

$\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ values in dental collagen as a proxy for age- and sex-related variation in foraging strategies of California sea lions

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Abstract We assessed the foraging habits of California sea lions, *Zalophus californianus*, from Isla Santa Margarita, BCS, Mexico, by analyzing $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values of dentin collagen. Since dentin is deposited annually in growth layer groups (GLGs), it can be subsampled to construct ontogenetic isotopic profiles at the individual level. We drilled 20 canine teeth and obtained 141 samples for isotopic analysis that were assigned to age-specific categories from GLG-based estimated ages. Pups' GLGs had the highest mean $\delta^{15}\text{N}$ values and the lowest mean $\delta^{13}\text{C}$ values, a pattern likely driven by the consumption of milk. Juveniles had $\delta^{15}\text{N}$ values between those of pups and adult females, which may reflect continued nursing into the second year or preferential consumption of coastal benthic versus pelagic prey. Significant differences were observed between the sexes of adults; adult females had lower mean $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values than adult males. Higher isotope values in adult males relative to females may reflect a

higher trophic position, but differences in foraging grounds cannot be excluded as a potential explanation because tracking data are not available at this time. Evidence of intra-specific foraging diversification may be related to a strategy to reduce competition within and among age and sex categories.

Introduction

The California sea lion (*Zalophus californianus*) breeds on islands adjacent to Southern California, Baja California, and in the Gulf of California. Its entire population is estimated to be ~245,000 individuals (Lowry and Maravilla 2005; Szteren et al. 2006; Carretta et al. 2007), of which around 75,000 individuals breed on the west coast of Baja California, Mexico (Lowry and Maravilla 2005). The southernmost breeding colony on the Pacific coast of Baja California is on Isla Santa Margarita in Bahía Magdalena, which contains ~3,000 sea lions (Bautista 2002).

Like most otariid species, the California sea lion exhibits marked sexual dimorphism, where adult males are ~450 % larger than adult females (Orr et al. 1970), a difference in body size that allows males to have a higher dispersal capacity (Weise and Costa 2007). Ultimately, this factor may enable males to avoid competition with adult females, which must restrict their feeding trips to areas in close proximity to their breeding grounds throughout the year (García-Aguilar and Aurióles-Gamboa 2003; García-Rodríguez and Aurióles-Gamboa 2004).

The most common technique used to determine diet in marine mammal ecology is scat analysis, which allows for the identification of specific taxonomic entities, but may underestimate the relative importance of some prey due to the loss or degradation of small structures as a result of

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digestion (Da Silva and Neilson 1985; Dellinger and Trillmich 1988; Orr and Harvey 2001). Another limitation of this technique is related to the short time period represented by each scat sample, which only reflects recent dietary inputs, unless frequent sampling is possible, but this requires an exceptional amount of effort. Nonetheless, it is impossible to acquire a temporal record of ecological information from a single individual via scat analysis.

Stable isotope analysis (SIA) is a useful tool to reconstruct the diet and movement patterns of top marine consumers such as the California sea lion (Owens 1987; Burton and Koch 1999; Graham et al. 2010; Newsome et al. 2010). This is due in part to the observation that both $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values show a stepwise increase with each increase in trophic level in a food web, such that a consumer has higher $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values than those of its prey (Owens 1987). It is important to note that SIA does not typically result in fine-resolution dietary information, such as the identification of prey to the genus or species level, but it can provide useful information related to trophic level/individual dietary specialization and habitat use of top consumers in marine environments (Post 2002; Lewis et al. 2006; Auriolles-Gamboa et al. 2006; Newsome et al. 2009).

A large number of laboratory- and field-based studies reveal that consumer tissues show an average increase of +3–5 ‰ in $\delta^{15}\text{N}$ values with respect to diet (DeNiro and Epstein 1978; Owens 1987; Minagawa and Wada 1984). $\delta^{13}\text{C}$ values also increase with increasing trophic level, but the stepwise enrichment is less than $\delta^{15}\text{N}$; consumer tissues are typically enriched by only +0.5–2.0 ‰ with respect to diet (France 1995; Hobson et al. 1997). Trophic discrimination factors (e.g., $\Delta^{15}\text{N}_{\text{consumer-diet}}$) are also tissue specific, being different for bone and dental collagen, which have higher $\delta^{13}\text{C}$ values than other commonly analyzed tissues (e.g., muscle, blood) because of their greater concentration of ^{13}C -enriched amino acids (e.g., glycine; Koch 2007). There can also be variation with growth rate, nutritional status, and among taxonomic groups that excrete different forms of nitrogen (e.g., urea, uric acid, ammonia) (Trueman et al. 2005; Martínez del Río et al. 2009; Newsome et al. 2009).

Variations in $\delta^{13}\text{C}$ values among primary producers in different habitats (marine/freshwater, coastal/oceanic, pelagic/benthic) are useful proxies for assessing habitat use in marine organisms, including marine mammals (France 1995; Hobson et al. 1997; Newsome et al. 2010). In marine ecosystems, spatial isotopic variation is related to a variety of physicochemical and biologic factors, such as (1) the isotopic composition and concentration of dissolved CO_2 available to primary producers (Goericke and Fry 1994), (2) the taxonomic composition and growth rate of phytoplankton (Fry and Wainright 1991), and (3) the influence of carbon derived from benthic macrophytes in coastal zones that are ^{13}C enriched in comparison to phytoplankton in

open-ocean pelagic environments (Michener and Schell 1994; France 1995). There is also a spatial variation in $\delta^{15}\text{N}$ values at the base of the food web that is negatively correlated with latitude in the Eastern Tropical and North Pacific Ocean (Altabet et al. 1999). These differences are strongly related to the presence of oxygen minimum zones at intermediate depths and the associated denitrification, which increases $\delta^{15}\text{N}$ values in particulate organic matter available to the base of the food chain (Wada and Hattori 1991; Voss et al. 2001).

