Intraspecific comparison of diet of California sea lions (*Zalophus californianus*) assessed using fecal and stable isotope analyses

A.J. Orr, G.R. VanBlaricom, R.L. DeLong, V.H. Cruz-Escalona, and S.D. Newsome

Abstract: The diet of juvenile and adult female California sea lions (*Zalophus californianus* (Lesson, 1828)) at San Miguel Island, California, was estimated and compared using fecal and stable isotope analyses to determine dietary differences by age. Fecal samples were collected during 2002–2006 and prey remains were identified. Stable carbon ($\delta^{13}C$) and stable nitrogen ($\delta^{15}N$) isotope values were determined from plasma and fur obtained from yearlings, 2- to 3-year-old juveniles, and adult females during 2005 and 2006. Juveniles ate more than 15 prey taxa, whereas adult females consumed more than 33 taxa. Relative importance of prey was determined using percent frequency of occurrence (%FO). *Engraulis mordax* Girard, 1854, *Sardinops sagax* (Jenyns, 1842), *Merluccius productus* (Ayres, 1855), genus *Sebastes* Cuvier, 1829, and *Loligo opalescens* Berry, 1911 were the most frequently occurring (%FO > 10%) prey in the feces of both juvenile and adult female sea lions, although their importance varied between age groups. Only yearlings had significantly different isotopic values than older conspecifics, indicating that older juveniles were feeding at a similar trophic level and in similar habitats as adult females. Whereas each method had biases, combining the two provided a better understanding of the diet of California sea lions and intraspecific differences.

Résumé : Des analyses fécales et des analyses d'isotopes stables nous ont permis d'estimer le régime alimentaire de jeunes et de femelles adultes du lion de mer de Californie (*Zalopus californianus* (Lesson, 1828)) à l'île San Miguel, Californie, et de comparer les différences alimentaires en fonction de l'âge. Nous avons prélevé des échantillons de fèces en 2002–2006 et identifié les restes de proies. Nous avons déterminé les valeurs des isotopes stables de carbone ($\delta^{13}C$) et d'azote ($\delta^{15}N$) dans le plasma et la fourrure provenant d'individus de l'année, d'individus de 2–3 ans et de femelles adultes en 2005 et 2006. Les jeunes consomment plus de 15 taxons de proies, alors que les femelles adultes en utilisent plus de 33. L'importance relative des proies est représentée par la fréquence d'occurrence en pourcentage (%FO). *Engraulis mordax* Girard, 1854, *Sardinops sagax* (Jenyns, 1842), *Merluccius productus* (Ayres, 1855), le genre *Sebastes* Cuvier, 1829 et *Loligo opalescens* Berry, 1911 sont les proies qui apparaissent le plus fréquemment (%FO > 10 %) dans les fèces des jeunes lions de mer et des femelles adultes, bien que leur importance varie selon les groupes d'âge. Seuls les individus de l'année présentent des valeurs isotopiques différentes de celles de leurs congénères plus âgés, ce qui indique que les jeunes plus âgés se nourrissent au même niveau trophique et dans des habitats de même type que les femelles adultes. Bien que chaque méthode ait ses sources d'erreurs, la combinaison des deux permet une meilleure compréhension du régime alimentaire des lions de mer de Californie et de ses différences intraspécifiques.

[Traduit par la Rédaction]

Introduction

Energy is essential for all animals, and many actively search, pursue, and handle several types of prey to survive and reproduce. Although it has been assumed that individuals seek to maximize their rate of energy intake during feeding (Schoener 1971), there are constraints on the rate of energy intake that can affect optimal foraging by animals (Pyke et al. 1977). One such constraint occurs in the foraging behavior of aquatic mammals.

Received 10 May 2010. Accepted 10 November 2010. Published on the NRC Research Press Web site at cjz.nrc.ca on 20 January 2011.

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Because foraging by aquatic mammals occurs during a breath hold, feeding depth and time spent searching, pursuing, handling, and consuming prey are constrained by oxygen reserves acquired before submergence. The physiological constraints that limit dive duration are highly correlated with an animal's size and age (Horning and Trillmich 1997; Burns 1999). Oxygen stores increase with body mass (Schmidt-Nielsen 1984; Kooyman 1989) and are depleted faster in smaller animals because of their higher mass-specific metabolic rates (Kleiber 1975; Thorson and Le Boeuf 1994). Therefore, young individuals theoretically are more limited in the depths that they can dive (aerobically) and the durations that they can stay underwater, resulting in differences in foraging behaviors compared with older conspecifics.

Several authors have suggested that other factors related to prey (e.g., prey species, behavior, energy content, size, swimming speed, abundance, density, and distribution) and predator species, age, sex, experience, social status, or conspicuousness may be more important than physiological limits of a breath hold to the diving and foraging patterns of aquatic mammals (e.g., Schoener 1971; Dunstone and O'Connor 1979; Costa 1991; Pierce and Boyle 1991). Such factors and constraints frequently are observed in the foraging behaviors of otariid pinnipeds. For example, lactating females are central place foragers and constrained in duration by their pups' fasting limitations to forage near rookeries during breeding season (Melin et al. 2000). Juveniles, which may be physiologically constrained to feeding in shallower depths, have less experience at acquiring prey or handling large prey and might not exploit the same range of food items as faster and larger adults. These differences in phenotype, physical capabilities, and biological requirements among conspecifics likely result in different patterns in diet, distribution, and habitat use related to feeding among age classes of otariids.

Various methods have been used to determine the diet of otariids (e.g., collection of stomachs, regurgitations, enemas, and lavages); however, fecal (scat) samples primarily are collected nowadays. Scats are useful because many can be collected quickly, inexpensively, and with little or no harm to animals (Harvey 1989). The distinctive morphology of otoliths and other diagnostic bones of teleost fishes, various structures of cartilaginous fishes, and beaks of cephalopods can be used to identify pinniped prey taxa.

Stable isotope analysis, among other biochemical methods, has been used to augment the more conventional techniques in assessing the diet of pinnipeds. In particular, the abundance of naturally occurring stable isotope ratios of carbon ($^{13}C/^{12}C$) and nitrogen ($^{15}N/^{14}N$) have been used to examine trophic relations and identify sources of prey or nutrients of pinnipeds in several systems (see review by Newsome et al. 2010).

Stable isotope analysis is based on the idea that the stable isotope composition of a consumer's diet is reflected in its tissues. Because of the preferential excretion of ^{14}N in urine, $\delta^{15}N$ values increase by approximately 3‰–5‰ per trophic level in marine food webs (DeNiro and Epstein 1978; Minagawa and Wada 1984; Owens 1987; Wada et al. 1991; Hobson and Welch 1992; Kurle 2002). Therefore, the relative amount of ^{15}N in tissues reflects the trophic level at which the consumer is feeding, with higher $\delta^{15}N$ values corresponding to higher trophic levels. The ratio of stable carbon isotopes varies little with trophic position (approximately 0.5‰–1.1‰ enrichment with increase of trophic level in marine food webs; Fry and Sherr 1984; Wada et al. 1991; Kurle 2002). Instead, $\delta^{13}C$ reflects the isotopic composition of primary producers at the base of the food web and has been used to indicate consumer foraging locations ($\delta^{13}C$ enrichment: fresh water > marine, nearshore > offshore, benthic > pelagic, low latitude > high latitude; Rau et al. 1982; Fry and Sherr 1984; Wada et al. 1991; France 1995; Burton and Koch 1999; Cherel and Hobson 2007).

In contrast to traditional methods, which reflect prey consumed by pinnipeds only during the most recent feeding events (Orr and Harvey 2001; Sweeney 2008), the stable isotope approach reflects the diet assimilated over a longer time period, ranging from a few days to years because of the dissimilar isotopic turnover rates of various tissues (Kurle and Worthy 2002; Dalerum and Angerbjörn 2005; Hammill et al. 2005). Although stable isotope analysis does not provide detailed information on dietary composition and interpreting isotopic data can be complicated, the use of stable isotope analysis is advantageous in avoiding the biases associated with using scat samples alone (e.g., Jobling and Breiby 1986; Dellinger and Trillmich 1988; Arim and Naya 2003; Sweeney 2008). Additionally, when using stable isotope analysis, ancillary information can be collected and intraspecific comparisons (e.g., age) are possible.

