The role of body size in individual-based foraging strategies of a top marine predator

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Abstract. Body size is an important determinant of the diving and foraging ability in air-breathing marine vertebrate predators. Satellite-linked dive recorders were used during 2003–2004 to investigate the foraging behavior of 22 male California sea lions (*Zalophus californianus*, a large, sexually dimorphic otariid) and to evaluate the extent to which body size explained variation among individuals and foraging strategies. Multivariate analyses were used to reduce the number of behavioral variables used to characterize foraging strategies (principal component analysis, PCA), to identify individually based foraging strategies in multidimensional space (hierarchical cluster analysis), and to classify each individual into a cluster or foraging strategy (discriminant analysis). Approximately 81.1% of the variation in diving behavior among individuals was explained by three factors: diving patterns (PC1), foraging effort (PC2), and behavior at the surface (PC3). Individuals were classified into three distinct groups based on their diving behavior (shallow, mixed depth, and deeper divers), and jackknife resampling of the data resulted in correct group assignment 86% of the time. Body size as an independent variable was positively related to dive duration and time spent ashore and negatively related to time at sea, and it was a key parameter in PC2 used to classify the three distinct clusters. Differences among individual-based foraging strategies probably were driven by differences in body size, which enabled larger animals to dive deeper and forage more efficiently by targeting different and perhaps larger prey items. The occurrence of foraging specializations within a species and age class has implications for quantitative modeling of population-level predator–prey interactions and ecosystem structure.

Key words: body size; California sea lion; diving behavior; foraging strategy; individual specialization; predator–prey interactions; sexual dimorphism; Zalophus californianus.

Introduction

Body size is a derived trait that evolves in response to a complex interaction between the organism and its environment that directly affects its ecology, behavior, and physiology (Peters 1983, Brown et al. 2004). Further, body size determines where, how, and what kind of prey can be eaten (Peters 1983). This is particularly important for air-breathing marine vertebrates for which diving ability is directly related to body mass (Schreer and Kovacs 1997, Halsey et al. 2006). Diving ability is determined by the difference in scaling between oxygen stores, which scales as mass$^{1.0}$, and the rate of oxygen utilization, which scales with mass$^{0.67–0.75}$. In contrast, absolute metabolic requirements increase proportionally with body mass, which means that larger individuals require more energy per unit time than smaller individuals (Peters 1983). Among marine mammals, sexual dimorphism is evident for many taxa, and the requirement for greater energy intake may lead to different foraging strategies and differences in ecology between sexes and among age classes.

A variety of marine bird, turtle, and mammal species either specialize or exhibit a combination of three distinct foraging strategies: epipelagic, mesopelagic, and benthic diving patterns (Tremblay and Cherel 2000, Costa et al. 2001, 2004). Each strategy is defined by functional characteristics related to dive patterns and searching effort, and inferences about the use of oxygen stores and target prey type, size, and vertical distribution (Houston and Carbone 1992, Thompson and Fedak 2001). Predators exhibiting the epipelagic foraging strategy dive in the upper part of the water column, search for prey throughout the entire dive cycle, and often eat small, schooling prey (Gentry et al. 1986, Costa et al. 2001). These prey vertically migrate upward during the night as part of the deep scattering layer; consequently, epipelagic predators often display a diel pattern with more frequent, shallow, short-duration dives during the night (Gentry et al. 1986). Mesopelagic predators also exhibit a diel pattern, but dive deeper for

longer durations to the midwinter column (>200 m), searching for fewer but larger prey items or small, numerous, energetically rich prey at the deepest portion of their dives (Costa et al. 2004). Benthic predators search at the deepest portion of their dives, usually on or near the bottom substrate for single, large prey items, and are restricted to the continental shelf or seamounts (Costa and Gales 2003). Benthic prey rarely migrate vertically, so benthic divers have no diel pattern (Tremblay and Cherel 2000, Costa and Gales 2003). In contrast to epipelagic predators, mesopelagic and benthic foragers exhibit longer duration dives as they spend more time in transit to the foraging depths. As a result they must maximize the time spent searching for prey at the bottom of the dive (Houston and Carbone 1992, Thompson and Fedak 2001); therefore, they commonly meet or exceed their calculated aerobic diving capacity (Costa et al. 2004).

Among air-breathing diving marine vertebrates, otariids (sea lion and fur seal) exhibit the most consistent and greatest degree of sexual size dimorphism, males being 2–4 times the mass of adult females and 1.5–2 times the length. Our understanding of the foraging ecology of otariids, however, is almost exclusively derived from studies of at-sea movement and diving behavior of smaller adult females (Shaffer and Costa 2006). Otariid females alternate periods at sea foraging with periods ashore provisioning their pups (Costa 1993). These patterns and their ease of handling facilitate the recovery of dive recorders, making lactating female otariids a favored research subject (Shaffer and Costa 2006). In contrast, studies of adult male otariids have been limited because of their large size, aggressive behavior, and the unpredictability of their rookery attendance, which makes instrument recovery difficult (Boyd et al. 1998). Recently, data compression techniques have enabled the transmission of detailed dive behavior data, negating the need to recover the instrument (Fedak et al. 2001). These techniques have been validated against more traditional archival instruments (Myers et al. 2006).

Because male otariids are not involved in parental care, they can maximize their fitness by traveling farther in search of prey than do females; this, in turn, reduces the potential for intraspecific competition for resources. Insights into male otariid foraging behavior have indicated that in some species males use different prey species than females (Page et al. 2005a) and use dramatically different foraging strategies by foraging farther from haul-outs (Green 1997, Hindell and Pemberton 1997, Boyd et al. 1998, Campagna et al. 2001, Kirkwood et al. 2002, Page et al. 2005b), spending more time at sea (Campagna et al. 2001), and diving deeper than females (Green 1997, Boyd et al. 1998, Page et al. 2005b).

