI	*Pleuronichthys verticalis*	3	B-D	-16.8	0.4	16.6	0.6
SMI	*Prionotus albirostris*	11	B-D	-18.1	0.5	15.8	0.5
SMI	*Prionotus stephanophrys*	3	B-D	-17.6	0.5	16.6	0.4
SMI	*Scorpaena guttata*	3	B-D	-14.3	1.3	15.6	0.7
SMI	*Sphoeroides lobatus*	9	B-D	-17.2	1.5	16.4	0.4
SMI	*Syacium ovale*	3	B-D	-17.4	0.4	16.6	0.0
SMI	*Symphurus fasciolaris*	3	B-D	-15.8	0.3	16.2	0.3
SMI	*Symphurus* sp.	3	B-D	-17.0	1.5	17.6	0.9
SMI	*Synodus scituliceps*	3	B-D	-14.1	0.4	17.1	0.3
SMI	*Synodus lucioceps*	10	B-D	-18.4	0.6	15.6	0.5
SMI	*Umbrina xanti*	3	B-D	-17.8	0.6	18.0	0.6
SMI	*Urobatis halleri*	3	B-D	-16.1	0.9	16.5	0.4
SMI	*Xenistus californiensis*	3	B-D	-20.2	0.3	17.9	0.2
SMI	*Balistes polylepis*	3	Pelagic	-17.5	0.5	18.0	0.2
SMI	*Squid*	3	Pelagic	-15.7	0.2	18.5	0.2
SMI	*Dosidicus gigas*	7	Pelagic	-17.9	0.8	16.1	0.4
SMI	Gobiidae	3	Pelagic	-17.7	0.3	18.3	0.2
SMI	*Larimus acclivis*	3	Pelagic	-16.0	0.1	17.9	0.6
SMI	*Lutjanus novemfasciatus*	3	Pelagic	-16.4	0.0	17.2	0.5
SMI	*Lutjanus argentivestris*	4	Pelagic	-16.4	0.6	15.6	1.3
SMI	*Paralabrax maculatofasciatus*	7	Pelagic	-16.0	1.2	15.7	2.1

Trophic (Isotopic) Niche
Stable Isotope Bayesian Ellipses in R (*SIBER*) (Jackson et al., 2011) was used to determine the isotopic niche of the adult female CSLs from SEI and SMI. The mean isotopic values of the vibrissae were used to define the isotopic niche space for the adult female CSLs captured at both colonies as a measure of the area of their isotopic resources at the population level. *SIBER* is a Bayesian version of Layman's metrics (Layman et al., 2007). Unlike Euclidean methods (e.g., convex hull), this technique incorporates uncertainties like sample biases and small sample sizes into the metrics of the niches (Jackson et al., 2011). Based on the Markov-Chain Monte Carlo (MCMC) simulation, this approach assigns uncertainty measures for constructing ellipse parameters in a manner similar to a bootstrap. The standard ellipse areas corrected for small sample size (SEAc) were used to obtain the isotopic niche (potential foraging areas) of the females from each colony (Jackson et al., 2011). Each vibrissa provided multiple δ^{13}C and δ^{15}N values (20 segments) that are not independent. To obtain the values for the corrected standard ellipse area (SEAc) in the *SIBER* analysis, we used a mean value for each vibrissa (one vibrissa = one individual) for each isotope to avoid violating the assumption of independence. The results of this analysis are interpreted in conjunction with the linear mixed effects model used to assess the individual variability in δ^{13}C and δ^{15}N within and between colonies. All statistical analyses were carried out using *R*, Version 3.4.1 (R Development Core Team, 2017), and all codes used for the *SIBER* analysis can be found in the *SIAR* (*Stable Isotope Analysis in R*) library (Parnell & Jackson, 2013).

Trophic Position
We wanted to explore how the CSL trophic position varies between these two colonies. To do this, we calculated the trophic position of adult female CSLs from SEI and SMI using a Bayesian model in "tRophicPositions" package (Quezada-Romegialli et al., 2017) in *R*, Version 3.4.1 (R Development Core Team, 2017). There is considerable spatio-temporal variation in baseline δ^{15}N values. Values are more enriched in the Gulf of California relative to the west coast of Baja California peninsula. In the North Pacific, values are less enriched in the north relative to the south (Aurioles-Gamboa et al., 2017). The analysis accounts for this variation in baseline δ^{15}N by considering the latitudinal position of the study sites before calculating the trophic position of female CSLs from each colony (Quezada-Romegialli et al., 2017).

