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BEHAVIORAL ECOLOGY – ORIGINAL RESEARCH

Foraging strategies of a generalist marine predator inhabiting a dynamic environment

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Abstract Intraspecific variability is increasingly recognized as an important component of foraging behavior that can have implications for both population and community dynamics. We used an individual-level approach to describe the foraging behavior of an abundant, generalist predator that inhabits a dynamic marine ecosystem, focusing specifically on the different foraging strategies used by individuals in the same demographic group. We collected data on movements and diving behavior of adult female California sea lions (*Zalophus californianus*) across multiple foraging trips to sea. Sea lions ($n = 35$) used one of three foraging strategies that primarily differed in their oceanic zone and dive depth: a shallow, epipelagic strategy, a mixed epipelagic/benthic strategy, and a deep-diving strategy. Individuals varied in their degree of fidelity to a given strategy, with 66 % of sea lions using only one strategy on all or most of their foraging trips across the two-month tracking period. All foraging strategies were present in each of the sampling years, but there were inter-annual differences in the population-level importance of each strategy that may reflect changes in prey availability. Deep-diving sea lions traveled shorter distances and spent a greater proportion of time at the rookery than sea lions using the other two strategies, which may have energetic and reproductive implications. These results highlight the importance of an individual-based approach in describing the foraging behavior of female California sea lions and understanding how they respond to the seasonal and annual changes in prey availability that characterize the California Current System.

Keywords Individual variability · Dive behavior · Sea lion · *Zalophus californianus* · California Current

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Introduction

Intraspecific variability in foraging behavior is widespread across a variety of taxonomic groups, even among individuals within the same demographic group (Bolnick et al. 2003; Araújo et al. 2011; Ceia and Ramos 2015). This variability may arise as a result of intrinsic factors such as individual differences in physiology, morphology, or behavior (Killen et al. 2011; Patrick and Weimerskirch 2014; Hoskins et al. 2015), or from external factors such as prey and habitat availability (Svanbäck and Bolnick 2005; Kernaléguen et al. 2015; Newsome et al. 2015; Rosenblatt et al. 2015). Population-level descriptions largely overlook this individual variability, which may result in incomplete descriptions of foraging behavior and obscure the responses of individuals and populations to environmental variability. Because the presence of intraspecific variability can affect population dynamics and the strength of species interactions, individual-based approaches are also important in understanding the structure and dynamics of ecological communities (Hughes et al. 2008; Bolnick et al. 2011; Violle et al. 2012).

Pinnipeds are a diverse group of carnivores that are often top predators in marine ecosystems. In the past decade, there has been increasing documentation of different foraging strategies within pinniped populations, with a particular focus on the various strategies used by individuals in the same demographic group (Cherel and Hobson 2007; Villegas-Amtmann et al. 2008; Weise et al.2010; Lowther and Goldsworthy 2011; Kernaléguen et al. 2012; Villegas-Amtmann et al. 2013). These foraging strategies often reflect the three basic diving patterns exhibited by air-breathing marine predators (epipelagic, mesopelagic, benthic), but also may be related to associations with oceanographic features, habitat use, or foraging site fidelity. Differences in diving behavior or spatial use are often assumed to reflect dietary differences, and studies that combine measures of at-sea behavior with diet estimation generally validate this assumption (Tinker et al. 2008; Lowther and Goldsworthy 2011; Lowther et al. 2011; Kernaléguen et al. 2016). The presence of multiple foraging strategies may buffer pinniped populations from environmental variability, and can have both management and conservation implications, especially if foraging strategies are spatially explicit (Villegas-Amtmann et al. 2008; Lowther et al. 2012; Augé et al. 2014).

California sea lions (*Zalophus californianus*) are the most abundant pinniped in the California Current System (CCS), which is a productive eastern boundary system characterized by oceanographic variability at multiple temporal and spatial scales (Checkley and Barth 2009). The US population of California sea lions has experienced exponential growth since federal protection in 1972, but there is some evidence that the current estimated population of 297,000 individuals is at or approaching carrying capacity (Carretta et al. 2015). As a species, California sea lions are opportunistic foragers that typically prey on seasonally abundant, aggregating species in neritic and offshore habitats (Weise and Harvey 2008; Orr et al. 2011). They are often described as shallow, epipelagic divers (Feldkamp et al. 1989; Kuhn and Costa 2014), although there is some evidence that individuals may have specialized foraging strategies (Weise et al. 2010; Villegas-Amtmann et al. 2011). Adult female California sea lions are good indicators of ecosystem conditions in the CCS because their reproductive success is influenced by small- and large-scale ocean conditions, particularly El Niño events that adversely affect pup growth and mortality rates (Melin et al. 2012). This sensitivity is likely because female sea lions have a restricted distribution during an energetically expensive time period (lactation), alternating foraging trips to sea (1–7+ days) with onshore nursing (1–2 days) at the rookery for the 10- to 11-month lactation period (Melin et al. 2000; Kuhn and Costa 2014; Harris 2016). Despite their abundance and importance as an indicator species, there

have been relatively few published studies on the at-sea behavior of adult female California sea lions (Feldkamp et al. 1989; Antonelis et al. 1990; Melin et al. 2008; Kuhn and Costa 2014). Previous studies have focused on describing population-level trends, although Melin et al. (2008) and Kuhn and Costa (2014) noted that adult females from the two largest US rookeries exhibited considerable individual variation in their at-sea behavior.