Foraging activities of apex predators can structure communities through trophic cascades or top-down predation pressure that can alter the number and/or strength of interactions among trophic levels (Estes et al. 1998). California sea lions are one of the most abundant apex predators in the California Current System (237 000 to 244 000 individuals; Carretta et al. 2005). Until recently, studies of foraging behavior of this species have been limited to adult females at rookeries in southern California (Feldkamp et al. 1989, Kuhn 2006). Weise (2006) observed diving behavior of male sea lions that was largely consistent with a shallow, epipelagic (<200 m) foraging strategy with a diving depth of 35 ± 4 m (mean ± SE), diving duration of 2.0 ± 0.1 min, and a strong diel pattern. However, variation in diving behavior among age (subadult and adult males; Weise 2006), sex (adult female sea lions; Feldkamp et al. 1989, Kuhn 2006), and region (Weise 2006) indicates the potential for individual-based foraging strategies. Sea lions in general have a diet that is temporally dynamic, with animals feeding on seasonally abundant schooling or aggregating prey, exploiting several species at a time that range in size from small, pelagically schooling prey (i.e., sardine, anchovy) to larger salmonids (Lowry et al. 1990, Weise 2006, Weise and Harvey 2008). An understanding of trophic interactions within coastal ecosystems along the West Coast of North America requires a more complete assessment of the foraging ecology of this large and abundant apex predator.

Individual-based foraging strategies have been identified among air-breathing marine vertebrates, including a broad taxonomic range of seabirds (Radl and Culik 1999, Kato et al. 2000), toothed whales (Ford et al. 1998, Laidre et al. 2002), pinnipeds (Lea et al. 2002, Austin et al. 2004, Staniland et al. 2004), and otters (Tinker et al. 2007). There are several hypotheses to explain the occurrence of alternative foraging strategies in air-breathing marine vertebrates, including (1) spatially explicit foraging strategies in which individuals target prey that are distributed at different depths and/or different geographic locations; (2) polymorphic foraging strategies in which individuals target different prey species in the same habitat; and (3) ontogenetic foraging strategies in which predators of different size or age consume different-sized prey and/or different species.

These same hypotheses may explain previously observed variation in diving behavior among individual male California sea lions (Weise 2006) and the potential for alternative foraging strategies among individuals that feed on a variety of prey types. In this study we used satellite-linked time–depth recorders to investigate variation in diving behavior among individual male California sea lions after the breeding season along the West Coast of North America, and examined the potential for individual-based foraging strategies. We used a multivariate analysis approach to examine variation among individual males and to identify and characterize individual-based foraging strategies. This approach may be applicable for studies of diving behavior in a broad range of air-breathing marine vertebrates.

METHODS

Handling of study animals

Male California sea lions were captured and instrumented in Monterey, California, USA (36°36.5′ N, 121°53.4′ W) from September to December 2003, using an aluminum enclosure (3 × 4 × 2 m) and squeeze cage (2.5 × 1.0 × 1.5 m; R. DeLong, National Marine Mammal Lab, *personal communication*; see Appendix: Fig. A1). Individuals were physically restrained in the squeeze cage, sedated with Midazolam intramuscularly at 0.20 mg/kg (mixed with atropine at 0.02 mg/kg) and then anesthetized with Isoflurane gas (0.5–5% dosage) vaporized and delivered in a mixture with O_2 at 5–15 L/min using a circular rebreathing circuit via gas mask or intubation. Once sea lions were quiescent, lengths and girths (±0.5 cm) were measured and mass was determined with a digital hanging scale (±0.5 kg; Dyna-Link MSI–7200; Measurement Systems International, Seattle, Washington, USA). Age data were not collected from individuals in this study; however, as accepted generally and in this study, adult males (mean 187 kg) were larger in body size than subadult males (mean 111 kg) and were distinguished by secondary sexual characteristics, such as a well-developed sagittal crest.

Data sampling

Male diving behavior and movement data were collected using satellite-relay data loggers (SRDL 7000, Sea Mammal Research Unit, St. Andrews University, Scotland) attached to the dorsal pelage at the point of maximum girth using 5-min epoxy. Onboard data were summarized and transmitted via the ARGOS system when the animal surfaced (Fedak et al. 2001). Tags recorded dive depth (minimum > 5.5 m), diving duration (minimum >10 s), and surface interval using a 4-s sampling frequency. Data from the first three SRDLs deployments were used to characterize diving behavior and optimize data acquisition, indicating that the minimum depth for a dive was 5.5 m and duration was 10 s. Behavior above 5.5 m was considered surface related, and included swimming, handling and consuming prey, and resting. For every dive, start and end time were recorded, and dive depth (±0.5 m), dive duration (±1 s), and surface interval were sampled every 4 s. Horizontal swim speed was calculated using a linear interpolation of time and distance between Argos dive positions (McConnell et al. 1992).

Summaries were transmitted for every 4-h period: mean and SD of percentage of time spent diving, swimming at the surface (<5.5 m and 10 s), and onshore resting; maximum depth and maximum dive duration; and number of dives. While the animal was in the water, surface swimming was recorded if no dives were recorded for 6 min. A haul-out period began after the tag was dry for 6 min and ended after the tag was wet for 40 s.

The SRDLs provided a combination of randomly sampled "profile dives," which in addition to depth and location, recorded water temperature (±0.1°C) every 4 s during one of the two deepest dives every 2 h during each 24-h period. Temperature profiles were compressed using a broken-stick method (McMahon et al. 2005), which produced 12 temperature–depth pairs.

Data analysis

Diel patterns in diving behavior were examined by transforming data to local time and calculating the mean of dive parameters for each hour of the day for each individual. Activity patterns (percentage of time onshore resting, swimming, or diving) were arcsine transformed. Trip duration was calculated by subtracting end time of haul-out period from start time of the next haul-out period, and only trips bounded by sequential haul-out periods were used in analysis. Activity patterns and diving frequencies were determined only from those days in which data were received for all 4-h summary periods.

Habitat was defined as the region of diving activity within the water column relative to the depth of the thermocline and distance from the seafloor. Thermocline was used because sea lions mostly prey on schooling, vertically migrating species, which occur over the continental shelf and shelf break in association with the thermal stratification of the water column (Weise 2006, Weise and Harvey 2008). Thermocline was estimated on "profile" dives by interpolating between the 12 temperature–depth pairs at 1-m intervals, and identifying a change in temperature gradient of 0.05°C/m over a minimum of three consecutive temperature points in either direction using purpose-built software in IKNOS Toolbox (Y. Tremblay, *unpublished software*). Least-squares regression was fitted to thermocline depth vs. diving depth for all dives with temperature profiles per individual, and residuals (difference between dive depth and regression line) from this relationship were used to compare diving behavior relative to the thermocline among individuals. We compared dive depth and seafloor depth as determined using the ETOPO2 Global 2′ elevations based on 2 × 2 minute grids from the national Geophysical Data Center (Smith and Sandwell 1994).