The next step in the analysis involved determining which type of environment CSLs preferred as feeding areas. To do so, the isotopic values from the vibrissa and fish muscle samples were separated into three functional groups: (1) predator (CSLs), (2) benthic-demersal prey (benthic-demersal baseline), and (3) pelagic prey (pelagic baseline). For each colony, the predator value was the mean δ^{13}C and δ^{15}N of all vibrissae. The values for the benthic-demersal and pelagic baselines were obtained from the fish species sampled around the two colonies (Table 1). For this stage of the analysis, it was necessary to incorporate trophic discrimination factors for both δ^{13}C and δ^{15}N; discrimination values between CSL vibrissae and their prey are not available, thus we used the values reported for phocids. Following Hobson et al. (1996), the discrimination factor between phocid vibrissae and prey muscle is 2.8‰ for δ^{15}N and 3.2‰ for δ^{13}C. In "tRophicPosition," the default trophic discrimination values are those reported by McCutchan et al. (2003) for different species of marine and terrestrial organisms; thus, we had to select the values closest to those reported by Hobson et al. (1996) as they were the most appropriate for this analysis. In this case, the value closest to the δ^{15}N was that for muscle (2.9 ± 0.29‰; McCutchan et al., 2003, do not specify to which species this muscle value corresponds), and the value closest to the δ^{13}C was that for brook trout (3.3 ± 0.29‰).

Results

Trophic (Isotopic) Niche
A total of 26 lactating or pregnant adult female CSLs were captured on both islands. One vibrissa was sampled from each of these 26 females: 10 from SEI and 16 from SMI. The mean vibrissa length at SEI was 14.9 ± 2.5 cm, while that at SMI was 17.1 ± 3.7 cm (Table 2).

Vibrissae from SEI were enriched by 1.3‰ in δ^{13}C (range -15.1 to -12.1‰) and 1.1‰ in δ^{15}N (range 19.8 to 22.9‰) compared to SMI (δ^{13}C ranged from -16.5 to -12.6‰; δ^{15}N ranged from 19.8 to 22.9‰) (Figure 2). The enrichment of the δ^{13}C and δ^{15}N values for SEI relative to those for SMI reflects important differences between these two colonies. Based on the analysis of the variance components of δ^{13}C, 17.3% of the variance was explained by between-individual isotopic differences, 26.4% was explained by within-individual isotopic differences, and 56.3% was explained by the sample colony ($p < 0.001$). For the isotopic variance in δ^{15}N, 5.4% was explained by between-individual isotopic differences, 15.6% was explained by within-individual isotopic differences, and 79.0% was explained by the sample colony ($p < 0.01$).

Table 2. $\delta^{13}C$ and $\delta^{15}N$ values (mean, SD, and SE) for vibrissae of adult female CSLs from SEI and SMI. Of the total vibrissa length, only 4 cm were analyzed for each sample.