The objective of this study is to examine individual variation in foraging behavior of adult female California sea lions, focusing specifically on the presence of multiple foraging strategies. To accomplish this, we used bio-logging devices to collect data on at-sea movements and dive behavior of female sea lions from one of the largest sea lion rookeries across multiple years. The specific objectives are to (1) identify and describe foraging strategies of female sea lions; (2) determine whether the prevalence of each strategy varies among years; (3) examine spatial use of each foraging strategy; and (4) determine if movement and haul-out behaviors differ among strategies. This individual-level approach will help to elucidate the potential trade-offs sea lions face in terms of physiological constraints, pup attendance, and energy expenditure that may impact overall fitness. It also provides insight into how female California sea lions respond to the seasonal, annual, and multi-year changes in prey availability that are characteristics of the CCS. This is particularly important in light of recent significant oceanographic changes in the CCS, including increased sea surface temperatures and reduced primary productivity that have affected the condition and survival of California sea lion pups (Leising et al. 2014; McClatchie et al. 2016).

Methods

Data collection

Lactating adult female California sea lions ($n = 41$) were captured in November of 2005–2008 at San Nicolas Island, CA (33.25°N, 119.5°W) using custom hoop nets. Sea lions were sedated using gas anesthesia (IsoFlurane) administered with oxygen via a field portable vaporizer. Each sea lion was instrumented with a satellite tag (Wildlife Computers, Redmond, WA or Sirtrack, New Zealand) that collected location data using ARGOS or Fastloc GPS, a time-depth recorder (Wildlife Computers), and a VHF tag (Advanced Telemetry Systems, Isanti, MN). Time-depth recorders had a depth resolution of 0.5 m and sampled at 1-, 2-, or 4-s intervals. Tags were mounted on a neoprene base and attached to mesh netting using cable ties. The instrument package was then glued to the dorsal pelage with a quick-setting epoxy. Morphometric measurements were collected at the time of initial capture. Sea lions were

recaptured approximately 2 months later to recover instruments and obtain the complete, archived dive record. We assumed that all sea lions were nursing a pup because they were lactating at the time of capture and continued to return to the rookery during the tracking period (Melin et al. 2000). One female did leave San Nicolas Island at the end of December and traveled south to Mexico, returning after 4+ weeks. We assumed that she had already lost or did lose her pup due to the long absence, and only included data from trips before this absence in the analysis.

Data processing

Location data were filtered using a speed and angle filter to remove erroneous locations. A continuous-correlated random walk (R package, *crawl*; ARGOS) or linear interpolation (GPS) was used to predict hourly locations along the foraging trip. Foraging trips were defined as the time between when a female departed to the time she returned to the rookery. The departure and arrival times of each foraging trip were identified using the wet–dry sensor on the time-depth recorder and the interpolated satellite locations (i.e., a sea lion had to return to San Nicolas Island for the foraging trip to end). While on foraging trips, sea lions often hauled-out at locations other than San Nicolas Island. The time spent ashore during these haul-outs was included in the total trip duration. Trips <1 day were excluded from further analysis because they generally had very few satellite locations associated with them.

The movement and haul-out behavior of sea lions during each foraging trip was described using seven variables: trip duration (days), maximum distance traveled from the rookery (km), total distance traveled (km), path straightness, the number of times that a female hauled-out during a trip, the time spent hauled-out during a trip (days), and the time spent hauled-out at the rookery following a trip (days). The maximum distance from the rookery was calculated as the straight-line distance between the rookery and the farthest location from the rookery. Total distance traveled was the sum of the distances between each interpolated location. Path straightness, an indication of the tortuosity, was calculated by dividing the round-trip straight-line distance by the total distance traveled. For sea lions instrumented with GPS tags that collected both ARGOS and GPS locations, only the GPS locations were used to calculate movement metrics. Differences in error measurements between ARGOS (0.5–11 km) and GPS locations (50–100 m; Costa et al. 2010) should not have affected comparisons because the mean (±SD) differences in movement variables between the two location types were relatively small compared with the actual measurements (0.4 ± 4.4 km for maximum distance traveled from the rookery and 7.1 ± 41.5 km for total distance traveled).

Dive data were analyzed using a custom built zero-offset correction and analysis program in MATLAB (IKNOS, Y. Tremblay). Only dives deeper than 4 m and longer than 16 s were analyzed. To standardize among years, dive data were subsampled to data collected at 4-s intervals. Dive bouts, which are periods of intensive diving activity, were identified using a custom R script (R. Beltran), which is a modification of the method described in Boyd et al. (1994). The minimum criterion for a bout was five dives with a maximum surface interval of 10 min or less between dives. Transiting bouts were identified as those with a mean dive depth of 8 m or less; these bouts (and all dives within) were excluded from further analysis (Melin et al. 2008).

The dive behavior of sea lions on each foraging trip was described using 16 variables. The following variables were calculated by averaging dive statistics for all dives that occurred within bouts across the foraging trip: maximum day and night dive depths (m), bottom time (s), number of vertical movements (wiggles) during the bottom phase of the dive, efficiency [(bottom time/{dive duration + post-dive interval})], and intra-depth zone (IDZ) index. The time period (day or night) of each dive was identified using the solar zenith based on the time and an interpolated location of the dive. Day and night dives were defined as dives with a solar zenith <90 (day) or >102 (night). The IDZ is a measure of the tendency to dive repeatedly to a given depth (Tremblay and Cherel 2000). An IDZ value of 1 was assigned to a dive if the maximum dive depth was within ±10 % of the previous dive; if not, a value of 0 was assigned to the dive. Because IDZ values were averaged across dives, values for trips ranged from 0 to 1. We also calculated a single value per foraging trip for the following variables: the percentage of time at sea spent diving, percentage of dives during the day and night, percentage of dives in each dive type (see below), and a diel index [(mean maximum day depth − mean maximum night depth)/larger mean maximum dive depth]. Values for the diel index theoretically ranged from −1 to 1, with negative values indicative of reverse diel diving. For example, a value of 0.5 would indicate that night dive depths were 50 % shallower than day dive depths, whereas a value of −0.5 would indicate the opposite. Lastly, a mean dive rate (dives h^{-1}) was calculated by averaging the dive rate for each bout across the foraging trip.