Twenty-two commonly used variables were used to describe diving behavior (Tremblay and Cherel 2000, Page et al. 2005b). Using principal component analysis (PCA), we reduced these 22 behavioral variables to 12 and then into a few dominant, orthogonal axes to characterize and compare foraging strategies among individuals. Variables excluded were mean and standard deviation of the ratio of dive depth to bottom depth; mean time at depth; season (as defined by Broenkow 1977); maximum dive depth, dive duration, and surface interval; and mean percentage of time diving, at surface, or hauled out. The appropriate number of components to extract was selected using the (1) latent root criterion,

which states that only factors with eigenvalues of 1 or above would be included, and (2) the criterion that more than 5% of the variance be explained (McGarigal et al. 2000). Collinearity among variables was eliminated by collapsing variables into uncorrelated orthogonals. Hierarchical cluster analysis of the factor scores from the PCA was used to detect discontinuous groupings or "clumps" of data points in multidimensional space (McGarigal et al. 2000), which were interpreted to represent distinct foraging strategies. Distance measure was the square of the Pearson product-moment correlation (r^2), because this measure maximized the cophenetic correlation coefficient and thus best represented the raw data structure (McGarigal et al. 2000). Ward's minimum variance method was used to link similar points, and the number of significant clusters was determined by graphical examination of the resulting dendrogram and scree plot of inter-cluster distance vs. the number of clusters (McGarigal et al. 2000). A discriminant analysis was then used to evaluate the effectiveness of classifying each individual into a cluster or foraging strategy, and to identify the key variables that contributed most to the classification.

Diving performance (mean dive duration/calculated aerobic dive limit, cADL; Weise and Costa 2007) among foraging strategies of male California sea lions was examined as a function of diving depth and duration for all individuals. Mean oxygen stores were scaled to body size using 47.3 mL O_2/kg (Weise and Costa 2007). Because of the hypometabolic response of sea lions to diving (Hurley and Costa 2001), cADL was calculated using a high metabolic rate (44.8 mL $O_2 \cdot kg^{-0.75} \cdot min^{-1}$; Weise 2006); low metabolic rate was (21.6 mL $O_2 \cdot kg^{-0.75} \cdot min^{-1}$; Weise 2006).

Summary data were reported as mean ± SE, unless otherwise noted (SD was used for variables in the PCA). Data were transformed where applicable using log transformation for non-normal data or arcsine transformation for percentage data. Differences between means were tested using a two-sample t test or ANOVA, and relationships were tested using least-squares linear regression analysis. Differences in diving behavior of three male foraging strategies throughout the day were tested by comparing the distributions of dive depths and durations during the day and night based on the times of sunrise and sunset along the California coast using two-way repeated-measures analysis of variance (ANOVA). Multivariate analysis was conducted with MATLAB 7.1 (MathWorks 2005), and all other statistical analysis was conducted using SYSTAT 11 (SPSS 2004).

RESULTS

Twenty-two male California sea lions were captured and instrumented in the Monterey harbor during 2003: seven were subadults (110.9 ± 26.6 kg, mean ± SE) and 15 were adult males (186.8 ± 50.4 kg; see Appendix: Table A1). From May 2003 to February 2004,

temperature-only SRDL tags remained attached for 23 to 127 days, logging 51,920 dives and 1781 temperature profiles (see Appendix: Table A1). Mean dive depth among foraging strategies ranged from 27.7 ± 0.56 (mean ± SE) to 35.8 ± 1.27 m, and mean dive durations ranged from 1.6 ± 0.03 min to 2.2 ± 0.04 min (Table 1).

Increasing body mass of males was positively related to dive duration ($F_{1,19} = 8.61$, $P = 0.009$, $r^2 = 0.31$, df = 22; Fig. 1a), negatively related to time at sea ($F_{1,19} = 5.19$, $P = 0.034$, $r^2 = 0.22$, df = 22; Fig. 1b), and positively related to time ashore ($F_{1,19} = 5.19$, $P = 0.034$, $r^2 = 0.22$, df = 22; Fig. 1c). Body mass had no effect on diving depth ($F_{1,19} = 0.16$, $P = 0.696$, $r^2 = 0.01$, df = 22). There also was no relationship between body size and trip duration ($F_{1,19} = 3.05$, $P = 0.097$, $r^2 = 0.14$, df = 22) or percentage of time at sea spent diving ($F_{1,19} = 1.08$, $P = 0.313$, $r^2 = 0.05$, df = 22). There was a decreasing trend, however, between increasing body size and the percentage of time spent surface swimming, although it was not statistically significant ($F_{1,19} = 3.76$, $P = 0.067$, $r^2 = 0.17$, df = 22).

Individual foraging strategies

Using principal components analysis, 81.1% of the variation among individuals in diving behavior was explained by three factors (Table 2); diving patterns (PC1), foraging effort (PC2), and behavior at the surface (PC3). PC1 explained 41.6 % of the variance, and was composed of mean and SD of dive depth, duration, and habitat use defined by mean and SD of the ratio of dive depth to thermocline depth. PC2 explained 22.6% of the total variance and was composed of dive frequency, trip duration, and percentage of time spent at sea, and PC3 was composed of surface interval and horizontal swim speed and explained 17.0% of total variance (Table 2).

Hierarchical cluster analysis of the three principal components indicated that individuals could be classified into three distinct groups based on their diving behavior (Fig. 2a). Individual sea lions were partitioned into three distinct behavioral groupings by discriminant analysis (Fig. 2b), and jackknife resampling of the data resulted in correct group assignment 86% of the time. Univariate analyses indicated that individuals in group 1 had the least body mass and were characterized by the greatest frequency of dives ($F_{2,18} = 13.15$, $P < 0.000$), dives that were the shallowest ($F_{2,18} = 0.915$, $P = 0.418$), shortest duration ($F_{2,18} = 2.70$, $P = 0.950$), and closest to the thermocline ($F_{2,18} = 1.44$, $P = 0.263$), and with the shortest surface interval among the groups ($F_{2,18} = 3.07$, $P = 0.710$; Fig. 3). This group also spent the greatest percentage of time at sea ($F_{2,18} = 3.86$, $P = 0.039$) during the longest duration trips ($F_{2,18} = 2.017$, $P = 0.162$) of the three groups, and swam the fastest at the surface ($F_{2,18} = 0.407$, $P = 0.671$). Individuals in group 2 made deeper, longer duration dives that were less frequent, with a greater surface interval, and they swam farther from the thermocline than did group 1 (Fig. 3). This group spent less time at sea than group 1, or the greatest percentage

TABLE 1. Diving behaviors (means with SE in parentheses) of 22 male California sea lions (*Zalophus californianus*) tagged in Monterey, California, USA, in 2003 and 2004.