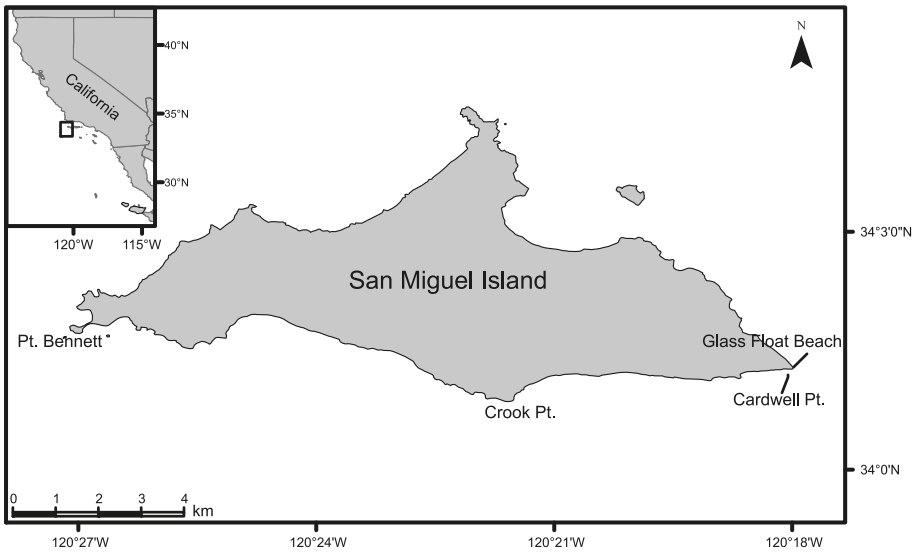
The California sea lion (*Zalophus californianus* (Lesson, 1828)) is the most abundant sea lion in the world, with an estimated population of 355 000 (Caretta et al. 2005; Aurioles and Trillmich 2008). Juveniles compose a significant proportion of this predator that occupies coastal waters and directly competes for food resources with humans, yet we know little about their foraging behaviors. Studies have been conducted to determine the diet of California sea lions throughout their distribution (e.g., Antonelis et al. 1984; Roffe and Mate 1984; Lowry et al. 1991; García-Rodríguez and Aurioles-Gamboa 2004), but the size distribution of prey and differences in diet according to age of sea lions (specifically juveniles) were not assessed. Information about juvenile diet is needed to provide insight into potential intraspecific competition, resource partitioning, and optimal foraging by conspecifics at different stages of their development. The objective of this study was to use fecal and stable isotope analyses to describe the diet of juvenile California sea lions and to compare them with those of adult females to examine age-related variation in diet between these age classes. Adult males disperse from rookeries during the nonbreeding season and many fast during the breeding season, therefore their dietary information was not included in this study.

Materials and methods

Fecal analysis

Scat and enema samples from California sea lions were collected at San Miguel Island (34.03°N, 120.44°W; Fig. 1) during July 2002; March, September, and October 2003; March 2004; March and April 2005; and February, March, and July 2006. Samples collected at Cardwell Point, Glass

Fig. 1. Map of San Miguel Island, California, where fecal and stable isotope samples were collected from California sea lions (*Zalophus californianus*). Fecal samples collected at Crook Point, Cardwell Point, and Glass Float Beach were from juveniles (1–3 years old), whereas those collected from the west end of the island near Point Bennett were from adult females (≥4 years old).



Float, and Crook Point beaches were from juveniles, whereas scats obtained on the west end of the island were from adult females (Fig. 1). Here, age class was based on the animals' morphological characteristics. Juveniles of both sexes were non-pups, 1–3 years old, approximately 1–1.5 m long, with coloration ranging from tan to brown. Adult females were ≥4 years old, 1.5–2 m long, and light brown or cream colored (descriptions summarized from Aurioles 1988; Aurioles and Zavala 1994). During the sampling periods, Glass Float and Crook Point beaches were used by juvenile sea lions and rarely used by other demographic groups. When older animals were present, an effort was made to collect samples that we subjectively determined to be excreted by a juvenile (e.g., relatively smaller in size and diameter). Only "fresh" scats (i.e., those with no obvious signs of desiccation) were collected to assure that prey species were consumed at or near to the time of collections. Each scat was collected into either a 124 μm mesh bag (3.8 L, 85–95 fine-mesh nylon paint strainers; Reaves and Company,[2] Durham, North Carolina, USA) or a plastic Whirl-Pak®[2] bag. Date, location, and suspected age class of the animal that expelled the sample were recorded on a card and placed with each sample. Scats were frozen until future cleaning and analyses.

Enemas were given to selected juvenile sea lions using techniques described by Staniland et al. (2003). Enema samples were collected in an effort to obtain information about the animal that excreted the sample so that dietary estimates accessed using two methods could be compared for each individual. Enema samples were stored in plastic bags and frozen for future cleaning and analyses. Because of limited samples sizes, ancillary information for animals given enemas was disregarded and enema samples were pooled with scats for further processing and analyses. All frozen samples were thawed overnight and prey remains (e.g., otoliths, bones, and lenses from teleost fishes; cartilage from cartilaginous fishes; and beaks, pens, and statoliths from cephalopods) were separated from other organic waste material by rinsing samples with water through a series of three sieves (mesh sizes 2.0, 1.0, and 0.5 mm; Murie and Lavigne 1985) or by placing them in mesh bags and cleaning using a washing machine (Orr et al. 2003). All prey hard parts were collected and stored in glass scintillation vials. Fish remains were stored dry and cephalopod parts were stored in a 50% isopropanol solution. Vials containing prey remains for each sample were labeled with a unique identification number, the area of collection, age class of predator, and the date.

Prey items were identified to the lowest taxon possible using an extensive reference collection at The Alaska Fisheries Science Center's National Marine Mammal Laboratory (Seattle, Washington), voucher samples verified by Pacific Identifications (Victoria, British Columbia, Canada), and comparative illustrations acquired from the literature. Unknown prey items were categorized as "unidentified" and "unidentifiable" (Browne et al. 2002). Remains that were categorized as "unidentifiable" were excluded from analyses. A subset of samples (approxmately 10%) was verified by a second identifier. Only fish otoliths and cephalopod beaks were used to estimate size of prey. Otolith length (to the nearest 0.05 mm) was measured parallel to the sulcus from the anterior tip of the rostrum to the posterior edge using a dissecting microscope and either an ocular micrometer or hand-held calipers. Otoliths with broken edges were not measured. The upper and lower rostral lengths of cephalopod beaks were measured (to the nearest 0.05 mm) using a dissecting microscope equipped with an ocular micrometer.