Because isotopic incorporation (or turnover) rates vary among tissues (Kurle and Worthy 2002; Sinisalo et al. 2008), isotopic analysis may provide a different temporal record of dietary information depending on the tissue(s) analyzed. The analysis of dental collagen provides a time series of information with near annual resolution at the individual scale (Hobson and Sease 1998; Newsome et al. 2009; Riofrío-Lazo et al. 2012) because dental collagen is deposited annually in growth layer groups (GLGs) from the fetal stage to death. GLGs are metabolically inert and are not resorbed after deposition (Klevezal 1996; Walker and Macko 1999).

In California sea lions, differences in dispersal behavior and diving capacities associated with body size between the sexes and ontogenetic classes likely result in differences in foraging behavior that may be recorded in $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values of dental collagen. In this study, we present evidence of sex- and ontogenetic-related differences in dental collagen $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values of 20 California sea lions from Isla Santa Margarita in Bahía Magdalena, Mexico. Using a high-resolution micromill, we obtained 141 GLGs samples from these 20 individuals and binned the samples into five different age and sex categories. Subsampling and analysis of tooth dentin allowed us to analyze aspects of the species biology from a life history perspective, such as those related to the length of the lactation period and sex-based differences in adult foraging habits. By utilizing this a high-resolution sampling strategy, we were able to assess this life history variation through an individual's ontogeny and extract foraging information for specific ages that are likely linked to particular foraging behaviors. Ultimately, our study may provide ecological information for a better status analysis of *Zalophus californianus* and its subsequent conservation.

Materials and methods

Sample collection and preparation

The samples of dentin collagen were sourced from a collection of California sea lions skulls curated in the Laboratorio de Ecología de Pinnípedos Burney J. Le

Table 1 Code, sex, and age of the 20 California sea lions, *Zalophus californianus*, from Isla Santa Margarita that were analyzed

Code	Sex	Age (years)
Z-ISM-123-220582	Female	5
Z-ISM-106-130382	Female	12
Z-ISM-112-130382	Female	10
Z-ISM-097-130382	Female	7
Z-ISM114-130382	Female	7
Z-ISM-099-130382	Male	13
Z-ISM-120-220582	Male	5
Z-ISM-109-130382	Male	3
Z-ISM-ANC-1982	Male	11
Z-ISM-095-130382	Male	6
Z-ISM-121-220582	Male	6
Z-ISM-104-130382	Male	5
Z-ISM-145-170483	Female	7
Z-ISM-135-170483	Female	6
Z-ISM-159-040683	Female	7
Z-ISM-136-170483	Female	5
Z-ISM169-101084	Female	7
Z-ISM-166-101084	Female	5
Z-ISM-167-101084	Female	7
Z-ISM-230-050385	Male	7

Z, *Zalophus*; ISM, Isla Santa Margarita; the last number of the code indicates the date (day/month/year) of the stranding for each individual and its skull sampling

Boeuf, at the Centro Interdisciplinario de Ciencias Marinas in La Paz, B. C. S., México. We selected 12 females of ages from 5 to 12 years and 8 males of ages from 3 to 14 years (Table 1) collected during the 1980s on Isla Santa Margarita, Bahía Magdalena in Baja California Sur, Mexico (Fig. 1). All individuals were fresh carcasses when skulls were collected; hence, all the years when the animals died are known. The corresponding skulls were grouped into sex categories based on criteria established by Peterson and Bartholomew (1967) and Orr et al. (1970): (1) subadult males exhibit a partially developed sagittal crest, while adult males present it in a fully developed manner; (2) adult females are easily differentiated from mature males because they do not exhibit a sagittal crest; (3) at the same age, males present larger canine teeth than females. For females, we only considered a single adult category after the juvenile stage because field observations focusing on physical characteristics and/or behavior do not allow us to distinguish subadults from adults, as in males.

Age estimation

Each tooth was cut longitudinally with an Isomet[®] low velocity saw (Buehler[®]), yielding two symmetric halves.

One of the halves was polished with fine grit sandpaper (400–600 grit) to obtain a smooth surface. The teeth were then immersed in a solution of 10 % formic acid for a period of 1.0–1.5 h to help define dentin growth layers, then rinsed with water and air dried (Newsome et al. 2006). The external outermost layer represents the youngest growth layer, which is partially formed during the fetal development (Fig. 2; Klevezal 1996). Individual age was estimated based on the number of GLGs, from the fetal layer inward (Scheffer 1950; Klevezal 1996). For all skulls, we knew the year when the sea lion had died, so we were able to assign a known year for each GLG.

Preparation of samples and isotopic analysis ($\delta^{15}\text{N}$ and $\delta^{13}\text{C}$)

We obtained a sample of dentin from each dentin growth layer using a high-resolution drilling system (Merchantek MicroMill System). We used a 300- μm wide drill bit and sampled each growth layer to a depth of $\sim 500 \mu\text{m}$ (Fig. 2). The width of the sampled layers varied depending on the total number of GLGs in the tooth; GLGs from older individuals tended to be thinner, especially GLGs representing the adult stage ($\sim 1 \text{ mm}$ width/GLG) in contrast to juvenile teeth with a smaller number of GLGs ($\sim 3 \text{ mm}$ width/GLG).