Foraging strategy	Animal ID	Dive depth (m)	Dive duration (min)	Surface duration (min)	Dive frequency (no. dives/ 4 h)	Trip duration (h)	Residual dive depth/ thermocline depth†	Time at surface (%)	Time diving (%)	Time in haul-out (%)
Group 1	28588	24.1 (0.58)	1.1 (0.02)	1.1 (0.02)	47.5 (0.87)	11.3 (0.3)	54.3 (0.9)	37.4 (0.6)	20.0 (0.3)	42.7 (0.7)
	28589	27.3 (0.22)	2.0 (0.02)	1.0 (0.02)	41.2 (0.47)	23.2 (0.7)	25.0 (0.6)	31.6 (0.6)	34.7 (0.6)	33.8 (0.6)
	37588	24.3 (0.87)	1.6 (0.04)	1.4 (0.04)	32.7 (0.66)	13.4 (0.4)	49.5 (2.2)	36.2 (1.1)	21.3 (0.6)	42.4 (1.3)
	37589	23.1 (0.37)	1.5 (0.03)	1.1 (0.02)	34.5 (0.94)	5.4 (0.1)	22.5 (0.3)	25.5 (0.6)	20.6 (0.5)	53.9 (1.3)
	37590	31.2 (0.69)	1.4 (0.03)	1.6 (0.03)	31.5 (0.69)	14.7 (0.6)	45.8 (0.9)	43.4 (1.0)	17.7 (0.4)	39.0 (0.9)
	37591	19.1 (0.30)	1.3 (0.02)	1.5 (0.01)	28.3 (0.49)	10.2 (0.2)	38.1 (0.6)	40.2 (0.5)	13.6 (0.2)	46.3 (0.6)
	37592	30.3 (0.42)	1.5 (0.02)	1.4 (0.02)	29.4 (0.50)	10.0 (0.3)	30.0 (0.3)	34.9 (0.6)	17.4 (0.3)	47.7 (0.8)
	44634	32.3 (0.60)	1.8 (0.03)	1.6 (0.02)	27.2 (0.69)	10.5 (0.3)	58.9 (1.1)	37.0 (0.7)	20.0 (0.4)	43.1 (0.8)
	44635	37.3 (1.00)	2.0 (0.04)	1.8 (0.03)	34.3 (0.67)	12.3 (0.5)	67.8 (1.6)	45.3 (1.1)	25.8 (0.6)	29.0 (0.7)
	Mean	27.7 (0.56)	1.6 (0.03)	1.4 (0.02)	34.1 (0.64)	12.3 (0.4)	43.5 (1.0)	36.8 (0.8)	21.2 (0.4)	42.0 (0.9)
Group 2	28587	37.4 (1.10)	3.8 (0.03)	1.5 (0.06)	26.9 (0.71)	8.8 (0.2)	64.1 (2.0)	23.6 (0.5)	25.1 (0.6)	51.3 (1.2)
	28590	47.4 (2.90)	1.7 (0.05)	1.3 (0.06)	36.2 (1.04)	11.8 (0.7)	116.4 (4.1)	37.2 (1.3)	18.4 (0.6)	44.3 (1.6)
	44637	21.7 (0.31)	2.1 (0.02)	1.4 (0.03)	27.1 (0.89)	10.2 (0.3)	37.0 (1.4)	24.5 (0.5)	21.8 (0.4)	53.8 (1.0)
	44639	25.3 (1.15)	1.5 (0.05)	1.5 (0.04)	24.2 (0.73)	18.3 (0.7)	53.1 (2.6)	29.2 (0.8)	15.1 (0.4)	55.7 (1.6)
	44640	46.6 (0.91)	2.1 (0.02)	1.6 (0.02)	26.1 (0.55)	15.2 (0.3)	108.6 (1.6)	38.4 (0.5)	21.7 (0.3)	39.9 (0.5)
	Mean	35.8 (1.27)	2.2 (0.04)	1.5 (0.04)	28.1 (0.80)	12.9 (0.5)	75.8 (2.3)	30.6 (0.7)	20.4 (0.5)	49.0 (1.2)
Group 3	37593	22.0 (0.78)	1.6 (0.05)	1.7 (0.03)	18.2 (0.96)	9.1 (0.4)	60.5 (2.0)	29.9 (0.8)	12.7 (0.3)	57.4 (1.6)
	37597	24.4 (0.51)	1.6 (0.04)	1.6 (0.03)	23.1 (0.76)	8.0 (0.3)	30.1 (0.5)	26.4 (0.6)	15.4 (0.4)	58.2 (1.4)
	37598	24.3 (0.35)	1.9 (0.04)	1.3 (0.03)	22.8 (1.00)	4.6 (0.2)	22.3 (0.4)	22.5 (0.6)	17.9 (0.5)	59.6 (1.6)
	44632	34.4 (0.59)	2.1 (0.03)	1.7 (0.03)	22.4 (0.76)	9.2 (0.4)	37.3 (0.4)	28.7 (0.6)	17.7 (0.4)	53.6 (1.1)
	44633	28.3 (0.69)	2.0 (0.04)	1.5 (0.03)	23.5 (1.20)	8.2 (0.5)	45.9 (0.8)	27.4 (0.7)	19.3 (0.5)	53.3 (1.3)
	44636	96.3 (2.76)	3.4 (0.06)	2.8 (0.07)	12.2 (0.58)	12.8 (0.4)	171.4 (3.0)	37.9 (1.0)	16.8 (0.5)	45.3 (1.2)
	44638	39.9 (1.22)	2.4 (0.05)	2.0 (0.05)	17.7 (0.70)	10.1 (0.5)	65.8 (2.0)	32.2 (0.8)	17.3 (0.4)	50.5 (1.3)
	Mean	34.6 (0.99)	2.1 (0.04)	1.8 (0.04)	20.0 (0.83)	8.9 (0.4)	61.9 (1.3)	29.3 (0.7)	16.7 (0.4)	54.0 (1.4)

Note: Sea lions were assigned to three distinct foraging groups based on diving behavior; see *Results: Individual foraging strategies* for details.