Dive types were initially identified by visually classifying a subset of dives into one of four dive types—epipelagic (<200 m), benthic (<200 m and at or near the bottom), mesopelagic (≥200 m), and deep benthic (≥200 m and at or near the bottom). Benthic dives were identified as dives that had a distinct square shape to the bottom phase of the dive, which is often, but not always indicative that the dive is at or near the sea floor (Schreer et al. 2001). Alternative methods to identify benthic dives, such as comparisons of

dive depth to bathymetry, could not be used due to error in estimates associated with the actual location of the animal or uncertainty in bathymetry (i.e., sea lions frequently dove deeper than the estimated depth at a given location). A principal components analysis of 10 dive statistics (a subset of those listed above) was used to create a new set of uncorrelated variables for the classified dives (~5000 dives). The dive classifications and principal component scores from factors with eigenvalues ≥1 were used in a discriminant function analysis to determine the effectiveness of classifying dive type based on dive variables alone. The effectiveness of this method was 85 % and was subsequently used to predict the dive types for the remaining dives. All benthic dives (shallow and deep) were subsequently combined into one dive type.

Statistical analyses

Foraging strategies were identified using a hierarchical clustering on principal components analysis of all dive variables (R package, *FactoMineR*). A principal components analysis was first used to reduce the number of variables into a few, uncorrelated variables. The principal component scores from factors with eigenvalues ≥1 were retained and used as variables in the hierarchical cluster analysis. The cluster analysis was conducted using Euclidean distances and Ward's method. The number of informative clusters was identified as the smallest number of clusters that minimized the decrease in within-group inertia when moving from q to $q + 1$ clusters (Le et al. 2008). The contribution of each variable to separation of a cluster was described using the following equation.

$$u = \frac{\overline{x}_q - \overline{x}}{\sqrt{\frac{s^2}{n_q}\left(\frac{N-n_q}{N-1}\right)}}$$

where $\overline{x_q}$ is the mean of a dive variable for group q and $\overline{x}$ is the overall mean, n_q is the number of trips in group q, N is the total number of trips, and s is the standard deviation for all trips. The calculated value (u) was used to test whether the mean of any given variable for a cluster was equal to the overall mean of that variable (Le et al. 2008). If not, it was assumed that variable was important in describing the cluster. A linear discriminant analysis of the principal component scores using leave-one-out cross-validation was used to assess the overall effectiveness of the cluster analysis.

The prevalence of each foraging strategy was determined by calculating the proportion of trips in each strategy per female, which resulted in one value for each strategy per female. This approach was used, instead of simply calculating the number of trips in each foraging strategy

per year, to ensure that females with many trips in one foraging strategy did not bias results. Proportions were arcsine transformed and used in an Analysis of Variance (ANOVA) to determine whether the prevalence of a strategy differed among years. Separate analyses were run for each foraging strategy. Multiple comparisons were made using a Ryan's Q test with Kramer's modification for unequal sample sizes.

The horizontal spatial use of each foraging strategy was described using a kernel density analysis of the location of dive bouts (Geospatial Modeling Environment, v. 0.7.3). The location of each dive bout was determined by averaging interpolated locations of all dives within a bout. We created a kernel density for each foraging strategy to describe the overall distribution across all years, and also for each foraging strategy per year. The bandwidth was determined using the plug-in estimator. Because dive bouts were used as the replicate, females with more foraging trips in one strategy (hence more dive bouts) contributed more than females with fewer foraging trips in that strategy. We chose not to include a weighting factor because we were simply interested in a qualitative description of the important core foraging areas of each foraging strategy.

Linear mixed-effect models were used to determine whether movement and haul-out variables differed among foraging strategies (R package, *lme4*). Separate models were run for each of the following six variables: trip duration, maximum distance traveled from the rookery, total distance traveled, path straightness, occurrence of haul-outs on the trip, and the duration of time spent hauled-out at the rookery following a foraging trip. The occurrence of haul-outs on a trip was either a value of 0 (no haul-outs) or 1 (at least one haul-out), and was modeled using a generalized linear mixed-effects model (GLMM) with a binomial distribution and logit-link function. The fixed effects included in the initial models were year, strategy, and the year:strategy interaction. Because the year:strategy interaction was not significant for 5/6 variables, it was not included in the final models for these variables. There was a significant year:strategy interaction for the occurrence of haul-out on trips and separate models were therefore run for each year. Individual was included as a random effect in all models. The significance of the fixed effects for each variable was determined using F-tests or a χ^2 test (GLMM only). Multiple comparisons were made using Tukey's HSD tests (R package, *multcomp*) where applicable. Residual plots were used to test assumptions and log-transformations were applied (and assumptions reevaluated) when necessary. Over-dispersion was checked for the model fit with a binomial distribution. Means are shown ± SD unless otherwise stated. Statistical significance was assessed at $P \leq 0.05$.