To account for degradation of otoliths during digestion, species-specific correction factors were applied to lengths of otoliths in "fair" condition (Orr and Harvey 2001). A correction factor of 1.3 was used for prey that did not have

[2] References to trade names or companies do not imply endorsement by the National Marine Fisheries Service, NOAA, or the University of Washington.

known correction factors (Harvey 1989; Orr and Harvey 2001). Because cephalopod beak size is not reduced significantly during digestion, correction factors were not applied (J.T. Harvey, G.A. Antonelis, Jr., and C.J. Casson, unpublished data). The length of several prey were estimated (to the nearest 0.1 cm) using species-specific linear regressions of otolith length to fish standard length (supplementary Table S1[3]; Walker 1996; Harvey et al. 2000) and beak rostral length to dorsal mantle length for cephalopods (Table S2[3]; Wolff 1982, 1984; Clarke 1986). Mass estimates (to the nearest 0.1 g) of several prey species were obtained using species-specific regressions of the estimated prey length (described above) and measured masses (Wolff 1982, 1984; Harvey et al. 2000; S. Osborne, personal communication, 1994; W. Walker, personal communication, 2009). Identifying species of rockfish (*Sebastes* spp.) was difficult, so the length and mass regression equations used for this genus were from bocaccio (*Sebastes paucispinis* Ayres, 1854). Bocaccio was selected as the representative rockfish because it was the most abundant rockfish in areas near San Miguel Island (Best and Oliphant 1965; Antonelis et al. 1984). Equations from clawed armhook squid (*Gonatus onyx* Young, 1972) were used to estimate the length and mass of all *Gonatus* species. Identified prey species obtained from fecal samples were pooled using age class (i.e., juvenile and adult female) and year. Differences among estimated prey lengths by age class were non-normally distributed, so a Mann–Whitney *U* test was conducted to determine if there were any significant differences in prey sizes consumed by different-aged sea lions.

Adequacy of sample size to describe diet was determined by creating mean cumulative prey diversity curves (±1 SD) based on the Shannon–Wiener (H') index (Krebs 1999), following an approach proposed by Ferry and Cailliet (1996) and Ferry et al. (1997) and modified by V.H. Cruz-Escalona (co-author) and C. Turren. Diversity curves were created by implementing a Matlab routine that computes 500 random permutations of the original data. If the prey diversity curve reached an asymptote, then we assumed that enough samples were analyzed to characterize the diet.

The relative importance of different prey taxa in the diet was determined using percent frequency of occurrence (%FO), which was defined as

$$\%\mathrm{FO}_i = \frac{\sum_{k=1}^{s} O_{ik}}{s} \times 100$$

where O_{ik} is the absence (0) or presence (1) of taxon i in sample k and s is the number of samples that contained identifiable prey remains.

The presence of taxon i in sample k was determined by using any structure of a particular prey taxon. %FO was calculated for each year and averaged for the study tenure (i.e., 2002–2006) for each age class. Relative frequency of prey taxa per year was used as a proportional metric rather than relative abundance because of the biases associated with relative abundance estimates (Cottrell et al. 1996; Laake et al. 2002). Prey composition was compared between age classes using a percentage similarity index (PSI)

$$\mathrm{PSI} = \sum(\text{minimum } p_{ij}, p_{ik})$$

where p_{ij} and p_{ik} were the proportions of prey item i of the total prey consumed by juveniles (j) and adult females (k), and the Morisita's index (M)

$$M = \frac{2\sum(p_{ij}p_{ik})}{\sum {p_{ij}}^2 + \sum {p_{ik}}^2}$$

(Krebs 1999). Indices range from zero (no similarity) to 1.00 (identical species composition). The level of significance was set arbitrarily at 0.65 for both PSI and M.

Prey array indices were calculated to describe differences in prey items consumed by juvenile and adult female sea lions. Indices calculated included the following: species richness (S; number of prey species); Simpson's diversity index (dominance; $D = \Sigma {p_i}^2$); Levin's measure of niche breadth ($B = 1/D$); Shannon–Wiener diversity index ($H' = |\Sigma p_i \cdot \ln p_i|$, where p_i is the proportion of individuals using prey i); prey evenness ($J = H'/H'_{\max}$, where $H'_{\max} = \ln S$); and index of specialization ($R = 1 - J$) (Krebs 1999). Prey array indices calculated for each year for both juvenile and adult female sea lions were non-normally distributed, so a Mann–Whitney *U* test was conducted to determine if there was any significant difference in mean prey array values between age classes.

Stable isotope analysis

During 2005 and 2006, blood plasma and fur samples were collected from known-aged yearlings (1–2 years old) and juveniles (2–3 years old); both age classes were referred to as "juveniles" in this study. These tissues also were collected from adult females. Plasma samples were collected in Vacutainer®[2] tubes containing the anticlotting agent sodium heparin, which has been determined not to alter isotopic values (Kurle 2002). Plasma was separated from blood cells after 10 min of centrifugation and approximately 1 mL was decanted into a 2 mL cryovial and frozen at –40 °C until further processing. Fur was collected by cutting a patch approximately 2 cm × 2 cm on the dorsal side of each individual at the pelvic girdle using scissors or electric clippers applied to the base of the shaft without removing the follicle. Fur samples were stored dry in paper envelopes until further processing. Once in the laboratory, frozen plasma and fur samples were placed into a lyophilizer for 24–48 h. Once dried, samples were ground into powder and homogenized using a glass rod (plasma) or a mortar and pestle (fur). They were weighed into tin capsules (8 mm × 5 mm) to a target mass of 1.0 ± 0.2 mg.

Nitrogen (δ^{15}N) and carbon (δ^{13}C) isotope values were determined using a continuous flow – isotope ratio mass spectrometer (20-20 PDZ Europa) at the University of California (UC) at Davis Stable Isotope Facility (Davis, California, USA) or using a Carlo-Erba elemental analyzer (NC 2500) interfaced with a Finnegan Delta Plus XL mass spectrometer in the light stable isotope facility at Carnegie Institution of Washington (Washington, D.C., USA). Correction factors of +1.7 (for δ^{15}N) and +1.0 (for δ^{13}C) were applied to samples sent to The UC Davis Stable Isotope Facility, owing to

[3] Supplementary Tables S1–S3 and Figs. S1–S3 for this article are available on the journal Web site (http://cjz.nrc.ca).

interlaboratory discrepancies between standards of known isotopic composition sent to both facilities. Isotopic results are expressed as δ values, $\delta^{13}C$ or $\delta^{15}N = [(R_{sample}/R_{standard}) - 1] \times 1000$, where R_{sample} and $R_{standard}$ are the $^{13}C/^{12}C$ or $^{15}N/^{14}N$ ratios of the sample and standard, respectively. The standards are Vienna-Pee Dee Belemnite (V-PDB) limestone for carbon and atmospheric N_2 for nitrogen. The units are expressed as parts per thousand or per mil (‰) and are calibrated to international standards through repeated measurements of a gelatin standard of known isotopic composition. The within-run standard deviation of acetanilide standards was ≤0.2‰ for both $\delta^{13}C$ and $\delta^{15}N$ values. As a control for tissue quality, we measured carbon and nitrogen concentrations (presented as [C]/[N] ratios) of each sample (Table S3).[3] The $\delta^{15}N$ and $\delta^{13}C$ ratios among age classes were not normally distributed, so they were compared using individual Kruskal–Wallis tests. Significance was set at $\alpha = 0.05$. When significant differences were detected, pairwise multiple comparisons among age classes were assessed using individual Mann–Whitney *U* tests. Statistical analyses were performed using SPSS version 13.0 for Windows (SPSS Inc., Chicago, Illinois, USA).

Results

Fecal analysis

The cumulative prey diversity curves for juveniles (except during 2002 and 2005) and adult females reached an asymptote, indicating that we had sufficient fecal samples to describe the diets of sea lions during the study period (Figs. S1, S2).[3] A lower number of juvenile samples were collected during 2002 and 2005, and curves did not reach an asymptote (Fig. S1).[3] Therefore, results of diet composition during those years should be viewed with caution. From 2002 through 2006 during 12 days of collection, 178 samples (166 scats, 12 enema samples) were collected in areas predominantly occupied by juvenile sea lions (Table 1). Additionally, 296 scats were collected in areas used by adult females during 11 days of collection. Of the 474 samples collected, only 3 (1 scat, 2 enema samples) contained no prey remains (i.e., blanks; Table 1). Adult female scats had a greater proportion of the different types of prey remains (e.g., fish otoliths and bones, cephalopod beaks) compared with juvenile scats (Table 1). Fish remains were found in 77.1% and 98.0% of juvenile and adult female samples with identifiable prey, respectively, and cephalopods in 34.9% and 43.2%, respectively. Only two scats (1 juvenile, 1 adult female) had remains of cartilaginous fish. Throughout the collection period, a majority of prey hard parts (>63% for juveniles, >76% for adult females) were identified to genus (Fig. S3),[3] representing at least 15 species (13 fishes, 2 cephalopods; Table 2) for juveniles and at least 33 species (25 fishes, 8 cephalopods; Table 2) for adult females.