† Ratio of the residual dive depth (difference between dive depth and regression line) and the calculated thermocline depth; this metric is used to compare diving behavior relative to the thermocline depth among individuals.

of time hauled out ($F_{2,18} = 6.79$, $P = 0.006$), the greatest amount of time at the surface while at sea ($F_{2,18} = 3.74$, $P = 0.044$), and had the longest duration trips among all of the groups. Group 3 was distinguished as the least frequent but deepest divers, far from the thermocline, and the greatest surface interval, although not the longest duration dives (Fig. 3). Group 3 spent the least percentage of time at sea diving and had the shortest trips (Fig. 3). There was no difference in the time period of tag deployment (see Appendix: Table A1) or geographic distribution in diving locations among the three foraging strategies with respect to direction or bathymetric gradient (Fig. 4).

In general, male sea lion diving in all three foraging strategies occurred at all times of day, although strong diel patterns were apparent with deeper, longer dives,

with greater surface intervals during nighttime hours (approximately between the hours of 18:00 and 06:00 local time) compared with daytime. Distribution of diving and surface durations among the three foraging strategies differed between day and night, although not significantly (dive duration, repeated-measures ANOVA: $F_{2,18} = 3.413$, $P = 0.115$; surface duration, repeated-measures ANOVA: $F_{2,18} = 2.41$, $P = 0.055$); however, there was no difference in dive depth among foraging strategies between day and night (repeated-measures ANOVA: $F_{2,18} = 1.140$, $P = 0.342$).

When we used estimates of oxygen storage capacity from tagged individuals and conservative (low) estimates of oxygen consumption, no individual male California sea lion among the three foraging strategies exceeded its calculated aerobic dive limit (cADL); whereas when we used higher estimates of oxygen consumption, two individuals (28588/group 1 and 44636/group 3) were at or exceeded cADL. There was no relationship between mean dive depth or duration as a function of mass-specific oxygen storage capacity (blood, muscle, and lungs).

DISCUSSION

Although individual-based foraging strategies have been identified previously among several air-breathing marine vertebrates, this study is the first to describe it among sexually dimorphic male otariids and within a sex. We used 12 of 22 diving parameters to classify the three distinct foraging strategies. Greater body size clearly influenced diving behavior in male sea lions and explained a strong component of the variability among individuals and foraging strategies. Although there was variability in diving behavior within individuals, there was greater variability among individuals that was consistent with foraging specializations. Our finding indicated that the three male sea lion foraging strategies were geographically overlapping along the California coast, with both spatially explicit and ontogenetic components. All three foraging strategies had a shallow-water component; however, the mixed and deeper diving strategies had a spatially explicit component with regard to vertical distribution of diving behavior, indicating that these sea lions probably ate larger or different prey species. Further, more than half of the animals in the shallow diving strategy were smaller, subadult male sea lions, indicating that age and development probably affected foraging behavior. Individual-based foraging strategies identified in this study indicated that some larger males frequently use deeper waters, extending the previously described dive depth range in this species from the epipelagic to mesopelagic (>200 m) environment.

Niche variation within a species has long been ignored in ecological studies because it was believed to be rare or weak or to have a trivial impact on ecological processes (Bolnick et al. 2003). More recently Bolnick (et al. 2003) reviewed evidence for individual specialization in 93
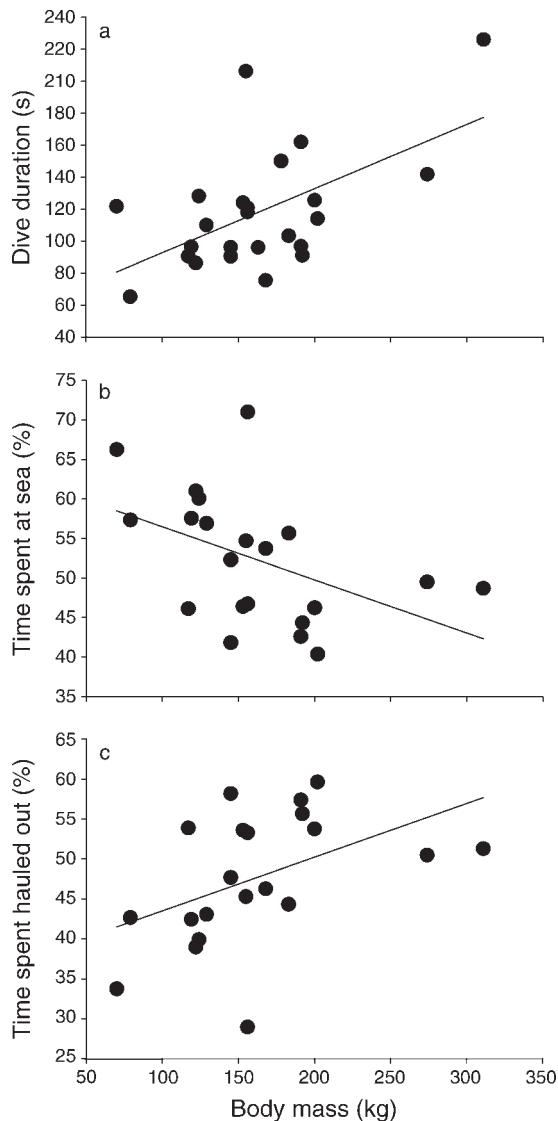

FIG. 1. Relationship of mean (a) dive duration, (b) time spent at sea (diving and surface swimming combined), and (c) time on land hauled out as a function of body mass of individual California sea lions (*Zalophus californianus*). Lines indicate a significant linear relationship between body mass and dive duration ($r^2 = 0.32$, $P = 0.009$), time spent at sea ($r^2 = 0.21$, $P = 0.034$), and time hauled out on land ($r^2 = 0.21$, $P = 0.034$).

species across a broad taxonomic range. Only a few studies, however, indicated distinct individual-based foraging strategies among air-breathing marine vertebrates, including a broad taxonomic range of seabirds (Radl and Culik 1999, Kato et al. 2000), toothed whales (Ford et al. 1998, Laidre et al. 2002), pinnipeds (Lea et al. 2002, Austin et al. 2004, Staniland et al. 2004), and otters (Tinker et al. 2007).

There is a diverse array of behavioral, ecological, and physiological or morphological mechanisms that can generate within-population variation that leads to

TABLE 2. Component loadings of 12 variables of diving behavior on the first three components, which collectively explained 81.1% of the total variance in the data.