| Female	Colony	Total length (cm)	$\delta^{13}C$			$\delta^{15}N$		
			Mean	SD	SE	Mean	SD	SE
1	SEI	11.9	-13.44	0.65	0.09	20.76	0.45	0.06
2	SEI	12.7	-13.65	0.47	0.06	20.86	0.36	0.05
3	SEI	13.2	-13.75	0.54	0.06	21.37	0.51	0.06
4	SEI	15.2	-13.53	0.50	0.06	21.21	0.36	0.04
5	SEI	15.4	-13.91	0.31	0.04	21.88	0.36	0.04
6	SEI	15.4	-13.99	0.60	0.08	21.20	0.31	0.04
7	SEI	16.1	-13.42	0.28	0.04	21.40	0.27	0.04
8	SEI	16.5	-13.81	0.22	0.03	20.91	0.29	0.04
9	SEI	17.5	-13.65	0.54	0.06	21.22	0.32	0.04
10	SEI	19.9	-13.81	0.32	0.03	21.37	0.38	0.04
11	SMI	17.0	-15.08	0.24	0.05	20.61	0.37	0.08
12	SMI	15.2	-15.17	0.16	0.04	20.20	0.27	0.06
13	SMI	16.3	-15.18	0.21	0.05	19.95	0.28	0.06
14	SMI	20.1	-15.26	0.37	0.08	19.62	0.36	0.08
15	SMI	17.7	-14.96	0.18	0.04	20.06	0.18	0.04
16	SMI	21.5	-13.28	0.41	0.09	20.07	0.19	0.04
17	SMI	20.8	-13.59	0.67	0.15	20.23	0.25	0.06
18	SMI	22.6	-14.42	0.53	0.12	20.49	0.33	0.07
19	SMI	10.2	-15.28	0.15	0.03	19.86	0.34	0.08
20	SMI	14.8	-15.69	0.13	0.03	20.43	0.28	0.06
21	SMI	15.5	-15.38	0.23	0.05	20.15	0.42	0.09
22	SMI	12.6	-14.99	0.26	0.06	20.45	0.13	0.03
23	SMI	16.0	-16.05	0.29	0.07	19.85	0.23	0.05
24	SMI	19.1	-14.71	0.18	0.04	20.14	0.27	0.06
25	SMI	21.9	-15.78	0.07	0.01	19.66	0.16	0.04
26	SMI	12.0	-14.87	0.10	0.02	19.98	0.19	0.04

The SEA$_C$ was 0.70 at SEI and 0.92 at SMI; the variation in the SEA$_C$ reflects differences between the two colonies in terms of the isotopic variance of $\delta^{13}C$.

Trophic Position
Although the $\delta^{15}N$ values were enriched at SEI (Figure 3a), the trophic position calculated for adult female CSLs from SEI was similar to that for female CSLs from SMI; however, their 95% credibility intervals were quite different (Figure 3b). The trophic position for SEI was 3.6 with a range of 3.0 to 4.4, while that for SMI was 3.5 but with a wider range (2.9 to 5.1). The contributions from the benthic-demersal

and pelagic baselines are different for each island (Figure 3c). In Figure 3c, only the first baseline is shown. At SEI, the contribution of the pelagic baseline is rather low, so the benthic-demersal baseline should be high. At SMI, the pelagic baseline contributes much more, but the 95% credibility interval ranges from 0.25 to 1.00.