The relative importance of each prey taxa was determined using %FO. The %FO for most prey taxa was greater when all structures were used rather than just fish otoliths or cephalopod beaks only, which traditionally were the only prey types used for analyses. Of the 376 prey occurrences in juvenile feces, 76.9% were fishes and 23.1% were cephalopods. Of the 731 prey occurrences in adult female scats, 78.9% were fishes and 21.1% were cephalopods. The ranking of importance of the predominant prey species varied between years and between age classes (Tables 3, 4). Interannual differences should be viewed with caution because of the disparity in sampling among years. However, when samples were pooled among years, northern anchovy (*Engraulis mordax*; 54.3% and 40.2%) and Pacific sardine (*Sardinops sagax*; 48.0% and 54.7%) were the predominant fish species consumed by juvenile and adult female sea lions, respectively; market squid (*Loligo opalescens*); 37.1% and 31.4%) was the predominant cephalopod eaten by juveniles and adult females, respectively. Other schooling fishes, such as Pacific hake (*Merluccius productus*) and rockfish, were also common prey in the diets of both juvenile and adult female sea lions; each occurring in ≥12% of the samples. Juvenile sea lions consumed only one other cephalopod species, East Pacific red octopus (*Octopus rubescens*). In contrast, at least seven additional cephalopod species were consumed by adult females, although infrequently (Table 4). Remains of elasmobranchs, identified to be from a skate (family Rajidae) and a spiny dogfish (*Squalus acanthias*), were recovered from one juvenile sample and one adult female sample, respectively).

There were no differences in diet composition between age groups when all years were pooled ($PSI_{total} = 0.84$, $M_{total} = 0.96$) or averaged (mean PSI = 0.63, mean M = 0.80). However, prey composition changed during 2002, 2005, and 2006 when PSI was used (for all PSI < 0.65). Prey composition was not determined to be different between age classes for any year when M was used (for all $M > 0.65$).

Fecal samples from juveniles contained 1–5 prey taxa (S; mean = 2.21, SE = 0.09), whereas those from adult females contained 1–10 prey taxa (mean = 2.83, SE = 0.11; Fig. 2). The majority of samples (84.7% juveniles, 73.8% adult females) contained 1–3 prey taxa (Fig. 2). Although fewer prey species per fecal sample were found from juveniles compared with from adult females, the difference was not significant. A higher diversity (H') of prey taxa was consumed by adult females (mean = 1.96, SE = 0.20, H'_{max} = 2.62) compared with juveniles (mean = 1.45, SE = 0.18, H'_{max} = 1.87; Fig. 3) during each year; however, the differences in diversity were not significant. Both groups had relatively high H' values in relation to their H'_{max} values; consequently, they had low dominance values (D; $mean_{juvenile} = 0.30$, SE = 0.05; $mean_{adult\ female} = 0.20$, SE = 0.04; Fig. 3) and low specialization values (R; $mean_{juvenile}$ = 0.21, SE = 0.03; $mean_{adult\ female} = 0.25$, SE = 0.02; Fig. 3). No significant differences in dominance or specialization were detected between age classes. Niche breadth values were in the low to mid-ranges when compared with the maximum value of number of species for juveniles (mean = 3.68, SE = 5.65, B_{max} = 7.40; Fig. 3) and adult females (mean = 5.65, SE = 0.84, B_{max} = 15.60; Fig. 3). There was no significant difference in B between age classes. Both age classes had relatively high evenness values (J; $mean_{juvenile}$ = 0.79, SE = 0.03; $mean_{adult\ female} = 0.75$, SE = 0.02; Fig. 3) and their values were not significantly different.

The estimated standard lengths (mean ± SE) and mass (mean ± SE) of fishes eaten by juvenile sea lions (that had regression equations in common with adult females) throughout the sampling period were 12.2 ± 0.2 cm and

Table 1. Summary of the number of prey hard parts retrieved from fecal and enema samples collected from juvenile (JUV) and adult female (ADF) California sea lions (*Zalophus californianus*) at San Miguel Island, California, during 2002 through 2006; five enema samples (two blanks) were collected in 2003, six during 2005, and one during 2006 from juvenile sea lions.

	2002		2003		2004		2005		2006		Total	
	JUV	ADF	JUV	ADF	JUV	ADF	JUV	ADF	JUV	ADF	JUV	ADF
No. of samples collected	14	94	75	98	56	35	6	49	27	20	178	296
With remains	14	94	72	98	56	35	6	49	27	20	175	296
With fish remains	4	89	47	98	56	34	4	49	24	20	135	290
With otoliths	0	28	20	64	12	15	2	30	10	16	44	153
With bones	4	86	47	98	56	34	2	49	24	19	133	286
With beaks	10	54	31	50	15	10	0	5	5	9	61	128
With cartilage	0	0	0	1	1	0	0	0	0	0	1	1

Table 2. Family, specific, and common names of prey found in fecal samples collected from juvenile (J) and adult female (A) California sea lions (*Zalophus californianus*) at San Miguel Island, California, during 2002 through 2006. Juveniles were 1–3 years old. Age indicates the age class of the sea lion.

Family	Species	Common name	Age
Fishes			
Bathylagidae	*Leuroglossus stilbius* Gilbert, 1890	California smoothtongue	J, A
Batrachoididae	*Porichthys notatus* Girard, 1854	Plainfin midshipmen	J, A
Bothidae	*Citharichthys sordidus* (Girard, 1854)	Pacific sanddab	A
Carangidae	*Trachurus symmetricus* (Ayres, 1855)	Jack mackerel	J, A
Clupeidae	*Clupea pallasii* Valenciennes in Cuvier and Valenciennes, 1847	Pacific herring	A
	Sardinops sagax (Jenyns, 1842)	Pacific sardine	J, A
	Clupeids	Herrings	J
Embiotocidae	*Cymatogaster aggregata* Gibbons, 1854	Shiner perch	A
Engraulididae	*Engraulis mordax* Girard, 1854	Northern anchovy	J, A
Gadidae/Merlucciidae	*Merluccius productus* (Ayres, 1855)	Pacific hake	J, A
Hexagrammidae	Hexagrammids	Greenling	A
	Oxylebius pictus Gill, 1862	Painted greenling	A
Myctophidae	Myctophids	Laternfish	A
	Stenobrachius leucopsarus (Eigenmann and Eigenmann, 1890)	Northern lampfish	J, A
	Symbolophorus californiensis (Eigenmann and Eigenmann, 1889)	California laternfish	A
	Tarletonbeania crenularis (Jordan and Gilbert, 1880)	Blue lanternfish	J, A
Ophidiidae	*Chilara taylori* (Girard, 1858)	Spotted cusk-eel	A
Pleuronectidae	*Lyopsetta exilis* (Jordan and Gilbert, 1880)	Slender sole	A
	Pleuronectids	Righteye flounders	A
Rajidae	Rajids	Skates	J
Sciaenidae	*Genyonemus lineatus* (Ayres, 1855)	White croaker	A
	Seriphus politus Ayres, 1860	Queenfish	A
Scomberesocidae	*Cololabis saira* (Brevoort, 1856)	Pacific saury	J, A
Scombridae	*Scomber japonicus* Houttuyn, 1782	Pacific or chub mackerel	J, A
Scorpaenidae	Genus *Sebastes* Cuvier, 1829	Rockfish	J, A
Serranidae	Serranids	Seabass	A
Squalidae	*Squalus acanthias* L., 1758	Spiny dogfish	A
Cephalopods			
Enoploteuthidae	*Abraliopsis felis* McGowan and Okutani, 1968		A
Gonatidae	Genus *Gonatus* Gray, 1849	Armhook squids	A
	Gonatopsis Sasaki, 1920		A
Histioteuthidae	*Histioteuthis hoylei* (Goodrich, 1896)	Flowervase jewell squid	A
Loliginidae	*Loligo opalescens* Berry, 1911	Market squid	J, A
Octopodidae	*Octopus rubescens* Berry, 1953	East Pacific red octopus	J, A
Ommasteuthidae	Ommasteuthids		A
Onychoteuthidae	*Onychoteuthis borealijaponicus* Okada, 1927	Boreal clubhook squid	A

Table 3. Percent frequency of occurrence (%FO) and mean rank of prey taxa retrieved from fecal samples collected from juvenile California sea lions (*Zalophus californianus*) at San Miguel Island, California, during 2002 through 2006 (N = 175).