Table 1 Principal component loadings by dive variable for the three principal component dimensions used in the cluster analysis. The percentage of variability explained by each dimension is shown below the column heading

	Dim 1 (34.6 %)	Dim 2 (30.2 %)	Dim 3 (15.6 %)
Day depth (m)	0.10	−0.78	0.30
Night depth (m)	0.10	−0.89	−0.22
Bottom time (s)	0.91	−0.21	0.20
Bottom wiggles	0.88	0.12	0.22
IDZ[a]	0.89	−0.19	0.10
Diel[b]	0.07	0.43	0.61
Efficiency[c]	0.68	0.67	−0.03
Dive rate (dives h^{-1})	−0.26	0.83	−0.17
Time diving (%)	0.18	0.51	−0.31
Day diving (%)	−0.36	0.11	0.85
Night diving (%)	0.42	−0.02	−0.85
Epipelagic (%)	−0.90	0.31	−0.10
Benthic (%)	0.86	0.46	0.10
Mesopelagic (%)	0.01	−0.91	0.01

[a] IDZ is a measure of the tendency to dive to repetitive depths

[b] Diel is a measure of similarity in mean dive depths between day and night

[c] Efficiency was calculated as bottom time/(dive duration + post-dive interval)

Results

A total of 35 adult female California sea lions had tracking and dive data that spanned at least three foraging trips to sea (2005 = 11, 2006 = 9, 2007 = 9, and 2008 = 6; Online Resources 1 and 2). The mean tracking duration per year ranged from 53 to 77 days, with an overall mean of 60 ± 16 days. The number of trips per individual ranged from 3 to 18, with an average of 9.9 ± 3.7 trips per individual and a total of 346 trips across all years. The total number of trips per year was 115 in 2005, 62 in 2006, 116 in 2007, and 53 in 2008. The mass and standard length of females ranged from 62.2 to 97.2 kg ($\bar{x}$ = 84.2 ± 9.3 kg) and 150 to 173 cm ($\bar{x}$ = 164 ± 6 cm), respectively.

Identification and description of strategies

The first three principal components had eigenvalues ≥1 and explained 80 % of the variability in the data (Table 1). The cluster analysis identified three distinct foraging strategies that were largely discriminated on the first two principal component dimensions (Fig. 1). Individual trips were reliably classified to the correct strategy with >97 % accuracy. The three foraging strategies could generally be described as a shallow, epipelagic strategy (Strategy 1), a mixed epipelagic/benthic strategy (Strategy 2), and a deep
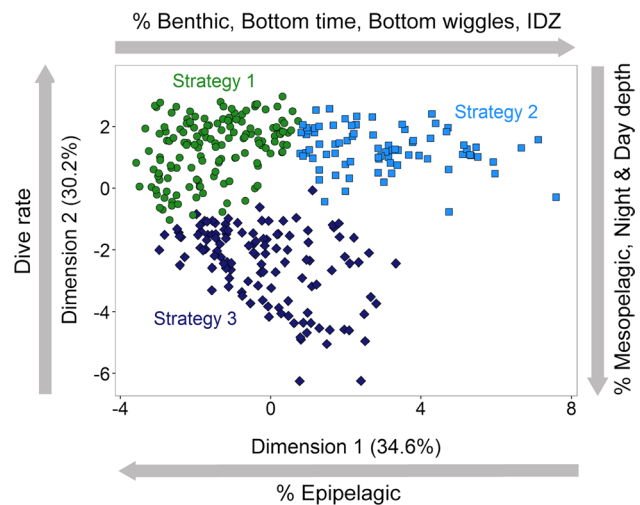

Fig. 1 The three foraging strategies exhibited by adult female California sea lions from San Nicolas Island as identified by a hierarchical cluster analysis on principle components. The location of each point, corresponding to one foraging trip and color coded by strategy, is shown on the first two principal component dimensions. The dive variables that loaded strongly (>0.7) on each dimension are above *arrows* indicating the direction of each relationship (color figure online)

epipelagic/mesopelagic strategy (Strategy 3; Fig. 2a–c). Females with foraging trips in Strategy 1 had a high dive rate and shallow dive depths during the day and night (<60 m), with 55 % of dive effort concentrated during the day (Table 2). Females in Strategy 2 dived slightly deeper during the day than females in Strategy 1, but to similar depths at night. The proportion of benthic dives, mean bottom time, IDZ, efficiency, and percentage of dives at night were all higher in Strategy 2 compared with the overall mean (Table 2). Females in both Strategy 1 and 2 exhibited occasional deep dives, but had a very low overall percentage of dives in the mesopelagic zone. In contrast, females in the third strategy had mean day and night dive depths over 100 m, with an average of 27 % of dives in the mesopelagic zone. Strategy 3 was also characterized by a reduced dive rate, a lesser percentage of time at sea spent diving, a higher IDZ, and a general lack of diel behavior compared with the overall mean (Table 2). In general, the mass range of females was similar across all three strategies; however, 93 % of females with foraging trips in Strategy 3 were heavier than 79 kg compared with 62 and 71 % for Strategies 1 and 2, respectively.