Variable	PC1 (41.6%)	PC2 (22.6%)	PC3 (17.0%)
Mean dive depth	**0.778**	0.054	0.515
SD of dive depth	**0.905**	0.118	0.232
Mean dive duration	**0.705**	−0.347	0.198
SD of dive duration	**0.914**	−0.308	0.129
Mean surface interval	0.543	−0.252	**0.723**
Mean horizontal swim speed	0.138	0.09	**0.849**
Mean ratio diving depth/thermocline depth	**0.870**	0.142	0.359
SD ratio diving depth/thermocline depth	**0.876**	0.154	−0.003
Mean trip duration	0.294	**0.730**	−0.176
Frequency of dives	−0.299	**0.725**	−0.414
Mean time spent at sea (%)	0.167	**0.861**	0.226
Body mass	0.431	**−0.748**	−0.197

Notes: Parameters accounting for most of the variability in each principal component are shown in bold. PC1 is related to dive patterns, PC2 to diving effort, and PC3 to surface behaviors.

distinct foraging strategies (Bolnick et al. 2003). Epipelagic to mesopelagic individual-based foraging strategies were identified among individual male California sea lions based on diving behavior. Similarly, variation in dive behavior within a species has been used to identify foraging strategies among other marine mammals, including toothed whales (Laidre et al. 2002), pinnipeds (Lea et al. 2002, Austin et al. 2004, Staniland et al. 2004), and otters (Tinker et al. 2007). In our study, ecological mechanisms were investigated by inferring feeding behavior from the examination of individual diving behavior and concurrent population-level prey use (Weise 2006). Although this approach has its limitations, within this framework we propose that spatially explicit (vertically) individual-based foraging strategies in male California sea lions are probably related to dietary specializations. Specialization resulted from decisions that individuals made in targeting different prey types that have similar horizontal distributions yet differ in their vertical distribution relative to thermal structure of the water column (Vaughan and Recksiek 1978, Chess et al. 1988, Reynolds 2003, Helser et al. 2006, Hill et al. 2006). In contrast, benthic-foraging California sea otters have different diving behavior and polymorphic prey specializations among individuals with almost identical home ranges (Estes et al. 2003, Tinker et al. 2007). Variation in dive strategies in Antarctic fur seals reflect differences in prey choice that are related to spatial and temporal variability in the availability and geographic distribution of prey species (Lea et al. 2002).

Prey preferences among male California sea lions may be partially dependent upon predator ontogeny and body size, which is directly related to foraging ability (i.e., ability to dive deeper, longer, and to handle large prey) and physiological diving capacity. Body mass is strongly related to diving behavior across all major groups of diving birds and mammals (Halsey et al. 2006). Many prey species identified in the diet of California sea lions in central California (Weise 2006)

occur in schools that are generally compact and patchily distributed (both vertically and horizontally), and probably account for variability in the behavioral differences among foraging strategies. Further, because males have relatively shallow dives, with distinct periods of diving, they are likely to visually search for prey from the surface while swimming between patches to minimize the greater transport costs associated with diving, similar to behavior described for fur seals (Boyd 1996). The three foraging strategies identified in this study were not mutually exclusive, and all three strategies included a shallow-water foraging component. The shallow diving strategy (group 1), observed mostly in smaller, subadult animals, probably served to focus their efforts on shallow-water schooling prey species. Larger males (groups 2 and 3), however, probably targeted shallow-water prey and larger prey items and species such as salmon depredated off lines from fisheries (Weise and Harvey 2005) and certain species of rockfishes and size classes of hake that are more typically distributed at deeper depths on or closer to the bottom (Chess et al. 1988, Reynolds 2003, Helser et al. 2006). Larger prey are more likely to meet the greater energetic demands of larger males, and increased intake by the larger sex has been observed in sexually dimorphic species including gray seals (*Halichoerus grypus;* Mohn and Bowen 1996) and giraffes (*Giraffa camelopardalis*; Ginnett and Demment 1997).

Larger adult male sea lions (groups 2 and 3) performed a number of dives to mesopelagic depths (>200 m), where they spent increased time underwater followed by increased surface intervals between dives, which could be explained by pushing or exceeding aerobic diving limits or needing to return to the surface to handle and consume prey. For diving air-breathing vertebrates, the prevailing view is that dives are primarily aerobic, although there are exceptions (e.g., Costa et al. 2001). In this study, there was no difference in oxygen storage capacity among foraging strategies; however, only 12 of 22 instrumented animals had an
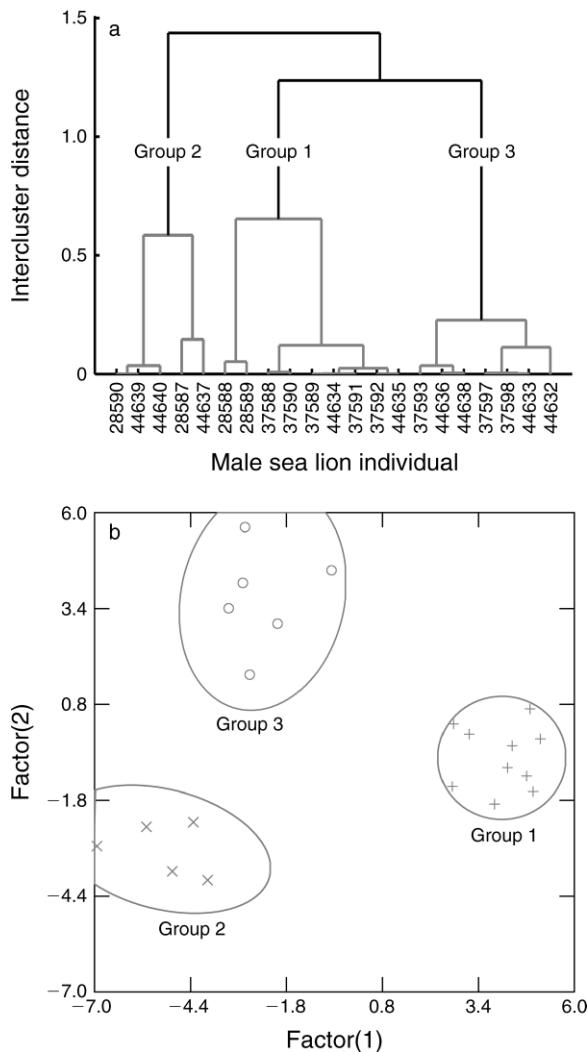
FIG. 2. (a) Dendrogram of hierarchical cluster analysis used to detect natural grouping in diving patterns, diving effort, and surface behaviors among individual male California sea lions. Three groups indicate distinct clusters representing different foraging strategies. (b) Plot of discriminant function analysis scores of two canonical variables showing the overall clumping of individuals into three different groups distinguished by foraging strategies. Ovals around clusters indicate 95% jack-knife confidence ellipses.

two individuals was an adult male (44636) from the mixed- or deeper-diving foraging strategies. Interestingly, this individual was among the smallest adult males in this study and exhibited the greatest surface durations among all tagged animals (2.8 min), so it is possible that pushing or exceeding cADL may explain greater surface intervals in this individual.