Prey	2002	2003	2004	2005	2006	Total	Mean rank
Engraulis mordax	21.4	44.4	60.7	66.7	81.5	54.3	2.0
Sardinops sagax	0.0	59.7	66.1	0.0	14.8	48.0	3.6
Loligo opalescens (cephalopod)	64.3	44.4	28.6	0.0	29.6	37.1	3.0
Merluccius productus	14.3	2.8	35.7	16.7	37.0	20.0	4.8
Sebastes spp.	0.0	25.0	3.6	0.0	3.7	12.0	6.4
Octopus rubescens (cephalopod)	50.0	8.3	5.4	0.0	0.0	9.1	6.0
Trachurus symmetricus	0.0	12.5	5.4	0.0	3.7	7.4	6.4
Scomber japonicus	0.0	0.0	1.8	0.0	7.4	1.7	8.6
Cololabis saira	0.0	4.2	0.0	0.0	0.0	1.7	8.4
Clupea pallasi	0.0	0.0	0.0	16.7	0.0	0.6	9.4
Rajids	0.0	0.0	1.8	0.0	0.0	0.6	9.4
Leuroglossus stilbius	0.0	1.4	0.0	0.0	0.0	0.6	9.0
Porichthys notatus	0.0	1.4	0.0	0.0	0.0	0.6	9.0
Stenobrachius leucopsarus	0.0	1.4	0.0	0.0	0.0	0.6	9.0
Tarletonbeania crenularis	0.0	1.4	0.0	0.0	0.0	0.6	9.0
Number of samples	14	72	56	6	27	175	

Note: Prey taxa not indicated as being a cephalopod are fishes. Juveniles were 1–3 years old.

21.3 ± 1.1 g, respectively. Fishes consumed by adult females were 12.0 ± 0.1 cm long and weighed 20.0 ± 0.5 g. There were no significant differences in the overall lengths of fishes consumed by juveniles and adult females; however, significant differences existed in mass of fishes (Mann–Whitney U test, P = 0.004). Estimated dorsal length (mean ± SE) and mass (mean ± SE) of cephalopods retrieved from juvenile fecal samples were 9.8 ± 0.2 cm and 21.0 ± 0.4 g, respectively. Cephalopods eaten by adult females were 10.5 ± 0.1 cm long and weighed 21.8 ± 0.2 g. There were no significant differences in the pooled mass of cephalopods consumed by juvenile and adult female sea lions; however, there were significant differences in the lengths of cephalopods (Mann–Whitney U test, P = 0.02).

Several prey consumed by juvenile and adult female sea lions were of different sizes. The estimated mean standard or mantle lengths and mass of northern anchovy, California smoothtongue (*Leuroglossus stilbius*), Pacific hake, rockfish, and East Pacific red octopus taken by juvenile sea lions were greater than those eaten by adult females (Figs. 4, 5; note that mass could not be determined for rockfish). There were significant differences in the sizes of Pacific hake (Mann–Whitney U test, $P_{\text{length and mass}} < 0.001$) and rockfish (Mann–Whitney U test, $P_{\text{length}} = 0.002$) consumed by both age groups. Estimated mean standard or mantle lengths and mass of market squid and Pacific sardine consumed by adult females were larger than those eaten by juvenile sea lions (Figs. 4, 5); however, none of these differences were significant. Adult females ate larger (length and mass) individuals of each prey species with the largest standard length and mass (Figs. 4, 5).

Stable isotope analysis

A total of 36 plasma (8 yearling, 14 juvenile, 14 adult female) and 49 fur (10 yearling, 18 juvenile, 21 adult female) samples were collected from California sea lions. We were able to separate yearlings from other juveniles because their ages were known. Plasma $\delta^{13}C$ values ranged from –15.0‰ ± 0.1‰ (mean ± SE) for yearlings and juveniles to –14.9‰ ± 0.1‰ for adult females (Fig. 6) and did not differ significantly among age classes. There were significant differences in plasma $\delta^{15}N$ values among age classes (Kruskal–Wallace test, P = 0.005). Yearlings (18.0‰ ± 0.1‰) and juveniles (17.8‰ ± 0.1‰) had significantly higher plasma $\delta^{15}N$ values compared with adult females (17.6‰ ± 0.2‰; Mann–Whitney U test, $P < 0.01$ for both comparisons; Fig. 6). Fur $\delta^{13}C$ values ranged from –13.8‰ ± 0.2‰ (mean ± SE) for yearlings to –13.3‰ ± 0.1‰ for adult females (Fig. 6) and did not differ significantly among age classes. On average, yearlings were enriched 1.3‰ in mean fur $\delta^{15}N$ values compared with juveniles and adult females (Fig. 6). There were significant differences in fur $\delta^{15}N$ values between yearlings and older age classes (Mann–Whitney U test, for all comparisons $P < 0.01$).

Discussion

Fecal analysis

To examine if the diet composition of animals in the wild is accurately reflected using fecal sample reconstruction, empirical and direct observations are required. This is logistically difficult for most aquatic consumers. Hammill et al. (2005) noted that a more feasible approach could be to compare diet composition estimates using alternative techniques applied to the same animals.

Dietary studies using fecal samples of California sea lions have been conducted at many areas throughout their geographical range, including San Miguel Island (e.g., Antonelis et al. 1984; DeLong et al. 1991; Melin 2002). Although little information has been reported on the diet of juvenile California sea lions, this study was in concordance with previous studies in determining that California sea lions (regardless of age class) are adept at feeding on a variety of prey species.

Table 4. Percent frequency of occurrence (%FO) and mean rank of prey taxa retrieved from fecal samples collected from adult female California sea lions (*Zalophus californianus*) at San Miguel Island, California, during 2002 through 2006 (N = 296).