The values for CSLs (predator), benthic-demersal prey (baseline 1), and pelagic prey (baseline 2) are given in Figure 4. The female CSLs are at the top of the trophic chain at each colony. A greater inter-individual variation is evident between the $\delta^{13}C$ values (range -16.7 to -13.3‰) for female CSLs from SMI relative to the range presented by female CSLs at SEI
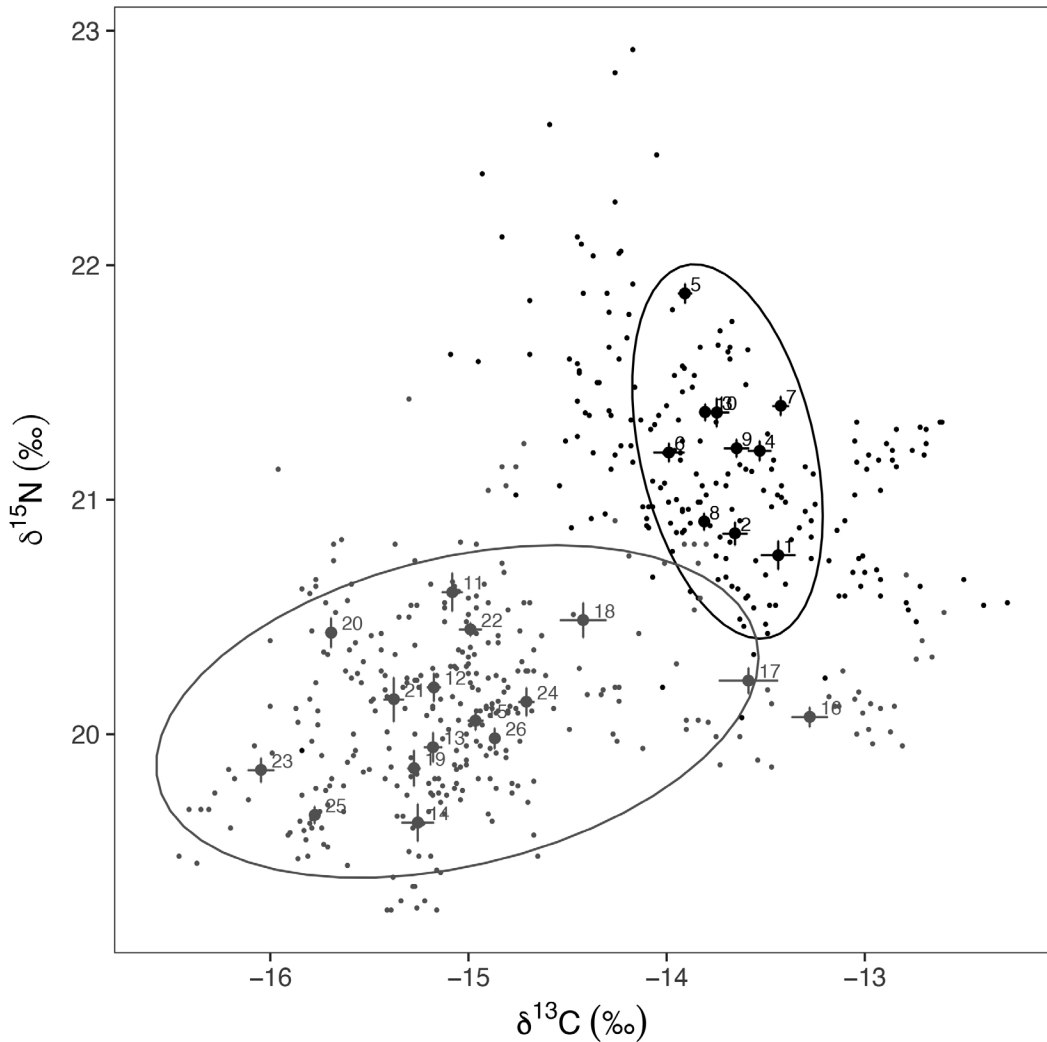
**Figure 2.** The δ¹³C and δ¹⁵N values for vibrissae from female California sea lions (CSLs; *Zalophus californianus*) at SEI (black dots) and SMI (grey dots). The estimated medians (± SE) for SEI are represented by black dots, and those for SMI are shown with grey dots. The ellipses represent the isotopic niches estimated for CSLs from SEI (black ellipse) and SMI (grey ellipse).

(-14.0 to -13.4‰). In terms of the δ¹⁵N values, female CSLs from SEI present more enriched values as expected based on the geographic location of the colony; however, the inter-individual variation is very similar between colonies for this isotope. The difference in the range of δ¹⁵N values at SEI (20.8 to 21.9‰) is slightly greater than that between the range of δ¹⁵N values at SMI (19.6 to 20.6‰).

The graphics along the top and right-hand side of Figure 4 represent the smoothed density estimates for δ¹³C and δ¹⁵N, respectively.