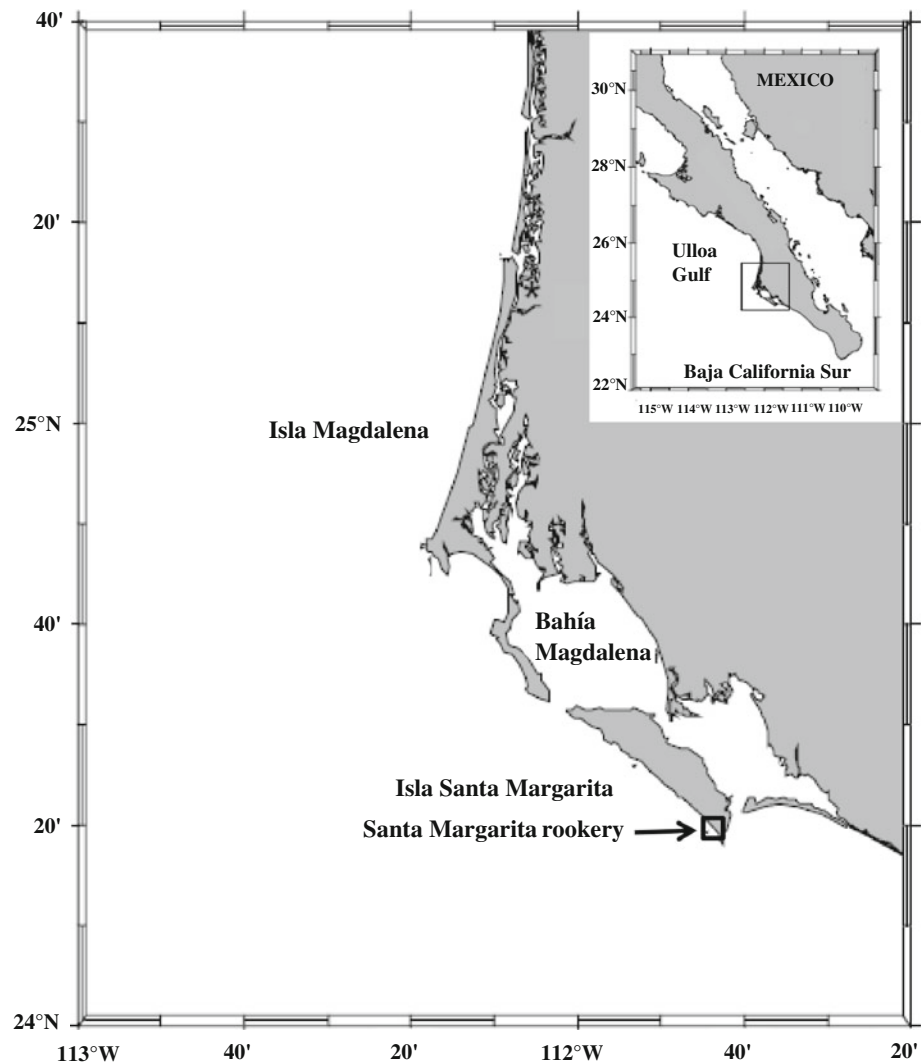
In order to isolate the collagen fraction, powdered dentin samples ($\sim 15 \text{ mg/sample}$) were demineralized with 0.1 M hydrochloric acid and then rinsed to neutrality with distilled water. Dentin samples were not lipid extracted prior to analysis because it does not contain appreciable quantities of ^{13}C -depleted lipids (Newsome et al. 2006, 2009). The atomic C/N ratio of all tooth dentin samples ranged from 2.8 to 3.0, which is within the range for unaltered, lipid-free collagen (DeNiro and Epstein 1978).

Approximately 1 mg of the demineralized sample was weighed into a $3 \times 5 \text{ mm}$ tin capsule. Carbon ($\delta^{13}\text{C}$) and nitrogen ($\delta^{15}\text{N}$) isotope values were determined using a Carlo-Erba elemental analyzer (NC 2500) interfaced with a Finnegan Delta Plus XL mass spectrometer (Carnegie Institution of Washington, Washington, DC). Isotopic results are expressed as δ values, $\delta^{13}\text{C}$ or $\delta^{15}\text{N} = 1,000 \times [(R_{\text{sample}}/R_{\text{standard}}) - 1]$, 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 atmos. N_2 for nitrogen. The units are expressed as parts per thousand (‰). Repeated analysis of a gelatin standard yielded a within-run standard deviation of $\leq 0.2 \text{ ‰}$ for both $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values.

Data analysis

Since several ontogeny stages or categories are present within each tooth, the isotopic values obtained from the

Fig. 1 Study area. Isla Santa Margarita, Bahía Magdalena in Baja California Sur, México



different GLGs corresponding to each stage were grouped into distinct categories (Peterson and Bartholomew 1967). For both sexes, the first GLG was assumed to represent the first year and was assigned to the pup category and the next three GLGs (corresponding to 2–4 years old) were assigned to the juvenile category (there were no significant differences between juveniles sexes, so they were considered as one category). For females, the successive GLGs from 5 years old to death were assigned to adult female category. For males, the fifth to eighth GLGs were assigned to the subadult category and all GLGs representing ≥ 9 years of age were assigned to the adult male category (Table 2).

The GLG values within one tooth cannot be considered as independent of each other, so they were taken as repeated measurements. The sphericity of the data was assessed by comparing the non-similarity (based on Euclidian distances) among individuals using a PERMDISP analysis as recommended by Anderson et al. (2008). Since we did not find significant differences ($p(\text{perm}) > 0.1$), a two-way

permutational multivariate analysis of variance (PERMANOVA) was performed (pair wise permutational comparisons). Sex and category were used as fixed factors and individuals as random effect nested on category (Anderson 2001; McArdle and Anderson 2001); as there are more categories in males than in females, category was nested on sex. Permutation implies random reassignment of the observations to the treatment groups under each variable, with subsequent recalculation of the F -statistics. This is repeated many times to create a distribution of F values, which then is used for comparison with the F value from the original dataset instead of tabulated values. The analysis was based on Euclidean distances. A total of 9,999 unrestricted permutations of raw data were used. The multivariate analysis was run using the computer programs PERMANOVA v. 1.6 (Anderson 2001; McArdle and Anderson 2001) and PERMDISP (Anderson 2004).