Prey	2002	2003	2004	2005	2006	Total	Mean rank
Sardinops sagax	33.0	61.2	80.0	65.3	55.0	54.7	1.8
Engraulis mordax	9.6	53.1	48.6	69.4	35.0	40.2	3.4
Loligo opalescens (cephalopod)	43.6	33.7	17.1	8.2	45.0	31.4	3.4
Merluccius productus	37.2	11.2	34.3	8.2	80.0	26.4	3.4
Sebastes spp.	13.8	20.4	2.9	8.2	10.0	13.5	6.4
Trachurus symmetricus	0.0	28.6	0.0	0.0	5.0	9.8	12.8
Octopus rubescens (cephalopod)	28.7	1.0	0.0	0.0	0.0	9.5	11.8
Cololabis saira	12.8	13.3	2.9	0.0	0.0	8.8	9.0
Symbolophorus californiensis	1.1	4.1	11.4	2.0	15.0	4.4	9.2
Gonatus spp. (cephalopod)	4.3	2.0	2.9	0.0	5.0	2.7	10.2
Ommasteuthid spp.	1.1	2.0	2.9	0.0	0.0	1.4	12.0
Tarletonbeania crenularis	1.1	1.0	5.7	0.0	0.0	1.4	12.8
Scomber japonicus	0.0	1.0	0.0	0.0	15.0	1.4	14.6
Citharichthys sordidus	1.1	2.0	0.0	0.0	0.0	1.0	13.2
Chilara taylori	2.1	1.0	0.0	0.0	0.0	1.0	13.4
Gonatopsis spp. (cephalopod)	2.1	0.0	2.9	0.0	0.0	1.0	14.4
Onychoteuthis borealijaponicus (cephalopod)	1.1	0.0	2.9	0.0	5.0	1.0	14.4
Cymatogaster aggregata	0.0	2.0	0.0	0.0	0.0	0.7	15.2
Abraliopsis felis (cephalopod)	2.1	0.0	0.0	0.0	0.0	0.7	15.6
Leuroglossus stilbius	2.1	0.0	0.0	0.0	0.0	0.7	15.6
Clupea pallasi	0.0	1.0	0.0	0.0	0.0	0.3	16.2
Genyonemus lineatus	0.0	1.0	0.0	0.0	0.0	0.3	16.2
Hexagrammids	0.0	1.0	0.0	0.0	0.0	0.3	16.2
Myctophids	0.0	1.0	0.0	0.0	0.0	0.3	16.2
Pleuronectids	0.0	1.0	0.0	0.0	0.0	0.3	16.2
Squalus acanthias	0.0	1.0	0.0	0.0	0.0	0.3	16.2
Stenobrachius leucopsarus	0.0	1.0	0.0	0.0	0.0	0.3	16.2
Histioteuthis hoylei	1.1	0.0	0.0	0.0	0.0	0.3	16.4
Lyopsetta exilis	1.1	0.0	0.0	0.0	0.0	0.3	16.4
Oxylebius pictus	1.1	0.0	0.0	0.0	0.0	0.3	16.4
Porichthys notatus	1.1	0.0	0.0	0.0	0.0	0.3	16.4
Seriphus politus	1.1	0.0	0.0	0.0	0.0	0.3	16.4
Serranids	0.0	0.0	0.0	0.0	5.0	0.3	17.6
Number of samples	94	98	35	49	20	296	

Note: Prey taxa not indicated as being a cephalopod are fishes.

During this study, California sea lions consumed a variety of different prey taxa. Because previous studies also showed them to eat a diverse array of prey, they have been regarded as opportunistic feeders (Antonelis and Fiscus 1980; Antonelis et al. 1984) and "prey switching" may be an important factor of their foraging behavior (Bailey and Ainley 1982; Antonelis et al. 1984). Despite consuming a large variety of prey, the diet of both juveniles and adult females averaged over all 5 years was dominated only by five prey types, specifically northern anchovy, Pacific sardine, Pacific hake, rockfish, and market squid. Additionally, less than three prey taxa were most frequently found in each fecal sample. Lowry et al. (1991) noted that California sea lions consumed seasonally abundant and accessible schooling or aggregating prey, and exploited a few species at a time, but their diet was temporally dynamic. The number of "important" prey (determined by several indices) was small in many studies on diet of California sea lions (e.g., Antonelis et al. 1984; Lowry et al. 1991; Melin 2002; García-Rodríguez and Aurioles-Gamboa 2004).

Prey diversity indices provided additional information on how the sea lions utilized their resources. Simpson's index (D) values were low and Shannon–Wiener (H') values were relatively high for both age classes, indicating that their diet was diverse. Mean values of both indices for adult females (lower D, higher H') indicated that they had a more diverse diet compared with juveniles. Values of species evenness (J) were relatively high, indices of specialization were low, and indices of niche breadth were intermediate for both age classes. This further supports the idea that California sea lions consume a variety of prey, but relatively few species compose the majority of their diet during a given time period. Additional information is needed about their prey selectivity or preference.

A variety of elements could affect the abundance and availability of prey species, including temporal (e.g., seasonal, annual) and spatial (e.g., diel–vertical migrations, schooling behavior) factors (Antonelis et al. 1984; Lowry et al. 1991). Prey distribution and size affects dietary composition of consumers that differ in size (Ashmole 1968). Juve-

Fig. 2. Frequency of number of prey taxa per fecal samples collected from juvenile (JUV) and adult female (ADF) California sea lions (*Zalophus californianus*) at San Miguel Island, California, during 2002 through 2006. Juveniles were all immature animals that were not pups (1–3 years old).

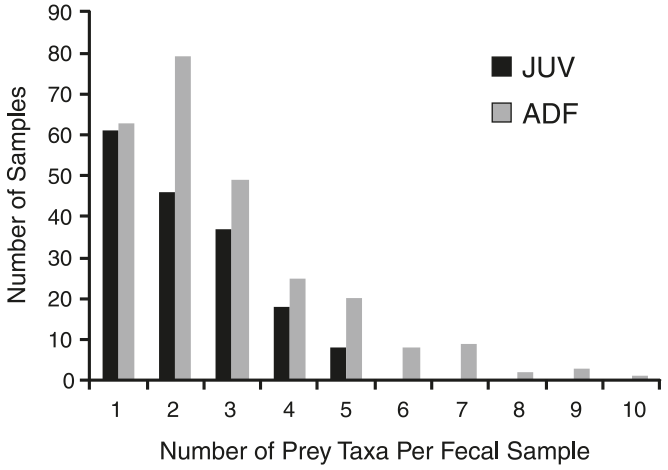
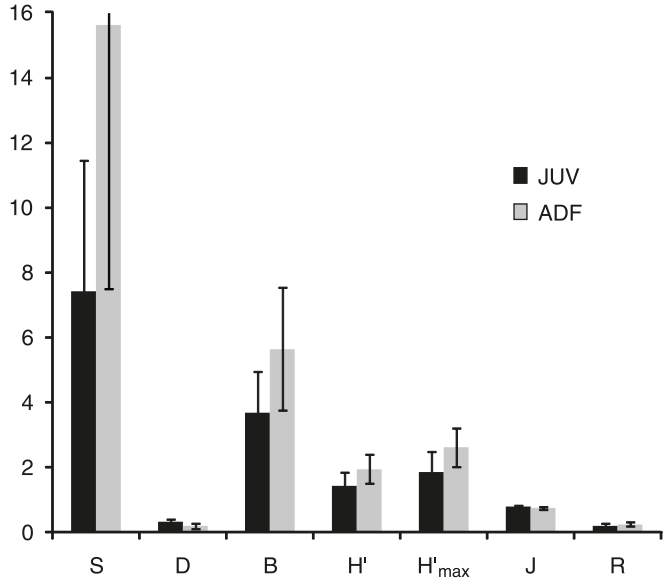


Fig. 3. Mean total variation of prey array indices calculated from scat and enema samples from juvenile (n = 178) and adult female (n = 296) California sea lions (*Zalophus californianus*) at San Miguel Island, California, during 2002 through 2006. Juveniles were 1–3 years old. Error bars indicate SD. Indices include species richness (S), Simpson's diversity index (D), Levin's measure of niche breadth (B), Shannon–Wiener diversity index (H'), prey evenness (J), and specialization (R).



nile sea lions fed on at least 15 different prey taxa, but adult females ate more than twice this number. Additionally, mean species richness (S) of adult females was twice that of their younger counterparts. Although adult females are central place foragers when providing nutrition for their dependent pups, they may be adept at capturing and consuming a greater array of food items in a greater variety of habitats compared with less experienced and more physiologically constrained juveniles. Additionally, because lactating females are nonmigratory and limited in the time (thus distance) that they can be away from the rookery, they may be more susceptible to the seasonal, annual, and multiannual fluctuations in the productivity of the system compared with individuals that are not obligated to return to the rookery (e.g., juveniles). Therefore, their foraging behaviors may be highly variable as they try to acquire energy stores for lactation, self-maintenance, and to sustain a pregnancy. Page et al. (2005) noted that according to central place foraging models, a lactating female might maximize her fitness by increasing milk delivery rates to her dependent offspring rather than foraging in the most productive habitats. Once weaned, juvenile sea lions are not obligated to return to the rookery until they are sexually mature. They only need to acquire energy for self-maintenance and growth. Although they are required to alter their behaviors in response to prey movements, they can afford to be more selective in prey choice or follow migrating prey for greater distances. However, because of their high energetic requirements for growth, they may need to exploit several prey items, but their selection may be limited because of their underdeveloped foraging abilities.