Our results suggest that female CSLs from SEI feed primarily on benthic-demersal prey, although the smoothed density for δ¹⁵N indicates that the two baselines (benthic-demersal and pelagic) overlap (Figure 4a). Female CSLs from SMI appear to feed in both benthic-demersal and pelagic environments, although prey from the benthic-demersal environment made a greater contribution to their diet. As was the case at SEI, the benthic-demersal and pelagic baselines overlap at SMI as well (Figure 4b).
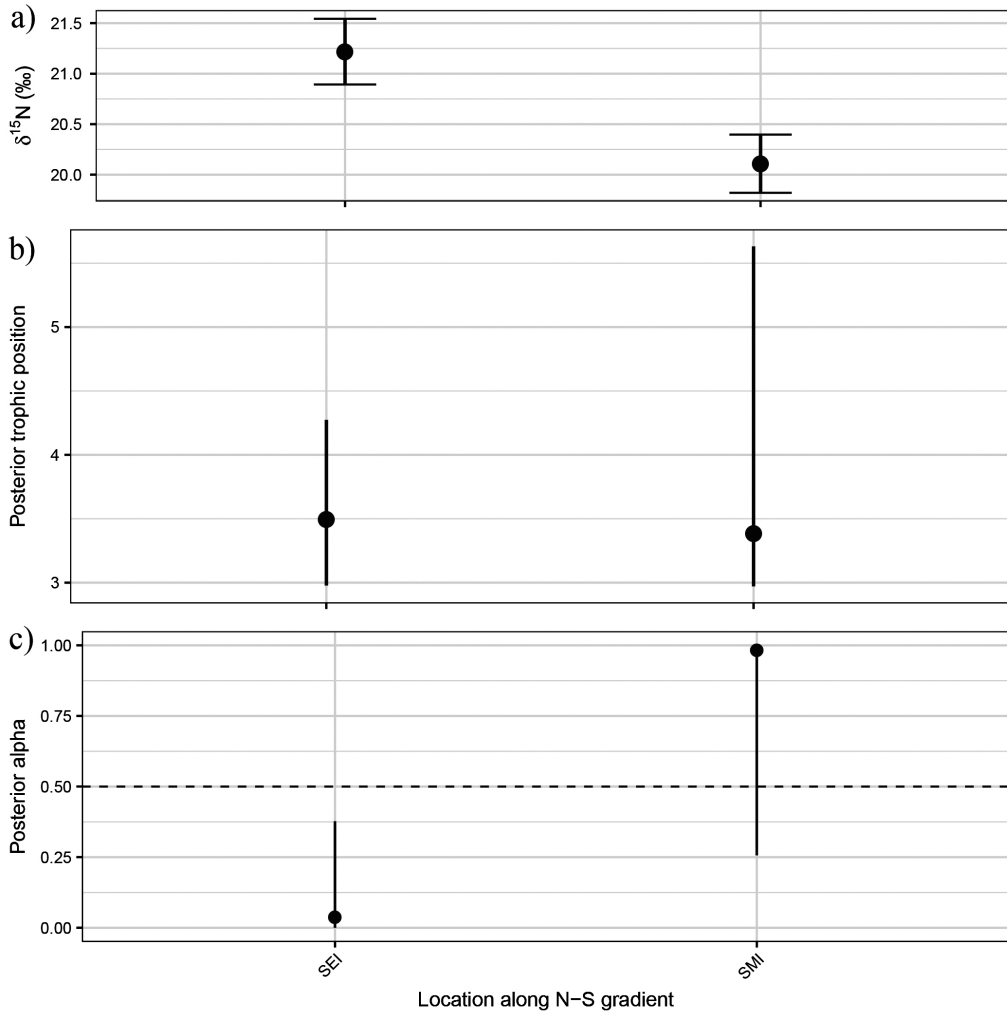
Figure 3. Diagram showing the trophic position, alpha, and estimated median ± SD for CSLs from SEI and SMI based on the median ± SD of the δ¹⁵N of the benthic and pelagic sources of each colony

Discussion

Trophic Niche

Our results indicate that CSLs exploit a variety of food sources to meet their energy requirements as reflected by the width of the $\delta^{13}C$ ranges for the isotopic niches at both colonies. The $\delta^{13}C$ isotopic range was wider at SMI than at SEI: CSLs at the former colony only consume benthic-demersal prey according to this model, while CSLs at SMI exploit both pelagic and benthic-demersal prey, including some inhabiting the Magdalena Bay lagoon environment. These results do not mean that none of the female CSLs at SEI consumed pelagic prey but, rather, that the contribution of

prey from this habitat was so low that the model did not detect it.

The difference in resource exploitation reflects the marine environments available to CSLs at each colony. The particular oceanographic characteristics around SEI provide the ideal environment for a variety of fish species (Castro-Aguirre et al., 1996), including the very abundant small pelagic sardine (*Sardinops sagax*) (Hammann et al., 1998) and the northern anchovy (*Engraulis mordax*) (Green-Ruiz & Hinojosa-Corona, 1997).