Time (calendar years) was considered as a co-variant; however, it was not possible to assess the interaction effect

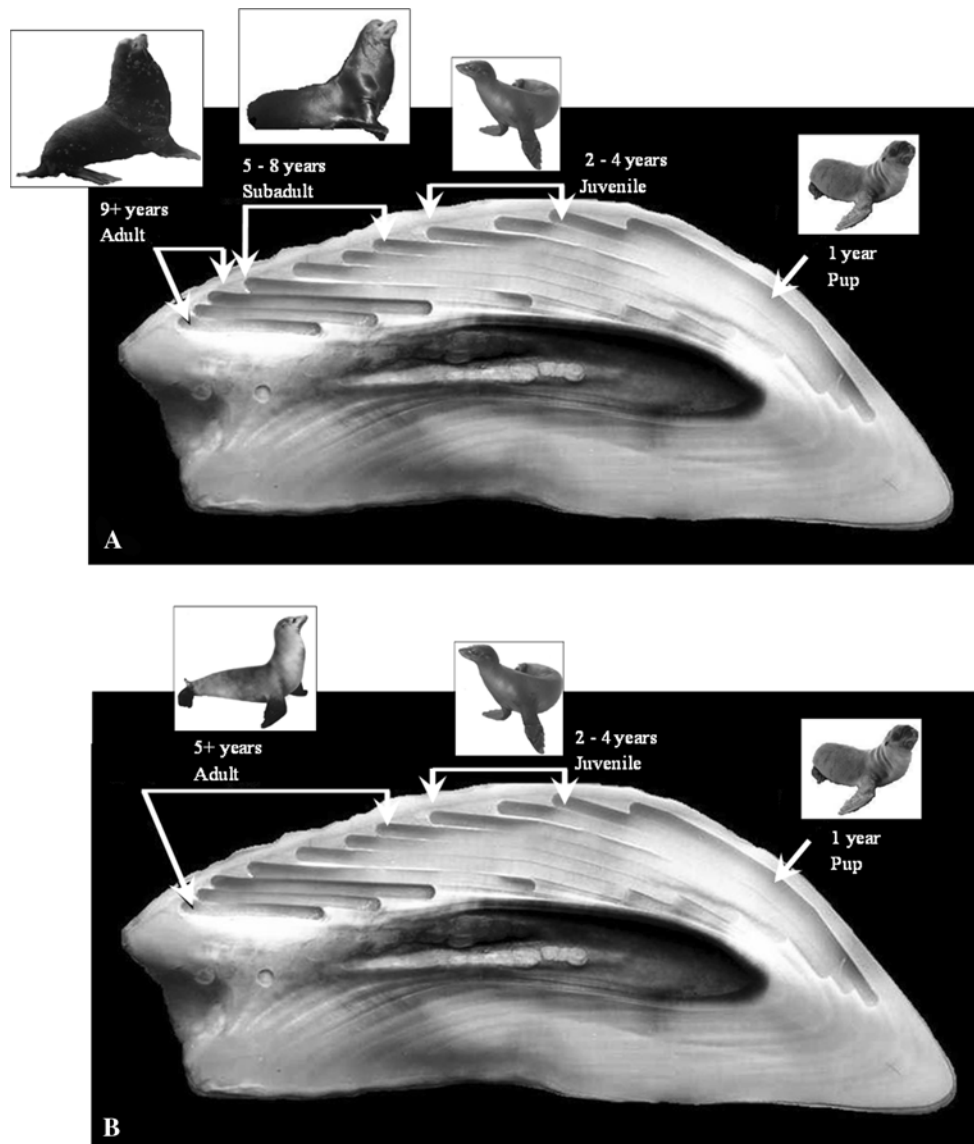


Fig. 2 Picture of sectioned adult California sea lion canine tooth representing the different categories for both sexes (**a** adult male; **b** adult female). The annual growth layer groups (GLGs) are observed in the *lower half* of the tooth and the marks *left* by the Micro Mill

System dentin sampling in the *upper half*. GLGs from the adult stage tended to be shorter (~7 mm) and thinner (~1 mm) in contrast to GLGs deposited during the early years of life, which are longer (20+ mm) and thicker (~3 mm)

Table 2 $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ values—mean and standard deviation ($\pm\text{SD}$)—of the sex and ontogenetic categories of 20 California sea lions from Isla Santa Margarita and the total number of Growth Layer Groups (GLGs) analyzed for each group

Sex/age category	Number of categories	GLGs	$\delta^{15}\text{N}$ (‰) Mean	$\delta^{15}\text{N}$ SD	$\delta^{13}\text{C}$ (‰) Mean	$\delta^{13}\text{C}$ SD
Pups	20	20	20.3	0.9	-13.2	0.6
Juveniles	20	59	18.4	1.0	-12.7	0.5
Subadult males	8	36	18.9	1.0	-12.7	0.7
Adult females	12	17	17.7	1.2	-13.1	0.7
Adult males	2	9	19.0	0.9	-12.0	0.3
Total/mean	62	141	18.7	1.2	-12.8	0.8

Each ontogenetic category is formed by a different number of GLGs (pups: 1, juveniles: 3, subadult males: 4, adult females (≥ 5 years of age) and adult males (≥ 9 years of age))

among each one of the involved factors because of the presence of empty cells in the original data matrix. Instead, we used a Spearman correlation between dental collagen isotopic values and calendar years for each of the age/sex categories to determine a significant temporal variation of the isotopic ($\delta^{13}\text{C}$ and $\delta^{15}\text{N}$) values. The correlation analyses were performed using the software Statistica 8.0 (Stat Soft).

Results

Sampling of tooth dentin collagen from multiple GLGs across 20 different California sea lion teeth collected at Isla Santa Margarita produced 141 samples. Mean (\pm SD) $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values of these dentin samples were -12.8 ± 0.8 and 18.7 ± 1.2 ‰, respectively.