Fidelity of females to one strategy across foraging trips varied, with 40 % of females using only one strategy, 26 % with strong fidelity to one strategy (>75 % trips in 1 strategy), and the remaining 34 % using 2 or all 3 strategies. All strategies were represented in every year, but the prevalence of Strategy 1 ($F_{3,31}$ = 3.24, P = 0.04) and Strategy
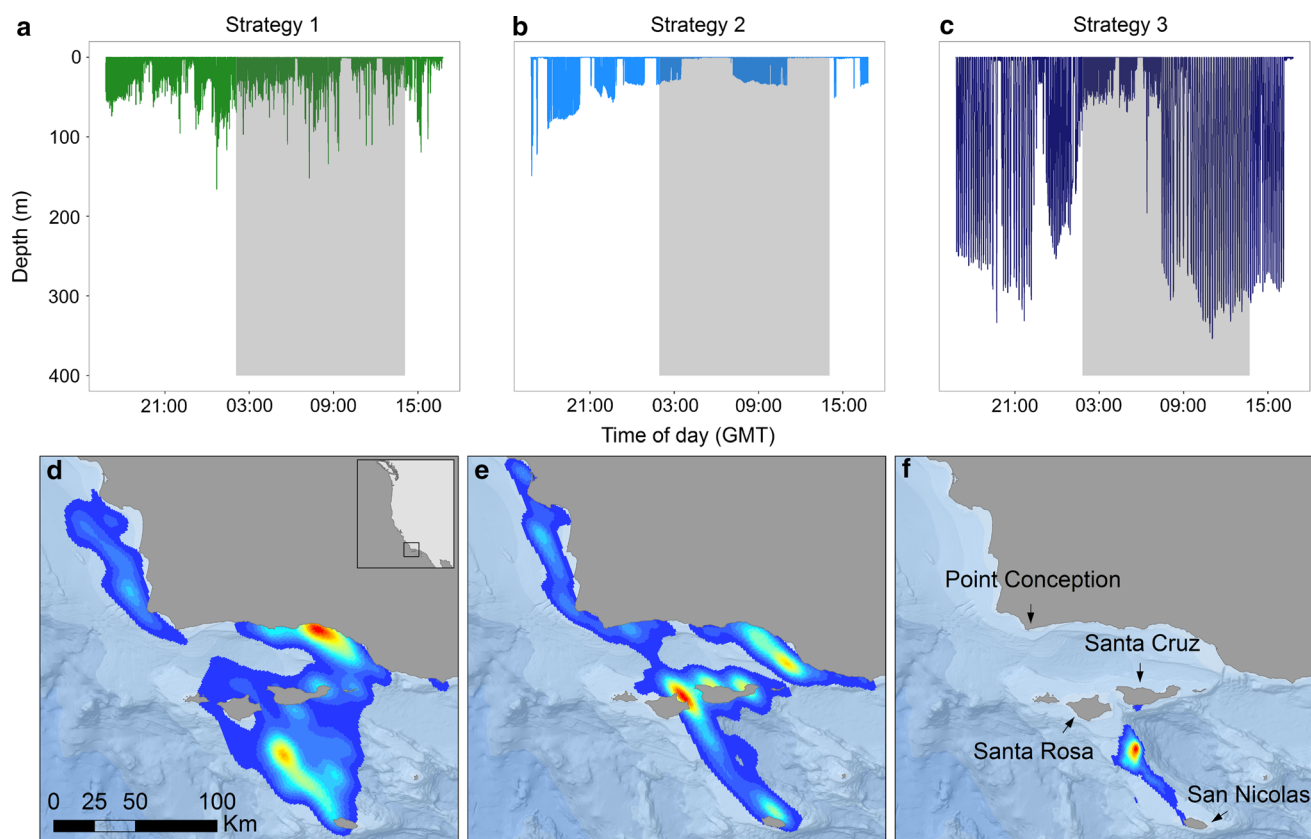
Fig. 2 Dive profiles for representative 24-h periods (**a–c**) and kernel density analysis of all dive bout locations between 2005 and 2008 showing 95 % utilization distributions (**d–f**) for each of the three foraging strategies exhibited by adult female California sea lions from San Nicolas Island. Strategy 1 is a shallow, epipelagic strategy, Strat- egy 2 is a mixed epipelagic/benthic strategy, and Strategy 3 is a deep epipelagic/mesopelagic strategy. In the *top panel*, local night is repre- sented by the *gray boxes*. In the *lower panel*, *warmer colors* indicate higher use and *cooler colors* represent lower use (color figure online)

2 ($F_{3,31} = 4.26$, $P = 0.01$) varied among years. For Strat- egy 1, the mean prevalence ($\pm$SE) was significantly higher in 2005 (average of 69 $\pm$ 13 % of a female's trips were in this strategy) compared with 2008 (15 $\pm$ 10 %, $P_{2005–2008} = 0.03$), but neither year was different from 2006 (39 $\pm$ 18 %, $P_{2005–2006} = 0.20$, $P_{2006–2008} = 0.72$) or 2007 (35 $\pm$ 13 %, $P_{2005–2007} = 0.21$, $P_{2006–2007} = 0.99$). Strat- egy 2 was uncommon in 2005, with a mean prevalence of 12 $\pm$ 17 %, which was significantly lower than 2008 (61 $\pm$ 14 %) and marginally non-significant from 2006 (44 $\pm$ 14 %, $P = 0.08$). The prevalence of Strategy 3 ranged from 17 to 45 %, but there was no significant differ- ence among years ($F_{3,31} = 1.07$, $P = 0.38$).