In contrast, SMI is located in the Magdalena Bay lagoon complex on the Pacific coast of Baja California Sur. The geographic orientation and physical characteristics of this lagoon complex
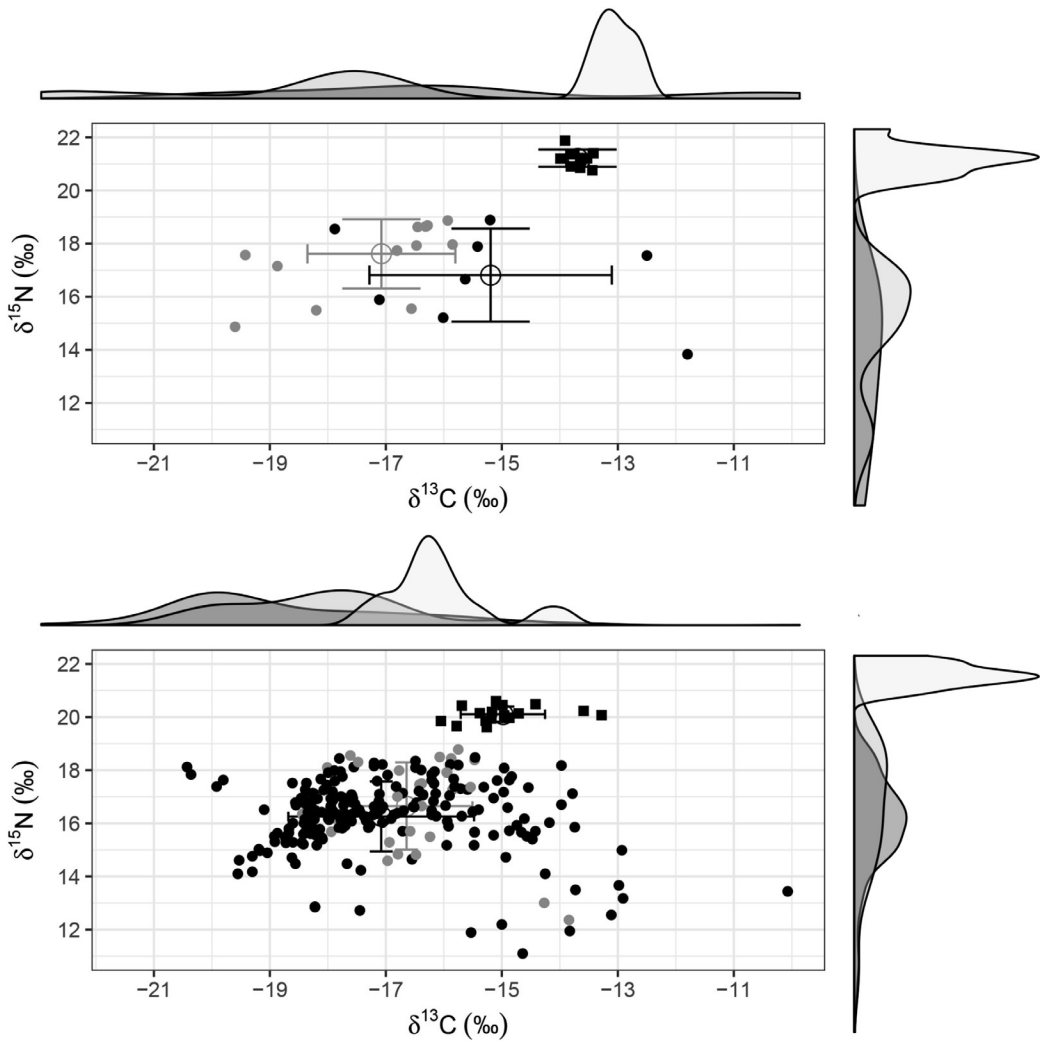
Figure 4. Biplot showing the values for the predator (CSL; black square), the benthic-demersal source (black dots), and the pelagic source (grey dots) for SEI (a) and SMI (b). The open circles represent the mean ± SD. The graphics along the top and right-hand side represent a smoothed density estimate for $\delta^{13}C$ and $\delta^{15}N$, respectively, facilitating identification of the predator's most important energy source (benthic or pelagic).

create a contiguous system of shallow canals, intertidal sandy areas, and highly productive and biologically diverse environments (Álvarez-Borrego et al., 1975). Moreover, SMI is located in a transition zone between tropical and temperate faunal regions (Castro-Aguirre & Torres-Orozco, 1993; Bizzaro, 2008). In contrast to SEI, the marine system around SMI includes a wide continental shelf and lagoon zone, as well as some mangroves and marine grasses surrounded by deeper waters that offer CSLs distinct habitats where they are able to feed on different fish, crustacean, and mollusk species (Bizzaro, 2008).