Temporal relationships in $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values within age and sex categories

Examination of $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values within age and sex categories over time produced four significant negative trends ($p < 0.05$). Significant negative trends were observed for $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ in subadult males between 1973 and 1985 and for $\delta^{15}\text{N}$ in adult and juvenile males between 1970 and 1983.

Isotopic variation among age categories

Statistical differences were found for $\delta^{15}\text{N}$ (PERMANOVA, Pseudo- $F = 12.08$, $df = 5$, 134 $p < 0.0001$) and $\delta^{13}\text{C}$ (PERMANOVA, Pseudo- $F = 4.18$, $df = 5$, 134 $p < 0.01$) among the different sea lion sex and age categories from Isla Santa Margarita (Table 3). We found no significant differences ($p > 0.05$) between sexes for pup and juvenile categories, so they were analyzed irrespective of sex. We observed four general trends in mean isotope values between sex and age categories: (1) pups had significantly different $\delta^{15}\text{N}$ values than other categories; (2) juveniles and subadult males had intermediate $\delta^{15}\text{N}$ values between pups and adult females; (3) adult females had the lowest mean $\delta^{15}\text{N}$ values among all categories; and (4) adult males had the highest mean $\delta^{13}\text{C}$ values (Fig. 3).

The pups had a mean (\pm SD) $\delta^{15}\text{N}$ value (20.3 ± 0.9 ‰) that was significantly higher than the other groups ($p < 0.05$; Table 2). Pups (-13.2 ± 0.6 ‰) and adult females (-13.1 ± 0.7 ‰) also had lower mean $\delta^{13}\text{C}$ values than adult males ($p < 0.05$); however, no significant differences were found between pups and juveniles (-12.7 ± 0.5 ‰) or subadult males (-12.7 ± 0.7 ‰) ($p > 0.1$). Adult males had significantly higher $\delta^{13}\text{C}$ values (-12.0 ± 0.3 ‰) than all categories ($p \leq 0.05$) (Fig. 3).

Table 3 Differences in $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ values determined using PERMANOVA analyses of two crossed, fixed factors, sex and category: category levels (pups, subadult, juvenile, adult female, and adult male) in *Zalophus californianus*

Source	df	SS	MS	Pseudo-F	$p(\text{perm})$	Perms
$\delta^{15}\text{N}$						
Sex	1	18.62	18.62	17.264	0.0001	9,828
Category (sex)	5	65.175	13.035	12.086	0.0001	9,954
Residual	134	144.53	1.0785			
Total	140	228.32				
$\delta^{13}\text{C}$						
Sex	1	0.452	0.452	0.78934	0.3712	9,839
Category (sex)	5	12.261	2.4522	4.1879	0.0058	9,956
Residual	134	12.261	0.29791			
Total	140	71.659				

$p(\text{perm})$ represents the permutational p value and $Perms$ denotes the number of permutations carried out. Significant p values (to 95 % significance level) are shown in bold

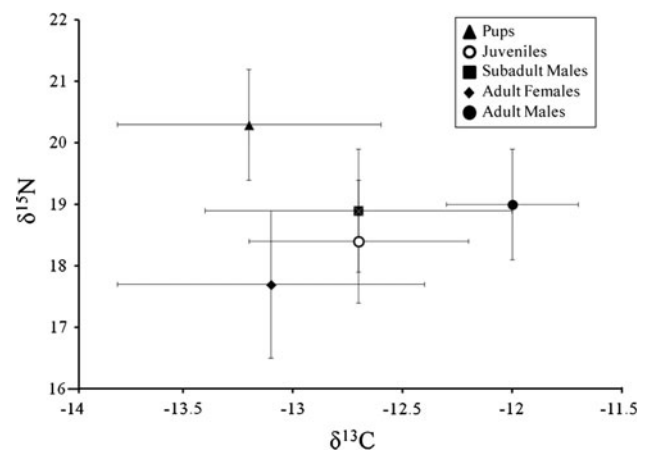


Fig. 3 Mean tooth dentin $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values of different age and sex classes of California sea lions from Isla Santa Margarita Baja California; error bars represent standard deviation

Juveniles (18.4 ± 1.0 ‰) had a lower mean $\delta^{15}\text{N}$ value than pups and slightly but not significantly higher ($p > 0.01$) than adult females (17.7 ± 1.2 ‰). The intermediate $\delta^{15}\text{N}$ value of juveniles (2–4 years old) between that of pups and adult females is presented as three distinct stages (juv1, juv2, juv3) representing the 3 years that correspond to this category. Since our approach allowed for an annual investigation of isotope values in canine teeth, it was possible to determine $\delta^{15}\text{N}$ values for each year in the juvenile category and there were no significant differences ($p = 0.96$) among these three juvenile years.

Subadult (18.9 ± 1.0 ‰) and adult males (19.0 ± 0.9 ‰) had similar mean $\delta^{15}\text{N}$ values ($p > 0.5$), but these were

significantly higher than the mean $\delta^{15}\text{N}$ value for adult females ($17.7 \pm 1.2 \text{ ‰}$; $p < 0.05$).

Isotopic variation within each age and sex category

Annuli $\delta^{15}\text{N}$ values ranged from 14.8 to 21.5 ‰ among all categories. Juveniles varied between 16.4 and 20.4 ‰, with most individual annuli ($\sim 60 \%$) in the range from 18.0 to 19.9 ‰. Adult females exhibited a wider range of $\delta^{15}\text{N}$ values (14.9–20.6 ‰), but most individual annuli ($\sim 40 \%$) range from 18.0 to 19.9 ‰. The combined group of subadult and adult males had $\delta^{15}\text{N}$ values that ranged from 18.1 to 21.2 ‰, with most individual annuli ($\sim 70 \%$) ranging from 18.0 to 19.9 ‰.