Optimal foraging theory (OFT) predicts that predators will choose prey sizes with the greatest energy return per unit time spent foraging (Stephens and Krebs 1986), and diving animals should maximize their foraging time by minimizing travel costs getting to and from depth and minimizing post-dive intervals (Houston and Carbone 1992, Costa et al. 2001). Given the energetic costs associated with attaining depth, mesopelagic (and
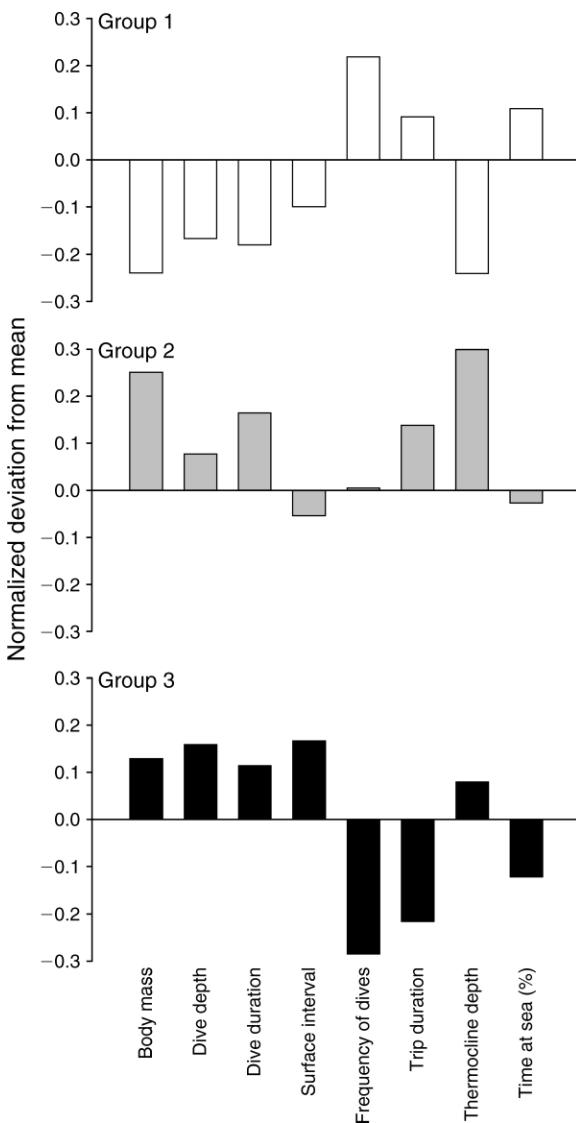

FIG. 3. Normalized deviation of mean dive characteristics among three foraging strategies identified in male California sea lions.

analysis of complete oxygen stores. Further, there was no relationship between mean dive depth or duration as a function of mass-specific oxygen storage capacity (blood, muscle, and lungs) that might be expected if animals were exceeding their cADL. Based on average individual dive behavior, no individual male California sea lions among the three foraging strategies exceeded their calculated aerobic dive limit (cADL) based on conservative (low) estimates of oxygen consumption. Also, only two individuals (28588/group 1 and 44636/group 3) were at or exceeded cADL based on higher estimates of oxygen consumption. One of these
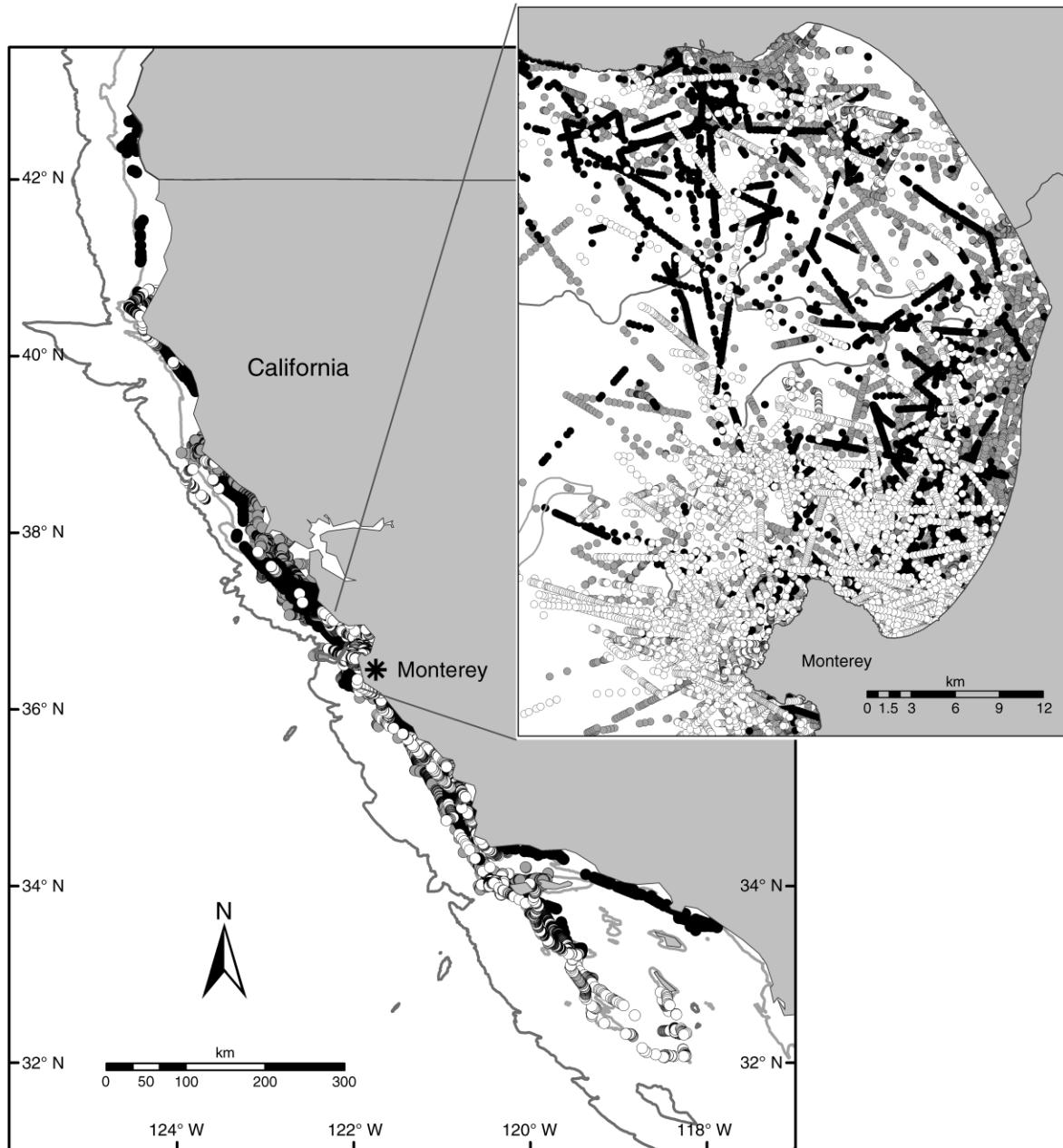
FIG. 4. Map of the distribution of diving locations for three foraging strategies identified in male California sea lions in relation to continental shelf (0–200 m, light gray line), shelf break (200–2000 m, dark gray line), and pelagic waters (>2000 m). Dive locations were determined by linear interpolation of time and distance between Argos positions, following McConnell et al. (1992). Foraging strategies include group 1 (shallow divers, gray circles), group 2 (mixed divers, white circles), and group 3 (deep divers, black circles). The inset is a map of diving locations of male foraging strategies on the scale of Monterey Bay, and in relation to tagging site in Monterey, California (continental shelf, light gray line; shelf break, dark gray line). White circles overlap gray and black, and gray circles overlap black.