Spatial use and movement/haul-out behavior

Core foraging areas were variable among strategies and years (Fig. 2d–f; Online Resource 3). Across all years, areas of high use were concentrated on the continental shelf along the mainland coast south of Point Conception (Strategies 1 and 2), close to Santa Rosa and Santa Cruz Islands (Strategies 1 and 2), and southeast of Santa Rosa Island (Strategies 1 and 3). There was considerable overlap in the spatial use of females using Strategies 1 and 2, and some overlap of core foraging areas between females using Strategies 1 and 3, depending on the year. Notably, the core foraging area of females using Strategy 3 was concentrated southeast of Santa Rosa Island along the shelf break and continental slope for all four years.

There were differences in the trip duration ($F_{2,23.5} = 7.51$, $P < 0.01$), maximum distance from the rookery ($F_{2,21.8} = 10.10$, $P < 0.01$), and total distance trave- led ($F_{2,23.8} = 14.80$, $P < 0.01$) among strategies. Foraging trips in Strategy 3 were significantly shorter in duration, closer to the rookery, and had less total distance traveled than the other two strategies (Table 3). In general, females using Strategy 3 tended not to haul-out on trips, whereas the probability of hauling-out for the other two strategies was much more variable depending on the year (Table 3). The only two years that there was a significant difference among strategies was 2005 ($\chi^2 > 100$, $P < 0.01$) and 2007 ($\chi^2 = 11.0$, $P < 0.01$), when females in Strategies 1 and

Table 2 Mean ($\pm$ SD) of dive variables for foraging trips of all animals combined and individually for each foraging strategy. A value of NA is shown if the dive variable was not important in clustering trips into a given strategy

	All	Strategy 1	Strategy 2	Strategy 3
Day depth (m)	92.7 ± 60.2	55.1 ± 30.1	72.5 ± 34.6	152.2 ± 54.8
Night depth (m)	68.3 ± 64.3	32.4 ± 20.1	35.9 ± 11.2	133.6 ± 69.3
Bottom time (s)	49.8 ± 19.0	35.8 ± 8.2	68.8 ± 17.1	54.3 ± 16.2
Bottom wiggles	3.7 ± 1.1	3.1 ± 0.8	5.0 ± 0.8	NA
IDZ[a]	0.35 ± 0.17	0.22 ± 0.09	0.54 ± 0.15	0.38 ± 0.12
Diel[b]	0.28 ± 0.38	0.34 ± 0.32	0.43 ± 0.25	0.11 ± 0.44
Efficiency[c]	0.23 ± 0.08	NA	0.34 ± 0.05	0.17 ± 0.04
Dive rate (dives h^{-1})	19.6 ± 6.8	24.7 ± 5.6	NA	13.2 ± 2.8
Time diving (%)	32.3 ± 11.8	36.3 ± 10.7	38.5 ± 8.3	23.3 ± 9.4
Day diving (%)	50.8 ± 16.2	54.6 ± 12.0	42.3 ± 15.5	NA
Night diving (%)	38.1 ± 17.2	34.8 ± 12.3	48.8 ± 15.8	35.1 ± 20.1
Epipelagic (%)	65.6 ± 17.1	79.5 ± 8.8	47.8 ± 11.8	NA
Benthic (%)	23.7 ± 17.9	18.0 ± 9.9	50.4 ± 11.9	13.2 ± 0.1
Mesopelagic (%)	10.8 ± 14.9	2.5 ± 3.9	1.8 ± 2.8	26.9 ± 14.8

[a] IDZ index ranges from 0 to 1, with higher values indicative of repetitive diving to similar depths

[b] Diel index ranges from -1 to 1, with values closer to zero indicative of similar night and day depths

[c] Efficiency was calculated as bottom time/(dive duration + post-dive interval)

2 were more likely to haul-out on foraging trips compared with females using Strategy 3 (Table 3). There were no differences in path straightness ($F_{2,21.8} = 0.14$, $P = 0.97$) or haul-out duration ($F_{2,18.4} = 2.45$, $P = 0.11$) among the strategies (Table 3).

Discussion

The presence of multiple foraging strategies for adult female California sea lions indicates that population-level approaches result in an oversimplification of foraging behavior, and highlights the importance of addressing individual variability when describing foraging behavior. Epipelagic foraging was important in all strategies, but the presence of a mixed epipelagic/benthic strategy and a deep-diving strategy in all years indicate that female sea lions also depend on prey in the benthic and mesopelagic zones.

The foraging strategies exhibited by adult females in our study were generally similar to those documented for adult male California sea lions from central California (Weise et al. 2010), adult female California sea lions from the Gulf of Mexico (Villegas-Amtmann et al. 2011), and adult female Galapagos sea lions (*Zalophus wollebaeki*; Villegas-Amtmann et al. 2008, 2013), which are closely related to California sea lions (Wolf et al. 2007). Sea lions from the genus *Zalophus* appear to be relatively unique among otariids with respect to their flexibility in diving strategies; most species usually employ one or two of the three diving patterns (Arnould and Hindell 2001; Chilvers and Wilkinson 2009; Kuhn et al. 2010; Villegas-Amtmann et al. 2013; Baylis et al. 2015), but both *Zalophus* species display all three (Villegas-Amtmann et al. 2008, 2011). This diversity in diving strategies may have developed in response to the dynamic nature of the oceanic regions inhabited by these two species, and likely has contributed to the successful recovery of California sea lions post-exploitation despite the occurrence of El Niño events and several regime-shifts that have affected the productivity and biological communities of the CCS (Hare and Mantua 2000; McGowan et al. 2003).