Annuli $\delta^{13}\text{C}$ values ranged from -14.5 to -11.4 ‰ among all categories, with most ($\sim 50 \%$) of the values ranging between -12.9 and -12.0 ‰ . The variation in $\delta^{13}\text{C}$ values was not as high as for $\delta^{15}\text{N}$, especially for the adult categories. Subadult and adult males showed a higher degree of variation in $\delta^{13}\text{C}$ ($\sim 4 \text{ ‰}$) than adult females and juveniles ($\sim 3 \text{ ‰}$).

Discussion

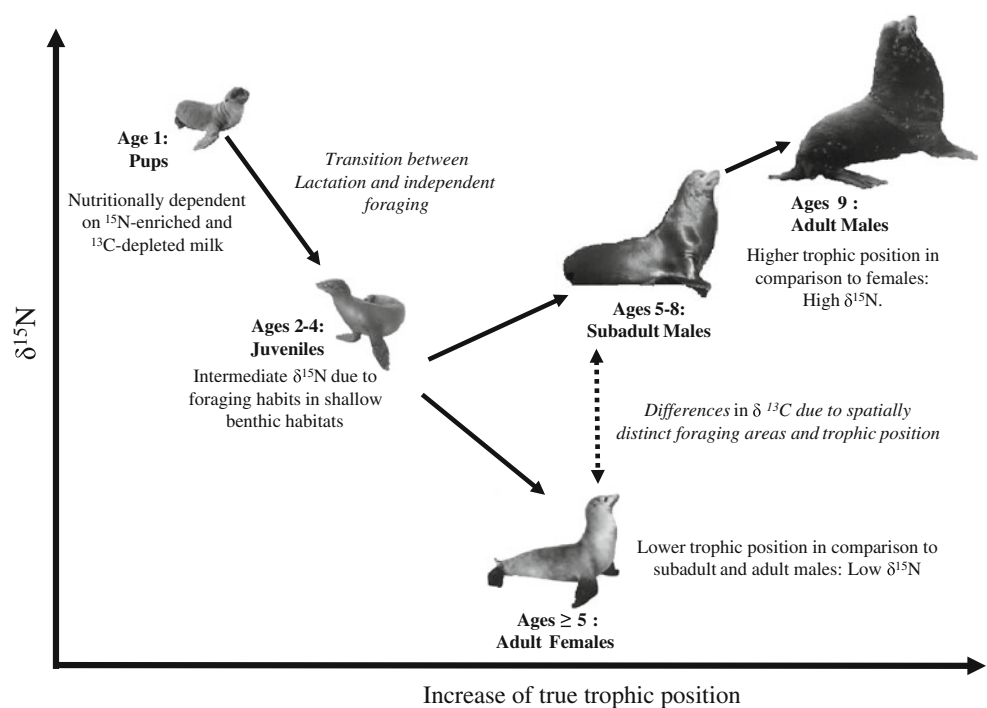
The subsampling of GLGs within individuals and the $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ analysis of tooth dentin allowed us to track ontogenetic dietary changes both within and among individuals. We found significant differences in mean $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ values among *Zalophus* sex and age categories, which

are likely driven by two factors. The first are ontogenetic shifts in diet, which include a transition from pups that are nutritionally dependent on milk, through the juvenile stage when foraging capabilities are not fully developed (Kuhn et al. 2006), and into the adult stage reflecting fully developed foraging habits. The second factor is related to a high degree of sexual dimorphism in *Zalophus*. Age- and sex-related differences in body mass may play an important role in dispersal abilities and variation in habitat utilization in this species (Fig. 4). Our findings were supported by previous investigations of *Zalophus* and other otariid species (Hobson and Sease 1998; Kurle and Worthy 2001; Newsome et al. 2006; Páez-Rosas and Aurióles-Gamboa 2010) and provide another example of the utility of stable isotope analysis to assess ontogenetic shifts in foraging ecology.

Pups

Irrespective of sex, *Zalophus* pups are dependent on their mother's milk during the first year of life; thus, the GLGs corresponding to this time period are marked by relatively high $\delta^{15}\text{N}$ values. Since adult female sea lions catabolize their own tissues (blubber and muscle) to produce milk (as occurs in many other mammal species), pups typically have higher $\delta^{15}\text{N}$ than lactating adult females by 2.0–2.5 ‰ (Hobson and Sease 1998; Newsome et al. 2006). This enrichment is similar to the trophic enrichment between consumer and prey. For $\delta^{13}\text{C}$, the expected trophic enrichment is complicated by the fact that pinniped milk

Fig. 4 Schematic synthesis of the ecological differences and increase of true trophic position among sex and age categories of the California sea lion from Isla Santa Margarita based on $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ values



contains a high percentage ($\sim 35\%$ for California sea lions; Pilson and Kelly 1962) of ^{13}C -depleted lipids (DeNiro and Epstein 1978), which can result in pups having lower $\delta^{13}\text{C}$ values than their mothers during the nursing period. These trends have been reported in muscle and bone collagen of northern fur seals (*Callorhinus ursinus*) and California sea lions (Hobson et al. 1997; Newsome et al. 2006), which suggests that pups can use carbon from ^{13}C -depleted milk lipids to synthesize non-essential amino acids during periods of rapid growth. Contrary to previous studies, our results showed similar dentin $\delta^{13}\text{C}$ values for pups ($-13.2 \pm 0.6\%$) and adult females ($-13.1 \pm 0.7\%$), which may be driven by direct routing of milk protein, and the amino acids from which they are constructed, rather than use of lipid-derived carbon (Jenkins et al. 2001; Martínez del Río et al. 2009; Newsome et al. 2010). More research is required to address the relative use of protein versus non-protein sources of carbon and nitrogen to tissue synthesis in animals that are experiencing rapid growth when resources are in high demand. Pinnipeds are an ideal group in which to test the relative use of protein and lipid carbon to tissue synthesis during periods of rapid growth because pinniped milk has a high fat content relative to other mammal groups, ranging from ~ 30 to 60% (Boness and Bowen 1996).