Despite adult females having a more diverse and species-rich diet compared with juveniles, PSI and M indices indicated that their diets were generally similar. This may be attributed to the fact that the prey which they had in common were dominant in their diet. In addition to several prey species, sizes of prey consumed by these groups of sea lions were similar. The range in mean length estimates of frequently occurring prey (4–33 cm) was not indicative of a great diversity in prey size. Antonelis et al. (1984) noted a similar finding and stated that this may reflect a prey size preference by sea lions feeding in waters off San Miguel Island. Rockfish, Pacific sardine, East Pacific red octopus, and Pacific hake attain larger sizes as adults (Eschmeyer et al. 1983; Wood 2009), therefore sea lions were feeding on juvenile individuals of these prey species. Length estimates of market squid and northern anchovy were within the size range of juveniles and adults (Eschmeyer et al. 1983; Wood 2009). There were significant differences only in the sizes of rockfish and Pacific hake consumed by both age classes. Because it is unlikely that different-aged sea lions are selecting a prey of a particular size in the midst of various sizes, it can be assumed that they are pursuing and capturing prey at different locations. The five dominant prey for both juveniles and adults throughout the study period (i.e., northern anchovy, Pacific sardine, Pacific hake, rockfish, and market squid) form large, dense schools, and are epi- or mesopelagic. Juvenile sea lions likely have attained the physiological capabilities to exploit these prey types in shallow habitats similar to adult females.

Results from fecal analysis indicated that there was an overlap in the type and size of prey consumed by sea lions of both age classes, but adult females exploited more resources. Interpretations were confounded because of the temporal scale that scats represent. Several studies have indicated that most prey remains pass through the alimentary tract of California sea lions within 48 h (Orr and Harvey 2001; Sweeney 2008). Therefore, scats primarily represent what

Fig. 4. Range, first, median, and third quartiles of estimated standard lengths of prey identified from otoliths or beaks (*n*) recovered from fecal samples collected from juvenile (JUV) and adult female (ADF) California sea lions (*Zalophus californianus*) at San Miguel Island, California, during 2002 through 2006. Juveniles were 1–3 years old. Plus signs indicate significant difference.

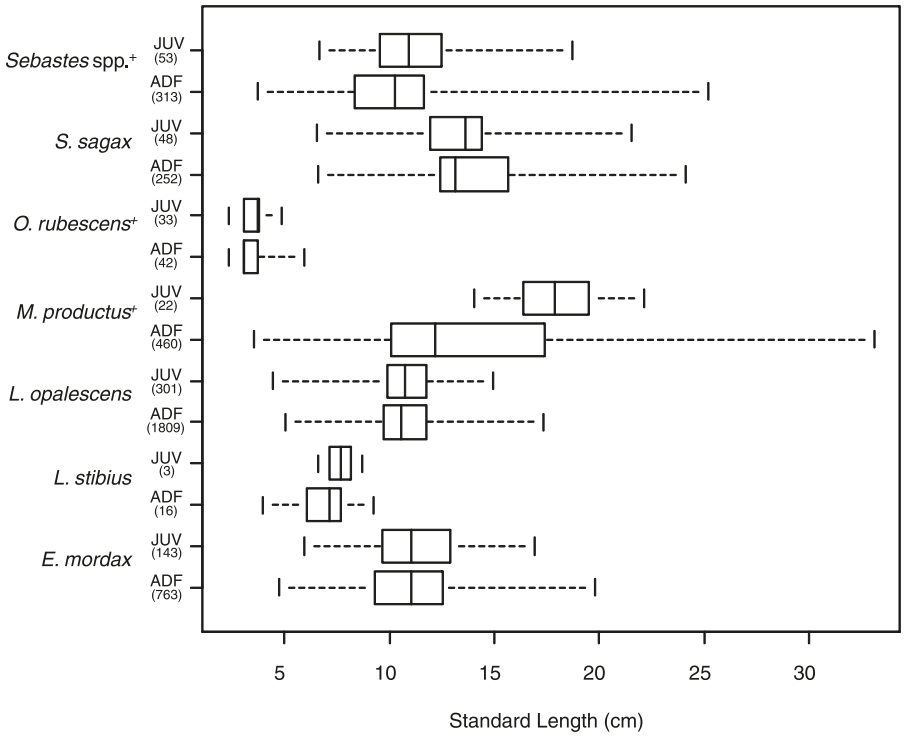


Fig. 5. Range, first, median, and third quartiles of estimated mass of prey identified from otoliths or beaks (*n*) recovered from fecal samples collected from juvenile (JUV) and adult female (ADF) California sea lions (*Zalophus californianus*) at San Miguel Island, California, during 2002 through 2006. Juveniles were 1–3 years old. Plus sign indicates significant difference. Maximum mass for *Merluccius productus* (not depicted in the figure) was 260 g.

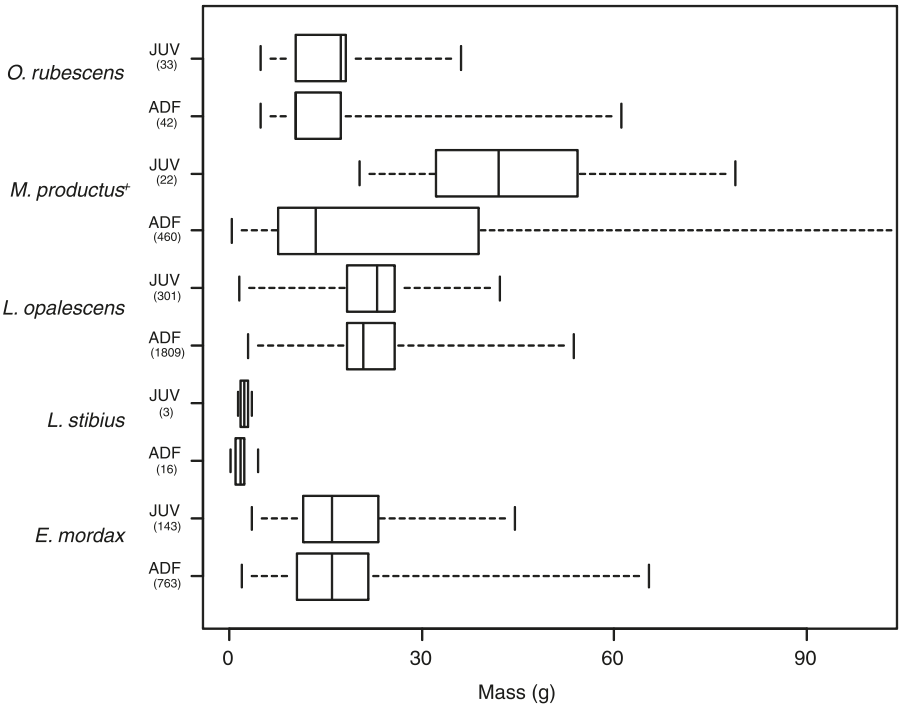
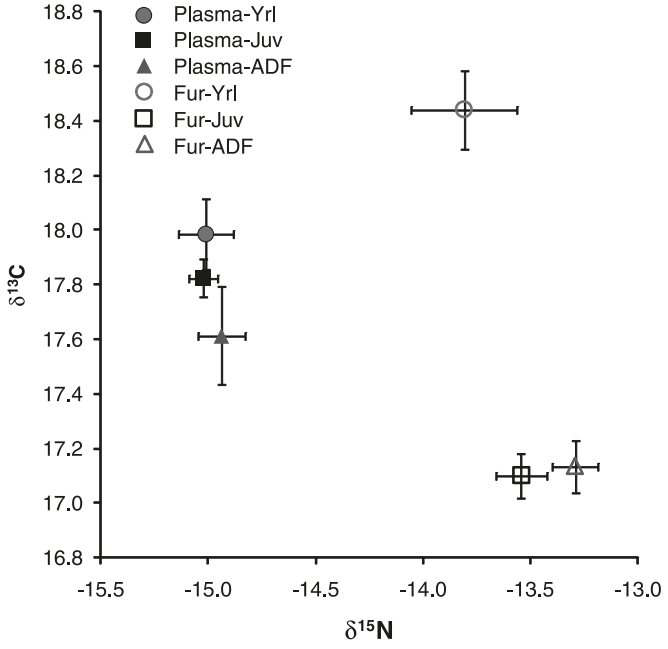