benthic) divers can optimize their energetic return by consuming prey at depth. In the case of large, energetically rich prey, however, prey cannot be consumed at depth and there is a trade-off between the greater energetic "payoff" of consuming larger prey and the increased time required to transport, handle, and consume large prey at the surface. Although the diet

of tagged individuals was unknown, large adult-size salmon were regularly observed being handled and consumed at the surface by adult male sea lions in the hook-and-line fisheries (Weise and Harvey 2005), and large salmon consisted of up to 11% of the seasonal mass consumed by the sea lion population in central California (Weise and Harvey 2008). Therefore, we

propose that mesopelagic diving patterns with increased surface intervals of larger male California sea lions represented increased "costs" associated with capturing and consuming large prey items at the surface, which were both facilitated and required by larger body size, rather than necessitated by a lack of oxygen storage capacity and/or management.

Although subadult male sea lions occurred in all three foraging strategies, the majority of younger animals occurred in the shallow-diving group 1, indicating that not only body size, but also ontogeny or age may be a covariant explaining variation in diving behavior among individuals. Previous studies have indicated that the diving ability of young marine mammals is constrained by lower oxygen stores than those of adults (i.e., Noren et al. 2001), faster use of oxygen stores than in adults, due to allometric relationships and costs associated with growth (i.e., Peters 1983), and more drag per unit mass (Schreer and Kovacs 1997). These constraints are pronounced in California sea lions, which have a surprisingly long period of development required for blood (1.5–2.5 years) and muscle (4–6 years; 125 kg) oxygen stores to reach adult values (Weise and Costa 2007). These physiological constraints in younger animals, coupled with lack of ability to handle larger prey in smaller animals, based on observations in salmonid fisheries (Weise and Harvey 2005), are likely to explain the shallower diving strategy observed in group 1. Potential differences in diet in subadult male sea lions, coupled with constrained diving behavior, may lead to differential survival among foraging strategies during environmental perturbations that cause changes in the abundance and distribution of prey species, and subsequent changes in behavior of sea lions (Weise et al. 2006).

The three male sea lion foraging strategies were highly overlapped geographically (two-dimensionally) along the west coast of the United States and, therefore, appeared to be polymorphic in nature, but the inclusion of the third dimension enabled us to tease apart spatially explicit behavior relative to depth. At the same time, Weise (2006) indicated that individual foraging behavior varied through time as a function of geographic location in northern and southern California. Although season was not a significant factor explaining the variation among strategies, this aspect needs to be further investigated in future studies, given the documented changes in seasonal and annual food habits of California sea lions (Weise 2006, Weise and Harvey 2008) and the paucity of sampling during some seasons. Considering the dynamic nature of the temporal and spatial variation in the physical structure of coastal waters and, in turn, prey distributions, future studies may offer insights into how this variation affects the stability and nature of alternative foraging strategies during fluctuations in prey availability resulting from environmental perturbations or as sea lions move into different oceanographic regions along the coast (southern California bight, central and northern California, Oregon and Washington).

Individual-based foraging specializations within a species of predator have important implications for the application and interpretation of population-level consumption models used to evaluate trophic interactions and ecosystem structure. In the California sea lion population, the implication is that individual males are likely to consume prey in unequal proportions and perhaps even totally different prey species. This may be further compounded by different strategies and target prey in females and younger age classes of animals. Foraging and dietary specializations have been recognized in a variety of species and in most marine vertebrate groups: otters (Tinker et al. 2007); penguins (Tremblay and Cherel 2000); odontocetes (Ford et al. 1998); mysticetes (Hoelzel et al. 1989); and otariids (Lea et al. 2002, Staniland et al. 2004). Such specializations are probably more widespread but undetected in other taxa. Predator impacts on specific prey species or subsets of prey populations may vary considerably more due to the occurrence of foraging and dietary specializations. These specializations may represent an adaptive response to reduced food resources and increased intraspecific competition and thus may be a useful index of population health with respect to the abundance of prey resources (Tinker et al. 2007). This is probably not the case with California sea lions, given the high productivity along the California coast; however, food limitation may be possible in localized regions, particularly during environmental perturbations. Although it is important to understand the underlying mechanisms that drive individual specializations, it is equally important to account for this variation in population-level models of trophic interactions.

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APPENDIX

Summary information on three foraging strategies of male California sea lions outfitted with Sea Mammal Research Unit SRDL tags and a photograph of the floating platform and aluminum enclosure used for passive capture of adult male sea lions (*Ecological Archives* E091-070-A1).