This benthic-demersal energy source makes a considerable contribution to the diet of CSLs at this colony; thus, the niche width is significantly influenced by the abiotic (habitat) factor.

There is a larger gradient in the $\delta^{13}C$ values for SMI compared to those for SEI. At least two adult female CSLs had $\delta^{13}C$ values suggesting they fed primarily in the lagoon environment, which was not observed in CSLs from SEI. At SEI, the gradient of $\delta^{15}N$ values indicates that the CSLs there consumed a variety of prey at slightly different trophic levels. The reduced gradient of $\delta^{13}C$ values suggests more uniform habitat conditions.

Our results indicate that the isotopic niche depends on the unique oceanographic characteristics and coastal physiography of each region, which, in turn, generate differences in the number and size of distinct habitats. At SMI, CSLs feed in the coastal lagoon or open ocean, whereas their counterparts at SEI focus on prey inhabiting the benthic-demersal environment. However, we must also consider the sampling strategy selected to obtain a representative dataset for each colony. Topography and the shape of each island largely determine the distribution of CSLs at each colony. There was a higher probability of capturing females with a variety of feeding strategies at SMI as CSLs typically are concentrated on a small strip of beach (less than 2 km); conversely, SEI has a perimeter of *ca*. 24 km, and CSLs are distributed throughout the island. For the SEI sample, only individuals in the northwest could be accessed; thus, it is very likely that we only captured females feeding in this area of the island, which is relatively shallow and where benthic prey abound. In species like the northern fur seal (*Callorhinus ursinus*) and the Galapagos sea lion (*Zalophus wollebaeki*), individuals living in distinct parts of the colony exploit different feeding areas (Robson et al., 2004; Páez-Rosas et al., 2014; Drago et al., 2016).

The female CSLs we sampled were pregnant and/or nursing. As lactation lasts 1 to 2 y (Newsome et al., 2009) and they have pups each reproductive season (Hernández-Camacho et al., 2008), it is possible that the reproductive state impacted the physiology of the females and, therefore, their isotope signatures. However, the low variability in $\delta^{15}N$ and $\delta^{13}C$ suggests that the isotopic values are independent of the physiological changes associated with gestation and lactation. In Antarctic (*Arctocephalus gazella*) and subantarctic (*A. tropicalis*) fur seals, reproductive state does not affect the isotopic values in vibrissae as the same isotopic cycles are present in males and females and the isotopic oscillations display the same periodicity in females of two otariid species with different lactation periods (Kernaléguen et al., 2012). Thus, we are confident that the isotopic changes observed in the vibrissae reflect the feeding habits of the female CSLs during the previous 19 mo.

Trophic Position
Many studies have used trophic position to characterize the functional role of organisms and facilitate estimations of the flow of energy or matter through ecological communities. This has been accomplished by inferring diet composition through the use of direct techniques like scat analysis and stomach content analysis, or indirect means such as stable isotope analysis or fatty acid analysis.

Studies based on scat analysis have assigned a trophic position of 4.1 to CSLs (Lowry et al., 1991; Pauly et al., 1998; Porras-Peters et al., 2008; Aurioles-Gamboa et al., 2009, 2013; Pablo-Rodríguez et al., 2016) making them secondary carnivorous predators (Mearns et al., 1981). According to this classification, this otariid's diet should be based primarily on benthic invertebrates, squid, small pelagic fishes, and a wide variety of demersal fishes (Pauly et al., 1998). However, the trophic position varies between colonies due to shifts in this pinniped's feeding habits. For example, values ranging from 3.4 (for SEI) to 4.6 (for Los Cantiles rookery) have been reported in the Gulf of California based on scat analysis (García-Rodríguez & Aurioles-Gamboa, 2004).