Juveniles

Juveniles had higher mean (\pm SD) $\delta^{15}\text{N}$ values ($18.4 \pm 1.0\%$) than adult females ($17.7 \pm 1.2\%$); however, the difference was not significant. If all juveniles were consuming milk, then they should have significantly higher $\delta^{15}\text{N}$ values than females, which they do not. Some juveniles are in a transitional stage between dependence on milk and the development of mature foraging capabilities, resulting in a mixture of maternal milk and solid prey after the first year of life (Newsome et al. 2006; Elorriaga-Verplancken 2009); however, this late weaning is not a consistent factor at a population level and cannot be considered as a dominant reason for the observed ^{15}N -enrichment in individuals of this category. *Zalophus* juveniles may forage in coastal benthic habitats because of (1) a limited capacity (relative to adults) to store oxygen (Kuhn et al. 2006) and (2) limited experience with hunting fast-moving prey in pelagic settings. Relative to pelagic ecosystems, benthic ecosystems can be ^{15}N enriched due to bacterial degradation of dead organic material as it sinks and is deposited on the ocean floor (Macko and Estep 1984; Young et al. 2010).

Because of the combination of milk consumption for some juveniles and foraging in benthic environments, we would expect juveniles to have even higher $\delta^{15}\text{N}$ values relative to adult females. There are two factors that may

play an important role in why the observed difference in $\delta^{15}\text{N}$ was only 0.7% . First, juveniles likely consume small prey at a lower trophic level resulting from a lack of foraging experience; this factor has been cited to explain isotopic differences among ontogenetic classes in other otariid species such as the northern fur seal (Kurle and Worthy 2001). In this region, lower trophic prey may include the pelagic red crab (*Pleuroncodes planipes*) that has $\delta^{15}\text{N}$ values of $14.5 \pm 0.6\%$ (Camalich-Carpizo 2011). Red crabs are abundant in Bahía Magdalena and are known prey items for *Zalophus* (Bautista 2002). Second, and perhaps not mutually exclusive from the previous factor, juvenile growth rates are faster than adults, which result in higher protein accretion rates and lower $\delta^{15}\text{N}$ trophic discrimination factors for young animals relative to non-growing adults. Theoretically, the isotopic composition of a consumer approaches that of its diet as more dietary protein is used directly for the synthesis of tissue protein to sustain growth (Trueman et al. 2005; Martínez del Río et al. 2009; Newsome et al. 2010).

High $\delta^{13}\text{C}$ values in juveniles ($-12.7 \pm 0.5\%$) relative to adult females may also be a consequence of foraging in coastal benthic habitats where primary production is largely influenced by ^{13}C -enriched macroalgae (Michener and Schell 1994; France 1995) and where phytoplankton have high growth rates resulting in high $\delta^{13}\text{C}$ values relative to offshore pelagic habitats (Fry and Wainright 1991; Laws et al. 1995).

Adult females and males

The significant difference in $\delta^{15}\text{N}$ values among adult females and subadult/adult males likely relates to the ability of males to travel greater distances from the breeding colony and also their capacity to dive deeper (Peterson and Bartholomew 1967; Odell 1975; Auriolles-Gamboa et al. 1983; Weise and Costa 2007). Variation in dispersal and diving capability between adult males and females is a consequence of significant differences in size/morphology and the limited ability of females to travel far from the colony while nursing a pup (Gautier-Hion 1980; Clutton-Brock et al. 1987). Spatial segregation in foraging areas used by adult males and females likely results in a reduction of resource competition during a time when females are carrying the cost of lactation (Estes et al. 2003; Lewis et al. 2006). Adult males breeding on the Channel Islands off Southern California make northward migrations to waters off Oregon, Washington, and British Columbia (Bartholomew and Boolootian 1960; Mate 1975). While there are no tracking data available for adult males breeding in Baja California, it is likely that they also migrate northward into the productive waters off Southern and Central California during the non-breeding season, which may help explain the winter peak in the numbers of

mature males observed on the Channel Islands (Odell 1975). Based on this theoretic framework, differences of $\delta^{15}\text{N}$ values between subadult/adult males and adult females observed in this study could be explained by the following two factors that are not mutually exclusive: (1) adult males forage on prey with a higher trophic position than females; (2) sexes utilize spatially segregated foraging habitats which have different baseline $\delta^{15}\text{N}$ values (Burton and Koch 1999; Aurióles-Gamboa et al. 2009).

Our data suggest that dietary differences may be more important in explaining the isotopic differences between adult females and subadult/adult males. $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ of both phytoplankton and particulate organic matter (POM) have been shown to be negatively correlated with latitude in the Eastern Pacific Ocean (Wada and Hattori 1991; Goericke and Fry 1994; Altabet et al. 1999; Michener and Schell 1994; Burton and Koch 1999; Aurióles-Gamboa et al. 2006). Thus, if spatial differences in baseline food web isotope values were the principal factor driving isotopic differences between adult sexes, then males should have lower $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ values than females. Instead, subadult/adult males have significantly higher $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ values. Thus, isotopic differences between the sexes are likely related to differences in diet and trophic position, with adult males consuming larger, higher trophic level prey to fuel their greater energetic demands.