Fidelity to a given foraging strategy varied across the 2-month period, with some sea lions exhibiting strong fidelity to just one strategy, whereas others used multiple strategies. Variability in fidelity did not appear to be linked to one particular strategy, as there were sea lions that exhibited fidelity to each of the three foraging strategies. Differences in individual behavioral consistency may have been driven by prey availability or individual foraging success, with individuals switching foraging strategies when they were unsuccessful in finding sufficient resources on their previous trip. Alternatively, this variability may be an indication that individual California sea lions may adopt either a generalist or specialist foraging strategy, which has been documented for both marine and terrestrial species (Araújo et al. 2010; Tinker et al. 2012; Cantor et al. 2013; Kernaléguen et al. 2016). Given that sea lions were only tracked across a 2-month period, we cannot make conclusions about whether these individual behavioral patterns may persist across longer temporal scales. Studies of other otariids have found that fidelity to a single foraging strategy is often retained across multiple years (Chilvers and Wilkinson 2009; Lowther et al. 2011; Kernaléguen et al. 2012; Baylis et al. 2015; Kernaléguen et al. 2016); however, many of these studies have focused on populations that inhabit less variable environments than the CCS. Villegas-Amtmann et al. (2011) found that adult female California sea lions from the Gulf of Mexico exhibited three foraging strategies during the warm, unproductive season, but only one during the cold season, indicating that the degree of intraspecific variability in behavior may be driven by

Table 3 Model means with 95 % confidence intervals of movement and haul-out variables by foraging strategy for 35 adult female California sea lions tracked over multiple foraging trips to sea

	Strategy 1	Strategy 2	Strategy 3	Difference[*]
Trip duration (days)	5.4 (4.7–6.2)	5.1 (4.3–6.0)	3.5 (3.0–4.0)	1 = 2 > 3
Max distance (km)[**]	98.6 (81.1–120.1)	86.9 (67.7–111.5)	55.9 (50.0–62.5)	1 = 2 > 3
Total distance (km)	348.3 (293.3–403.4)	303.7 (246.4–361.1)	167.3 (142.2–192.5)	1 = 2 > 3
Path straightness[a]	0.7 (0.7–0.8)	0.7 (0.7–0.8)	0.7 (0.6–0.7)	No
Haul-out—2005[b]	0.3 (0.3)	NA	0.1 (0.1)	1 > 3
Haul-out—2006	0.6 (0.1–1.0)	0.03 (0.001–0.6)	0.2 (0.01–0.9)	No
Haul-out—2007	0.2 (0.05–0.5)	0.5 (0.2–0.9)	0.01 (0–0.1)	1 = 2 > 3
Haul-out—2008	0.4 (0.05–0.9)	0.1 (0.02–0.5)	0.2 (0.02–0.9)	No
Haul-out duration (days)[c]	1.4 (1.3–1.6)	1.4 (1.1–1.6)	1.2 (1.1–1.4)	No

[*] Significant differences were assessed at $P \leq 0.05$

[**] Back-transformed values from log transformation

[a] Path straightness is a measure of the tortuosity of the path with values closer to one indicative of a straighter path

[b] Values for haul-out for each year represent the probability of a female hauling-out while on a foraging trip. A value of NA is shown for Strategy 2 in 2005 because there were only three trips in this strategy

[c] Haul-out duration represents the amount of a time a female spent hauled-out at the rookery following a foraging trip

prey availability. We did detect inter-annual differences in the prevalence of the shallow and mixed benthic strategies, which provides an indication that some sea lions likely switch foraging strategies in response to seasonal or annual changes in the availability of prey resources.

Adult female California sea lions from southern California prey on a diverse range of taxa (20 + species), but their diet is mainly comprised of northern anchovy (*Engraulis mordax*), sardine (*Sardinops sagax*), Pacific hake (*Merluccius productus*), rockfish (*Sebastes* spp.), and market squid (*Doryteuthis opalescens*; Orr et al. 2011). The importance of specific prey species in the diet fluctuates annually (Lowry et al. 1988; Orr et al. 2011; Melin et al. 2012), which as mentioned above, is likely why we found differences in the prevalence of some strategies among years. We did not have diet data from the instrumented females nor are there published diet estimates for California sea lions at any of the southern California rookeries for the time period that adult females were tagged. Scat collected from adult female sea lions at San Miguel Island between July and September indicate that sardine was the dominant prey species in 2005 (Melin et al. 2012), the year that had a high prevalence of foraging trips classified to the shallow epipelagic strategy (Strategy 1). In 2006, when the mixed epipelagic/benthic strategy (Strategy 2) was prevalent, sardine and anchovy were still important prey items, but juvenile hake and juvenile and adult market squid also occurred frequently in scat samples (Orr et al. 2011). In addition, hake and market squid either horizontally or vertically overlap with the at-sea distribution of females using Strategy 2; juvenile hake rest on the bottom during the day and migrate into the water column at night (Livingston 1983; Buckley and Livingston 1997), and market squid lay eggs in benthic habitats within 1–3 km of the northern Channel Islands and mainland coast from November to April (Zeidberg et al. 2012). Thus, we hypothesize that sea lions using Strategy 1 may primarily target schooling fishes, whereas hake and market squid may be important prey items for sea lions using Strategy 2. The spatial consistency of females using the deep-diving strategy (Strategy 3) and the lack of inter-annual differences in the prevalence of this strategy suggest these sea lions may either target prey species whose abundance is relatively predictable, or that the oceanographic or bathymetric features of that area predictably concentrate prey resources. Mesopelagic fishes are found in scat samples of California sea lions (Lowry et al. 1988; Orr et al. 2011; Melin et al. 2012), and while not an important prey item at the population level, it is possible that at least a portion of sea lions using Strategy 3 target these species.