The mean $\delta^{15}N$ value for the vibrissae of female CSLs was 3.5 at SEI and 3.6 at SMI. Thus, at least in the case of SEI, the trophic position values (~3.5) are consistent between studies despite the use of distinct techniques (scat analysis vs stable isotope analysis) during different years. The trophic position reported by García-Rodríguez & Aurioles-Gamboa (2004) is based on analysis of scat samples collected in 1995 and 1996. In contrast, in the present study, we collected vibrissae in 2011, and the time period encompassed by the trophic information varies from 2 to 4 y (calculated using the rate of 0.07 mm d^{-1} proposed by McHuron et al., 2016). Thus, it appears that for more than 15 y, the trophic position of these CSLs may have remained consistent, suggesting that the CSLs from this colony consume a specialist diet. However, Lowry et al. (1991) found that this pinniped prefers some species over others and is able to temporarily modify its specialist diet to include the most abundant or accessible prey during a given season, making them plastic specialists. The dearth of studies during the previous decade and a half has impeded the detection of these seasonal changes in the CSL diet (Aurioles-Gamboa et al., 2017). García-Rodríguez & Aurioles-Gamboa (2004) noted that the diet of CSLs from SEI was based primarily on species like Pacific cutlassfish (*Trichiurus lepturus*), sardines, lanternfish, and squid during their 2-y study.

These are all pelagic prey, contrasting to our findings of mostly all benthic-demersal prey at SEI. However, this may be due to the fact that at SEI we only sampled adult females in the northwest of the island. Thus, it is very likely that we only captured females feeding in relatively shallow areas where benthic-demersal prey abound.

Despite the difference in the methods used (scat vs stable isotope analysis) and the distinct diets identified (pelagic vs benthic-demersal), the result was the same: the trophic level of CSLs at SEI

has not changed over several years. Nonetheless, we recommend using both techniques as each provides distinct yet complementary information. Scat analysis is limited to providing information on the days prior to sample collection; thus, unless continuous sampling is performed, the time period that can be assessed is limited, and this technique does not offer a record of fluctuations in diet due to environmental changes. However, this technique does permit identification of the specific prey consumed (Lowry et al., 1991; Darimont & Reimchen, 2002; Porras-Peters et al., 2008). In contrast, stable isotope analysis of vibrissae provides information about diet over a longer period of time (from months to years depending on the vibrissa length analyzed); thus, the information contained in this tissue reflects both intra- and interannual variation in diet (Hirons et al., 2001; Cherel et al., 2009). However, stable isotopes do not permit us to directly identify the prey species consumed.

The trophic position of each species is determined by the gradual enrichment of the δ^{15}N values that occurs between links moving up the trophic web— that is, from the trophic base to apex predators. Thus, when using the δ^{15}N signatures of consumers as a measure of their trophic position, it is important to consider the δ^{15}N of the base of the trophic web (Fry, 1988; Zanden & Rasmussen, 1999). In this study, the trophic position estimates for CSLs at SEI and SMI were similar (3.6 and 3.5, respectively) despite the fact that the isotopic δ^{15}N values of the vibrissae of CSLs from SEI were enriched by ~1.1‰ relative to the values for CSLs from SMI. At first glance, this increase in δ^{15}N values might appear to reflect a diet composed of species from a higher trophic level. However, this enrichment is due to the values that predominate in the trophic base around SEI.

In the Gulf of California, all levels of the food web have enriched δ^{15}N values relative to other regions due to the denitrification in the oxygen minimum layer of the Eastern Tropical Pacific (Altabet et al., 1999; Sigman et al., 2009; Aurioles-Gamboa et al., 2017). Moreover, the δ^{15}N values increase progressively each year (Aurioles-Gamboa et al., 2017). Thus, the CSLs that inhabit this region present the most enriched values of δ^{15}N throughout the species' full geographical distribution (Aurioles-Gamboa et al., 2017).

Finally, although the trophic position was similar for both colonies, CSLs at SEI and SMI do not necessarily feed on the same prey. Female CSLs from SEI feed on benthic-demersal prey, while their counterparts at SMI consume prey from both benthic-demersal (lagoon) and pelagic habitats. It is important to complement this study with analyses of hard structures in scat samples to determine whether the differences detected in the trophic levels and trophic niches are the product of differences in diet.

Female CSLs are permanent residents of the colonies they inhabit because lactation forces them to remain at their reproductive colonies throughout the year (Hernández-Camacho et al., 2008; Newsome et al., 2012). This has led to the establishment of specific foraging areas over time, suggesting a partitioning of their trophic niche either by consuming different diets or by exploiting different foraging areas. Thus, the accurate evaluation of geographic variation in the trophic position of female CSLs allows us to better understand how these marine mammals utilize the distinct resources available in the habitats they occupy.

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