Higher $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ values in adult males may also be related to their diving capability, which allows them to forage in ^{13}C - and ^{15}N -enriched benthic habitats (Michener and Schell 1994; France 1995) on the continental shelf that are not easily accessible to adult females due to physiologic diving constraints (Weise and Costa 2007). Scat analysis suggests that subadult/adult males consume demersal prey within Bahía Magdalena, which is probably local foraging location for these age categories (Aurióles-Gamboa et al. 1983). Demersal fishes such as smooth stargazer, (*Kathetostoma avertuncus*), Panama hake (*Merluccius angustimanus*), longfin sanddab (*Citharichthys xanthostigma*), perch (*Diplectrum* sp), lizardfish (*Synodum* sp), and prowspline cusk eel (*Lepophidium* sp) are consumed by *Zalophus* in this area (Bautista 2002). These prey collected in Bahía Magdalena have mean $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values that range from -18.3 to -17.6 and 15.3 to 16.8 ‰, respectively (Camalich-Carpizo 2011). Application of suitable trophic discrimination factors to *Zalophus* dentin collagen suggests that these demersal species are important prey for subadult males and juveniles from Isla Santa Margarita. It is important to acknowledge that while there is a decent amount of information on the Bahía Magdalena *Zalophus* diet from scat analysis, there is little isotopic information available for potential prey. Further collection and isotopic analysis of prey in this region is required for more detailed assessment of *Zalophus*' foraging strategies.

Table 4 Spearman correlations results (r values) between mean isotope values and calendar years for each of the sex/age categories

	Pup	Juvenile	Subadult	Adult
<i>Males</i>				
$\delta^{15}\text{N}$	0.29	-0.45	-0.78	-0.87
$\delta^{13}\text{C}$	-0.37	-0.41	-0.76	-0.54
<i>Females</i>				
$\delta^{15}\text{N}$	-0.34	-0.14		-0.22
$\delta^{13}\text{C}$	0.40	0.14		-0.16

The significant values ($p < 0.05$) are presented in bold. Negative r values imply a negative correlation with time (years)

Lastly, the absence of tracking data for adult males from Isla Margarita limits our interpretations, and the possibility that *Zalophus* males from Isla Santa Margarita may not be migrating northward cannot be completely discarded. Additional movement data are needed to compare migration patterns of sea lions breeding in Baja California and Southern California.

Plausible effect of temporal isotopic trends

In some juveniles, we observed a significant negative trend (~ 0.4 ‰) in $\delta^{15}\text{N}$ between individuals collected in the late 1970s versus the early 1980s. We also found a significant negative trend in isotope values from the 1970s to 1980s in subadult (~ 0.5 ‰ in $\delta^{15}\text{N}$ and ~ 0.7 ‰ $\delta^{13}\text{C}$) and adult males (~ 0.5 ‰ in $\delta^{15}\text{N}$) (Table 4). These findings cannot be discarded as one of the factors that caused a significant difference between adult females and subadult and/or adult males. Higher $\delta^{15}\text{N}$ values in juveniles, subadult and adults males relative to adult females, however, lend support to our hypothesis that isotopic differences are primarily driven by foraging preferences. We acknowledge that there is a higher degree of uncertainty in the interpretation of these results because of the potential for temporal shifts in isotope values at the base of the food web (i.e., baseline shifts).

Isotopic variation within sex/age categories

There was a greater degree of variation in $\delta^{15}\text{N}$ versus $\delta^{13}\text{C}$ values within a given sex/age category. This pattern likely relates to higher sensitivity of $\delta^{15}\text{N}$ values to changes in trophic position relative to $\delta^{13}\text{C}$ (Michener and Schell 1994). Variation in isotope values within age/sex categories, however, may also relate to limitations in our sampling scheme since teeth were only collected over a 4-year period (1982–1985). In addition, samples within one category are derived from different years, so temporal variation in baseline isotope values could also be a source of observed isotopic variation in *Zalophus*.

We also observed isotopic variation among GLGs within categories, providing evidence for inter-individual differences in foraging strategies under similar conditions. Inter-individual variation in foraging preferences has been reported for other otariids, such as the Galapagos sea lion, using satellite tracking and stable isotopes analysis (Villegas-Amtmann et al. 2008; Páez-Rosas and Aurióles-Gamboá 2010). Adult females may be particularly susceptible to inter-individual differences in prey preferences as they are restricted to foraging in habitats within close proximity (~30 mile radius) of the breeding colony throughout the year (Kuhn et al. 2006) because their income-based maternal strategy requires frequent trips back to the rookery to provision pups (García-Aguilar and Aurióles-Gamboá 2003). As a result, adult females may experience greater inter-individual competition, a potential selective force that can drive diversification of foraging strategies at the individual level (Estes et al. 2003). For males or juveniles, other factors may be important in shaping individual foraging diversification. Adult males exhibit remarkable dispersal and diving capability (Weise and Costa 2007), which may translate to a greater degree of variation in individual foraging strategies to reduce intra-sexual competition, as observed for northern elephant seal adult males (Le Boeuf et al. 1993). Juveniles may also display variation in foraging behaviors as a result of two factors: (1) nursing can extend into the second or even third year of life (Newsome et al. 2006; Elorriaga-Verplancken 2009) and (2) foraging inexperience during the transition from nursing to nutritional independence (Eberhardt and Sinnif 1977).

Although stable isotope analysis does not typically provide information regarding the taxonomic identity of prey, a wide range of $\delta^{15}\text{N}$ values within sex and age categories suggests that foraging diversification occurs within and among groups analyzed in this study (Post 2002; Lewis et al. 2006; Wolf et al. 2008; Newsome et al. 2009; Páez-Rosas and Aurióles-Gamboá 2010).

Our results suggest that inter-individual differences in dietary preferences may be driven by both ecological (i.e., competition) and body size in *Zalophus*. Our isotopically derived foraging data generally agree with expected ontogenetic dietary shifts in *Zalophus*; however, additional information is required to better constrain potential interpretations discussed above. Complementary datasets from telemetry, scat analysis, and additional isotopic analysis of potential prey would allow for a better assessment of the relative importance of latitudinal baseline isotopic gradients versus diet composition in driving the observed trends among the age and sex categories analyzed in our study.

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