The identification and behavioral characterization of foraging strategies is an important first step towards understanding the energetic and reproductive consequences of intraspecific variability in foraging behavior. These consequences may be most pronounced for individuals exhibiting long-term fidelity to a single foraging strategy, but even short-term behavioral decisions have the ability to affect pup growth and survival for an income-breeding species with limited energy (blubber) reserves. Energy expenditure of other otariids are influenced by variability in at-sea behavior (Arnould et al. 1996; Costa and Gales 2000), supporting the assumption that females using different foraging strategies likely experience different energetic costs. It is, however, difficult to make definitive conclusions about the relative energetic costs of each strategy given there do not appear to be consistent patterns among

species in the relationships between energy expenditure and behavior. For example, the rate of energy expenditure of female Antarctic fur seals (*Arctocephalus gazella*) was negatively related to both the proportion of time at sea spent diving and dive rate, which was attributed to an increased time spent traveling between prey patches (Arnould et al. 1996). In contrast, Costa and Gales (2000) found that dive depth was the only behavior that affected energy expenditure of New Zealand sea lions (*Phocarctos hookeri*), with deep-diving sea lions experiencing lower rates of energy expenditure than shallow divers. There are no studies that have specifically investigated the energetic tradeoffs among foraging strategies for otariids (i.e., previous studies focused on single behavioral variables), although benthic diving is often assumed to be an energetically expensive strategy because benthic-diving species have higher rates of energy expenditure than species that primarily forage in the pelagic zone (Costa et al. 2004). Based on these findings, we hypothesize that females using Strategy 2 experience higher rates of energy expenditure than females using the other two foraging strategies, as they have a greater dependence on benthic dives, dive to relatively shallow depths, and also travel greater distances while at sea than females using Strategy 3. For many central-place marine foragers, individuals may offset higher energy costs with an increased dependence on energy-dense prey (Staniland et al. 2007; Rayner et al. 2010; Lowther et al. 2011). This may not hold true for sea lions because hake and market squid have a relatively low energy content compared with prey that is likely targeted by females using Strategies 1 and 3, such as schooling and mesopelagic fishes (Huynh and Kitts 2009; Litz et al. 2010). A similar pattern, that high cost does not equal high reward, has also been suggested for foraging strategies of New Zealand sea lions (Chilvers and Wilkinson 2009) and northern fur seals (*Callorhinus ursinus*; Costa and Gentry 1986). Energetic data in support of these hypotheses are lacking for California sea lions, yet should be a focus of future research because of the influence of maternal energy balance on pup growth and survival.

The reproductive implications of foraging strategies for income-breeding species are also influenced by the tradeoff between the time a female spends foraging versus delivering energy to her dependent offspring. California sea lion pups are solely dependent on milk to meet their energy needs for the majority of lactation and do not accompany their mothers on foraging trips (Melin et al. 2000); thus, the fasting duration of a pup increases with the duration of the foraging trip. There were differences in trip durations among foraging strategies, which were primarily the result of greater travel distances for Strategies 1 and 2, although in 2005 and 2007 the increased tendency for females using Strategies 1 and 2 to haul-out while on foraging trips also likely contributed to longer trip durations. These differences in trip durations have the potential to

negatively affect pup growth rates because the amount of time spent at the rookery appears similar irrespective of foraging strategy. Thus, sea lions using Strategies 1 and 2 spend proportionally less time of the maternal cycle (trip duration + time at the rookery) at the rookery than those using Strategy 3 (21 vs. 26 % of maternal cycle). For example, in 1 month, an average female sea lion using Strategy 3 would spend 7.7 days at the rookery compared with 6.2 days for a sea lion using either of the other 2 strategies. The potential negative impact of reduced time spent at the rookery may be offset by the female through increases in milk fat content or total milk delivery (Arnould and Boyd 1995; Arnould and Hindell 1999), or by the pup through an increased time spent suckling (Ono et al. 1985; Goldsworthy 2006). Assessing these compensatory mechanisms requires detailed information on maternal foraging behavior, milk energy content and delivery, and pup activity budgets, which was outside the scope of this project.

The dynamic nature of the CCS may contribute to the diversity of foraging strategies exhibited by adult female California sea lions, but the simultaneous presence of all three strategies suggests that this is not the sole factor driving intraspecific variability in foraging behavior in this demographic group. The availability of prey resources appears to affect the relative importance of each foraging strategy at any given time, and thus the simultaneous presence of all three strategies may be a mechanism to reduce intraspecific competition resulting from the large number of female sea lions foraging in the southern California Bight. The noticeable absence of small females from the deep-diving strategy and the presence of individual variability in fidelity to a given strategy raise some interesting questions about the role of intrinsic factors in a sea lion's decision to use a particular strategy and her willingness to switch foraging strategies in the face of environmental change. Further research is needed to determine if the patterns we detected in individual fidelity persist across longer time scales, and the specific energetic and reproductive tradeoffs experienced by sea lions using different foraging strategies. Because we detected differences in movement variables among strategies irrespective of year, caution should be used in interpreting the causes of seasonal or annual shifts in these variables if foraging strategies are not taken into consideration. Collectively, these results contribute to a growing body of literature that highlights the importance of accounting for individual variation in understanding the foraging behavior of marine and terrestrial predators, and provide insight into characteristics that may enable species to be successful in dynamic or changing ecosystems.

Compliance with ethical standards

Conflict of interest The authors declare that they have no conflict of interest.

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