Fig. 6. The relationship between stable carbon ($\delta^{13}C$) and stable nitrogen ($\delta^{15}N$) isotope ratios of plasma and fur collected from California sea lions (*Zalophus californianus*) of various age classes (Yrl, yearlings; Juv, juvenlies; ADF, adult females) at San Miguel Island, California, during 2005 through 2006. Ages of individuals were known because they were marked as pups. Yearlings were 1 year old, whereas juveniles were 2–3 years old. Error bars indicate SE.



was consumed during the most recent foraging trip or prey consumed near the island. This may explain the similarity in diet of individuals within these age classes.

Stable isotope analysis

Similar to fecal analysis, interpretations of stable isotope analysis were complex. To reconstruct consumers' diets using the isotopic composition of their tissues, prey of interest must be isotopically distinct (Gannes et al. 1998). Using fecal analysis, it was determined that California sea lions consumed several prey taxa. Isotopic models have been developed to calculate the relative contribution of particular food items to a predator's diet, even when the number of prey sources is large (e.g., IsoSource (Phillips and Gregg 2003); SOURCE and STEP (Lubetkin and Simenstad 2004); MixSIR (Semmens and Moore 2009)), as was the case in this study. However, sources should be accounted for when using these models. There was a lack of isotopic information for many of the prey consumed by sea lions during this study and it was beyond the scope of this study to collect such data, therefore we were unable to quantify the diet of sea lions using stable isotope analysis. However, other useful dietary data were ascertained, including more detailed information on different-aged "juveniles".

Stable isotope ratios assessed from consumer tissues with high turnover rates (e.g., blood plasma) reflect recent dietary inputs. Isotopic incorporation rates of mammals primarily have been determined from small species, and these rates increase with body mass and growth rate of the individual (e.g., MacAvoy et al. 2005; Martínez del Rio et al. 2009). Based on studies of other large carnivores, plasma reflected the assimilated diet of sea lions on the order of weeks to a couple of months (Hilderbrand et al. 1996; Kurle 2002; Zhao et al. 2004). Foraging behaviors during the relatively short temporal scale that plasma isotopic data reflect and the diet discerned from scats were in general agreement. Yearlings, 2- to 3-year-old juveniles, and adult females had similar plasma $\delta^{15}N$ values, indicating that they were feeding at approximately the same trophic level. Individuals within these age classes also had similar plasma $\delta^{13}C$ values, indicating that they were feeding in similar areas or that the spatial distance between foraging areas was not far enough apart to result in significantly different $\delta^{13}C$ values among age classes. Up to four other pinniped species, including northern fur seals (*Callorhinus ursinus* (L., 1758)), Pacific harbor seals (*Phoca vitulina* L., 1758), northern elephant seals (*Mirounga angustirostris* (Gill, 1866)), and Guadalupe fur seals (*Arctocephalus townsendi* Merriam, 1897), inhabit or feed near San Miguel Island. Perhaps interspecific competition affects the level of intraspecific variation of diet, resulting in similar foraging by conspecifics.

Metabolically inert tissues (e.g., fur) record diet assimilated during the period of tissue formation (i.e., up to a year for sea lions, which molt annually). Unlike plasma, dietary information obtained from fur isotopic data indicated significant differences in foraging behaviors among age classes. Yearlings were enriched in $\delta^{15}N$ compared with older juveniles and adult females. This enrichment, indicating that yearlings were feeding at a higher trophic level, may reflect that some of these individuals were still suckling during the period of tissue formation. The enriched $\delta^{15}N$ values may be due to suckling individuals consuming milk, which is derived from remobilized body tissues of lactating females; suckling offspring are essentially consuming their mother's tissues during lactation (Hobson and Sease 1998; Newsome et al. 2006; Newsome et al. 2009). These individuals may have been supplementing their diet acquired at sea with milk from their mothers. A prolonged lactation period has been observed in other otariids, including Galápagos sea lions (*Zalophus wollebaeki* Sivertsen, 1953), Steller sea lions (*Eumetopias jubatus* (Schreber, 1776)), Australian sea lions (*Neophoca cinerea* (Péron, 1816)), Galápagos fur seals (*Arctocephalus galapagoensis* Heller, 1904), and South American fur seals (*Arctocephalus australis* (Zimmermann, 1783)) (Boness and Bowen 1996; Schulz and Bowen 2004).

The lower mean fur $\delta^{13}C$ values of yearlings compared with older juveniles and adult females also might have been a reflection of a mixed diet of milk and solid food (e.g., fish and cephalopods). If some yearlings were suckling, then their lower $\delta^{13}C$ values were likely a result of the high lipid content in milk because lipids are ^{13}C depleted compared with protein (Polischuk et al. 2001; Kurle 2002; Newsome et al. 2006). The fur $\delta^{13}C$ values of 2- to 3-year-old juveniles indicated that young, nonmigrating males and nulliparous females were completely weaned and fed in similar foraging habitats as adult females.

The results from stable isotope analysis indicated that there were differences in the foraging behaviors of "juveniles", reflecting their continual development and transition from relying on their mothers for sustenance to foraging in

the marine environment. The similarities in isotopic values of multiple tissues of older juvenile and adult female sea lions suggest that these animals were exploiting similar prey in similar areas. Adult females consumed twice the number of prey taxa as younger conspecifics; differences in development, energy requirements, or preferences are plausible explanations for this discrepancy and warrant further investigation.

In conclusion, data presented in this study provide the most comprehensive and recent information available on the diet of juvenile California sea lions. Dietary information for juvenile sea lions is needed to better our understanding of the foraging ecology of this species, which has several management implications. There has been a greater focus on an ecosystem-based approach to fisheries management (Cochrane et al. 2004; Scandol et al. 2005; Field and Francis 2006). A vital constituent of this approach is information about both temporal and spatial prey consumption by marine apex predators (Furness 2002; Reid et al. 2004), including members of all age classes not just adults. For future studies, it would be beneficial to collect ancillary information for fecal samples (as can be ascertained using enemas) so that information collected from these samples and other dietary metrics can be used simultaneously to describe the diet of an individual. Additionally, baseline isotopic patterns of the environment, as well as isotopic data of prey, are needed so that stable isotope analysis can be used more effectively in discerning the foraging ecology of California sea lions or other marine mammals.

Acknowledgements

Gratitude is extended to S. Melin, A. Gemmer-Pecharich, J. Scordino, H. Ziel, R. Jenkinson, G. Orr, T. Goldstein, F. Gulland, J. Jenniges, M. Tennis, E. Hamblen, and C. Kuhn who helped collect scat samples, obtain enemas, and (or) procure tissue samples for stable isotope analyses. Special thanks go to E. Siek and W. Walker for their help in identifying prey remains. W. Walker also provided data for regression equations for several prey taxa for this study. Appreciation is extended to the Channel Islands National Park Service and Channel Islands Aviation for logistical support. Special thanks go to I. Williams (Channel Island National Park Service) for his logistical and field support. This manuscript was improved by helpful comments from B. Fadely and M. Gosho, as well as from two anonymous reviewers. This study was conducted in accordance with National Marine Fisheries Service Permit #782-1812-00.

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